Walter Hugo de Andrade Cunha

EMOTION IN THE CIRCUMSPECT PROCESSION

Ant trails as a way to discovery in Psychology and Ethology

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Walter Hugo de Andrade Cunha
Translated by Luís Carlos Borges

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IN MEMORIAM

To the two Berthas, wife and daughter, and my son-in-law, Geraldo.

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I am indebted to my grandchildren, Julia, Braulio, and Bruno, for their interest and help in putting this book together; Professor Gerson Yukio Tomanari for his appreciation of this work and efforts towards its publication; Ana Maria de Almeida Carvalho for her support and assistance with improvements; Luciana Rodrigues dos Santos and her brother, André, who kindly redesigned a number of illustrations in the book; Henrique Cesar Ullbrich for his attention and help with it; Maria Ivani da Silva Moço, Arnaldo de Oliveira Moço, and Eliane Maria da Silva Felix for their everyday help and Antônio Jayro da Fonseca Motta Fagundes for his solidarity. I am indebted to Deisy das Graças de Souza and the Sociedade Brasileira de Psicologia for the publication of this work as an e-book, and to Edevaldo Donizeti dos Santos for his careful page layout.

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PREFACE

Writing a preface to Professor Walter Cunha´s book is a challenge, not only on account of its wisdom and depth, but also the many aspects in which it represents a unique contribution to Brazilian psychology.

First of all – though not necessarily most importantly – this is, in more than one sense, a historical document: it portrays a life devoted to searching for answers to questions raised in his young days, and driven by curiosity, the fascination before the apparently unknown, and the resulting intellectual unrest that is the hallmark of great scientists. As it is wont to occur in their work, it documents the willingness and humility to, unrestrained by rigid doctrinal tenets, experiment with different theoretical interpretations, even mutually conflicting ones, and, at the same time, to venture and propose one's own views, even when they are in disagreement with prevailing interpretations.

In a wider sense of historical relevance, Professor Walter Cunha's work also marks the birth of Brazilian Ethology, at a time when Ethology was virtually unknown to American Comparative and Animal Psychology; it is also a pioneer in that it introduces in Brazil the work carried out by the founders of this approach – Konrad Lorenz, Niko Tinbergen, and Karl von Frisch, who would be awarded the Nobel Prize in 1973. It is worth remembering that Brazilian Ethology, now internationally renowned, was also a pioneer in using the term *Psychoethology*, proposed by the author, in an attempt to articulate the perspectives of Psychology and Ethology, evolved, respectively, out of Philosophy and the biological sciences – once again an early example of interdisciplinarity.

It also documents some moments in the history of Brazilian universities: the observations and experiments described in it, a number of them carried out at his own home, are marked by the simplicity of conditions in which they were undertaken, the creativity and inventiveness of the devices used in these experimental alterations, thus portraying an age in which access to research aids and technological resources was insufficient and almost always limited to the so-called hard sciences.

From an equally significant perspective, the text also provides teaching material of great relevance for the training of researchers, something which will be readily noticed by those responsible for this task: the meticulousness in describing situations of observation and experimentation, the attention paid to the language of description and to variables with a potential to influence the interpretation of results, the recognition and testing of alternative explanations in successive experiments, are lectures in scientific methodology and clearly evince the value of and the need for the naturalistic observation that marked the birth and development of Ethology – as stressed by the author in a well-known text, widely used in research training and included in the Introduction to this book. All students, including myself, who had the privilege of attending his lectures and/or having him as a tutor, will recognise and rediscover this fundamental contribution of Walter Cunha's work.

The potential importance of this work is not limited to Animal Psychology or Ethology, where it was born and developed, but also to other areas of thought and research. Showing the effects of psychological factors – the memory of past experiences – on the alarm reactions of ants faced with a crushed nest-mate is a bold challenge to those venerable hypotheses in Myrmecology claiming that these events are strictly physiological and related to the presence of pheromones on their trails. On the other hand, the postulation regarding the relationships between Psychology and Ethology pose an epistemological question which the author, who has a degree in Philosophy, is not reluctant to face with the same honesty and flexibility he has shown when considering the possibility of alternative interpretations, as mentioned in the Introduction, throughout his long, persistent, and fruitful path.

Ana M. A. Carvalho
PSE-IPUSP

INTRODUCTION

THE NATURE OF THIS INVESTIGATION, ITS APPROACH AND OBJECTIVES

It must be pointed out in this introduction that this book basically deals with my experience, since 1960 to quite recent times, in the research on ants from the perspective of Ethology and Psychology – a subject that has occupied my attention more than any other. My approach to this investigation was that of a naturalistic or ecological observation. One of the earliest and certainly most influential adopters of the naturalistic approach to animal behaviour was Charles Darwin, especially in his work on the expression of emotion in men and animals (Cf. Darwin, 1972). In this work, Darwin inferred the existence of emotion even in insects, even though he did not demonstrate this proposition through precise and detailed observations, as he did in the case of men and other mammals such as monkeys, dogs, cats, horses, etc. Naturalistic observation is generally less strictly bound by a previous theoretical frame and relies on observations and experiments that are less refined and strict than those found in current experimental laboratories. It does not follow that naturalistic observation could be dispensed with. It should be the first step when approaching the typical behaviour of any animal species in its natural environment, and for this reason it will always have a major role in the investigation of the more than one million animal species that remain to be studied; and also in pointing out facts and problems in investigation with relevance for a more detailed analysis, refined by the experimental approach of laboratories.

Naturalistic observation, since the time when Darwin carried out his remarkable work on the evolution theory, the ascent of man, and especially, the expression of emotions in men and animals, has been responsible for major discoveries of great naturalists, such as Wallace, Houzeau, Bates, and Belt on the relatively unknown fauna of many countries; as well as Huber, Fabre, Wasmann, Emery, Claparède, Forel, and the Peckhams on the habits of arthropods, Hartmann on anthropoids, Spinas on the social life of animals, Poulton on the colours of animals, Jennings on the genetics and behaviour of unicellular animals, Yerkes on the compared psychology of apes, etc. Naturalistic observation acquired more defined and precise contours with the development of Ethology since 1935, in the work of such authors as Konrad Lorenz, Nicholaas Tinbergen, Karl von Frisch, and many others. Creators of a new scientific discipline, adopting Darwin's theoretical perspective of evolution in the biological study of behaviour (Cf, Ades, 2009 a, 2009 b e 2012,), they surveyed and described many varieties of behaviour exhibited by certain species in their natural environment, considering their probable survival value and the circumstances in which they occur, formulating hypotheses about their causation, probable survival value, and assumed evolutionary course – a topic in which researchers normally resort to comparing a certain behaviour with those of related species. Acknowledging the advancement resulting from their studies on behaviour in natural environments, the three scholars mentioned above were awarded the Nobel Prize in 1973. In my article "Convite-justificativa para o estudo naturalístico do comportamento animal", published in 1965 in Jornal Brasileiro de Psicologia and reprinted in "Etologia; Uma Perspectiva Histórica e Tendências Contemporâneas", edited by Garcia, A., Tokumaru, R. S, and Borloti, E. B., in which it is referred to as the manifesto for Ethology in Brazil, I showed the various aspects in which the research on animal behaviour conducted in psychology laboratories, generally restricted to rats and other animals in individual cages, could gain relevance, and depth in their choice of topics, if seconded by naturalistic observation in natural environments. As I see it, this article is still relevant nowadays or, at least, historically important in our country, an opinion apparently shared by the organizers of the 31st Annual Ethology Meeting, held on 10-13 November 2013 at the Psychology Institute, University of São Paulo. On the occasion, in an effort to honour me as the founder of Brazilian Ethology, an English translation was published, alongside with that of another article I had written in 1983 on the historical development and principles of Ethology. For this reason, and since it reflects the spirit in which the research for this book was conducted, I have chosen, notwithstanding its old age, to include this article as one of three appendices to this book. On the other hand, the influence of psychology laboratories on naturalistic studies of animal behaviour has been small and sometimes even harmful in that it seems to discredit naturalistic observation for its relying on experiments less technically stringent than those conducted in laboratories. This difference in rigour is real, as already recognized, but it is often irrelevant as well, since the experiments in psychology laboratories, even though more technically controlled, have not generally been conducive to new discoveries or the explanation of behaviours observed in a natural environment. This is undoubtedly of far greater importance than the artificial setting in the creation and shaping of behaviours, for it is there, not in artificial environments, that the really important effects of natural selection manifest themselves. I must remind the scientific community that practically all doctoral and master papers by my post-graduate students at the Experimental Psychology Institute, University of São Paulo, honourably working there and at other Brazilian universities, rely on the naturalistic method, as well as many of my students all over the country. All investigative works presented at the Annual Ethology Meetings are precious testimonials to the importance and fruitfulness of naturalistic observation in animal behaviour studies. Also, as I noticed after an internship at an American university, it has proved a good alternative for the investigation of animal behaviour and a great part of human behaviour in Brazil, since we do not have material and financial conditions to emulate or even copy laboratories found in more developed countries. After my Ph. D., in 1967, I was able to create and maintain, until my retirement from the USP Psychology Institute, a laboratory, well equipped with optical and comparative psychology recording instruments, praised by foreign visitors, and meant as an incentive for users to carry out investigations in animal behaviour and train post-graduate students of psychology and other subjects such as biology and zoology, in the naturalistic observation of animal behaviour. With this purpose in mind, we relied especially on the observation and description of the behaviour of a leafcutter species, *Atta sexdens rubropilosa* Forel, 1908, kept at first in some ten colonies, secured by a special method devised by me. This laboratory was to be reproduced in other federal and state universities, and inspired the creation of a new discipline, at the Experimental Psychology Department of the University of São Paulo and other universities in Brazil, for training students in the naturalistic observation of human behaviour. However it is, naturalistic observation was of crucial importance for me; if not for it, I would not have made the discoveries described in this work, which have implications in the interpretation of psychologically mediated behaviour in humans.

In fact, although my immediate interest in this work are ants and their activities, my considerations aim at a considerably broader horizon. Therefore, dear reader, I think I am setting before you an investigation that may have important implications for current conceptions about behaviour, the mind, and the nature of Psychology, and the need of reformulating what has been taken as its basic principles, and the relationship that must exist between this science and Ethology.

It should be explained that my main objectives in this book have been, first, to determine the causes of behaviour modifications exhibited by ants – especially *Paratrechina fulva* – when faced with a sudden modification of their trails or familiar behaviour environments; second, to show two things: that pheromones are not either enough or necessary for bringing about the so-called alarm reactions observed in these insects, in opposition to what has been claimed by most zoologists, biologists, and myrmecologists, especially since the 1950's; that these responses, as well as other forms of modified behaviour, occur whenever there is a sudden alteration in their usual or familiar behaviour environment, to which they had been adjusted; that these behaviour modifications reflect a temporary impairment in their ability of relying on their memory of a usual behaviour environment to attain their required aims, and which will persist until a new readjustment is accomplished; that these behaviour modifications, since they are influenced by a memory of individual experiences, are therefore psychological and emotional. And then, this book aims at reinterpreting both the normal and disturbed behaviours of ants, and this has entailed developing new explanatory principles, centred on the phenomena of mnemic adjustment to behaviour environments and the possibilities this adjustment opens up to animals endowed with a Psychology, humans included. Regarding this point I tried to demonstrate that these principles originated in the activity, in certain organisms, of an ethological mechanism, evolutionarily directed towards the use of a memory of individual experiences in predicting and preparing for future actions with an adaptive purpose; I consider this as the most primitive phenomenon giving rise to processes of a psychological nature. These principles, applied in the explanation of psychologically mediated behaviour, are widely different from those still advocated by psychologists for the same purpose, based on the phenomena of habituation, sensitization, classical conditioning, and operant conditioning. These principles are the principle of mnemic adjustment to habitual behaviour environments, proper to animals endowed with a psychology, including humans, the principle of reintegration, of assuming as present, when a new adjustment environment is presented, aspects or elements of a habitual behaviour environment that follow from a given element even when this element has not actually been represented by stimuli; and, finally, the principle of using these reintegrated aspects as a path to results required in a psychologically purposeful behaviour. The mechanism responsible for this use of individual memory is an ethological mechanism, in addition to the older mechanisms of reflex, fixed-pattern action, and random activity, which are also structural and preserved in the phylogenetic memory of some animal species. Finally, in the two final chapters, I show how individual memory is present in ants, and how it is used, not only in going over a trail, but also in other behaviours exhibited by them. I also offer a comparative study of behaviour modifications caused by encounters with crushed nest-mates using a number of local ant species, and a discussion of phylogenetic and social factors in this causation, stressing the latter over the former. As for the three articles appended to the book, the first one deals with the naturalistic approach to behaviour, which had an influence on the way this investigation was conducted; the second one with major aspects in the ethology and psychology of ants, whereas the third one details how the explanatory principles discovered are applied in the interpretation of psychologically mediated behaviour, especially human behaviour.

Walter Hugo de Andrade Cunha

CHAPER I

INTRODUCTION

1 THE ORIGIN OF MY INTEREST IN ANTS; THE HISTORY OF A FASCINATION

Ants, perhaps, had been among my cogitations for quite a long time, even without my being aware of it. My mother said that, even as a small boy, in the quiet small town where we lived, I would spend hours on end, sitting at the doorstep of our house, looking intently at the pavement. It is possible that ants were already helping me to fill with thoughts my long empty afternoons.

However, it was only as a young man that, on a certain day, probably in May or June of 1952, in São Paulo, where I have lived for most of my life, that our destinies were definitely entwined. It was evening, and I was back from school, to the rented backyard room I shared with one of my brothers, who, by a coincidence, had also gone through a momentous experience that very day.

I was surprised to see my brother when I arrived; he was supposed to be travelling and I was used to his being absent for many nights and days. More than a month before, he had interrupted his business administration course in order to attend a practical course in tractor-driving and agricultural techniques at the state-owned Ipanema Farm, Sorocaba. I expected his return only a few days later.

He was sad because he had been expelled from the course a few days before its completion, without any explanation. He was attending the course simply for pleasure – missing, perhaps, the long-gone days of his childhood in the countryside – and with the secret hope of making use of it in the future. Apparently, some of the people in charge had found it strange that he had not taken to any group, that, during the infrequent moments of leisure, he would prefer to roam around, taking pictures of desolate sites and bizarre buildings. Since he had not come straight from an agricultural environment nor had any prospects of working in this area after completing the course, and fearing perhaps that he might be a spy, prying into whatever important matters they might have, a solemn meeting was held, and he was dismissed.

Half-lying, half-sitting on the bed, his back half-turned to the wall, my unfortunate brother told me of his Kafkaesque plight. Then, on the wall behind him, I saw a trail of minute tawny crazy ants. Originating in the wooden ceiling, a well-defined trail came down the wall behind the bed; upon reaching the floor, the ants went up a table leg and onto the top, where some food scraps had been left, and then retraced their steps back to the ceiling. Upset, intent on his narrative, my brother crushed a few ants.

What I saw then left me astonished and I had to approach the trail to see it better. The ants, up to then neatly organized, were in turmoil, and the trail was disrupted in the area where their nest-mates had been crushed. Most of them, either coming down or going up, would halt and shudder, and go back along or out of the trail in an undulating course. A few of them slowed down their steps near the disturbed area, left the trail for a moment, and then sped around it in an undulating march. Some of them, generally as a first signal of having sensed something abnormal on the trail, would exhibit a kind of shudder, a jolt; a few would even fall off the wall. Many would shake their antennae as they walked; others would assume a rigid stance and stand up with their abdomens raised and mandibles open; sometimes, the disturbed area was deserted.

I tried, to no avail, to call my brother's attention to the strange event, in part because I was really surprised, in part because I wanted to entertain him and take his mind away from his sorrows. He barely deigned to look at it, and, given his distress, I had no opportunity to go on observing the ants. Later, he seemed not even to remember the event, so upset and engrossed he was in his personal drama. As for me, it was quite different; I would preserve the memory of the event, and, on many occasions, recall and try to understand and explain it, as I did during the lectures and readings for the philosophy course I attended from 1953 to 1956 at the College of Philosophy, Sciences and Letters of the University of São Paulo.

I believe I was fascinated by this phenomenon because it appeared to me as surprisingly emotional, and emotion, as I then thought, was too complex a process to be found in insects. Now, there are instances when a universally accepted solution for a problem is debunked by an alternative solution, found by someone unaware that a solution had been found and deemed definitive and unique. This is perhaps my case, or maybe I have only introduced an unsuspected bit of complexity into this field of inquiry or added to a solution that had already been found. The reader will decide.

In fact, I was unaware at the time, and so remained, even when I started to study the phenomenon a few years later, that it was known by biologically oriented researchers under the name of "alarm behaviour" and was explained by them as an automatic, phylogenetically determined, response to "alarm pheromones". According to them, these pheromones, as explained below, are glandular secretions found in ants and other insects, used to communicate alarm to conspecifcs, either spontaneously, as when facing a threat, or artificially, as when they are crushed. However, and this is still an issue for me, if these behavioural phenomena are an evolutionary development, an automatic response to alarm substances, why should they not manifest themselves in flight, as straight and fast as possible, from the place signalled as dangerous instead of engaging in this profusion of shudders, twitches, wavering motions, and individual variations that may be anything but efficient escape responses? Is it not possible that psychology – a mechanism that, I suppose, has evolved with the purpose of making an adaptive use of individual experience, like reflexes and instincts do with the experience of the species – could have evolved before alarm pheromones or even have made them possible? In other words, is it not possible that alarm pheromones are secondary in relation to emotional phenomena, a later development, and still undergoing a process of elaboration, shaped by chance adaptive advantages in social communication, like the use of flags and branches by humans to signal the site of an accident and thus avoid other similar occurrences?

Although the behaviour I had witnessed seemed emotional and psychological, rather than automatic, it gave the impression of not being totally devoid of intelligence, for it was apparent that most of the ants, even when in flight, did not act randomly, but based on the main elements of the situation, to wit, the trail, its modification, their nest, and the food source, however distant they could be. For instance, although some of the ants trying to avoid the disturbed area by making a detour were not successful and returned to the trail before overcoming the obstacle, one could not say they were not looking for an adequate solution to the problem. Indeed, they would soon try it again, or, upon returning to the food source, would not immediately start to suck it, but would instead hide beneath it or inside any crevice, and use it as a shelter rather than as food. If by any chance, in trying to escape the "obstacle", they entered a crevice in the ground, they would stay there for a while, perfectly still, occasionally showing their shivering antennae, as if probing the outside. Again I ask, how could one recognize emotion and persistence in reaching a target in such tiny, insignificant animals, mere "creatures of reflexes and instincts", as we then read sometimes?

The fact that this phenomenon might be naturally and spontaneously interpreted as emotional by a lay observer was confirmed when I read a short story by Bráulio Pedroso (1962)[1], published two years later, when I was Assistant Professor of Psychology at the University and engaged in this investigation. With the privilege of the literary talent I lacked, the author described how the anguished narrator, arriving late at night in his apartment, comes upon a trail of sugar ants in his kitchen. Among other things, he writes: *"So many they are, they awaken in me a wish to kill. An impulse arising from my passiveness claims for an end to this silly affliction. A finger randomly extended, I choose one in the pageant. I crush it. The one coming just after it halts, although no remains of the victim are left. I see the others dare not cross the invisible barrier. I repeat the experience, and the same display of terror is repeated. I then proceed to shower neuroses upon the circu-*

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[1] PEDROSO, B. "The Ants" (short story). Suplemento Literário, *O Estado de São Paulo*. 1962.

mspect procession. I am amused by my experimental science and even lament the loss of a scientific vocation".

Unlike the author I did not lament the loss of a scientific vocation, but, just like him, derived great amusement from my experiments for many years. Not only amusement, however. I was often annoyed by the lack of opportunities to devote myself to research, my mistakes, meanderings, and difficulties to reconcile conflicting results and encompass them in a coherent interpretation. However, from the humble vantage point I have reached in a path which is certainly far from its completion, I have learned to value the unsuccessful efforts and the mistakes incurred in, for, with Wittgenstein, I understand that no truth can be safely established unless it is the result of relentless elimination and correction of mistakes.

2 The ants especially considered in this study

Most of my observations concerned *Paratrechina (Nylanderia) fulva* Mayr and took place in a domestic environment (backyards, gardens, kitchens...) or some vacant lots where they happened to flourish, in São Paulo, the city where I still live. There were some reasons for this choice: it was the species in which I had first observed the phenomena in which I was interested; it was more readily available and easier to handle than the others, as well as more plastic.

I observed other species in these and other environments, and they will be mentioned where appropriate. However, among the species I observed, *Paratrechina fulva* ants would become my favourites because they are lively, plastic, and easily attracted by food.

Workers have legs and antennae that seem very long when compared with the stocky and short thorax (Cf. Figure 1, below). They are about 2.5 mm long. Their colour is a gingery brown, resembling the colour of honey or lion fur (*fulva* means tawny, gingery). After feeding, they look considerably larger, their abdomens dilated and somewhat transparent, with alternating brown and yellowish bands when seen against the light. Marion R. Smith, taxonomist at the Insect Identification and Parasite Introduction Section, United States Department of Agriculture, in a letter dated 4 January 1961, in answer to my request for identification of specimens sent through Professor Charles D. Michener, at the time I was attending post-graduate lectures in Experimental Psychology at the University of Kansas, wrote:

"*Paratrechina (Nylanderia) fulva* Mayr, one of the larger and more common species of the subgenus. The species has been reported from Argentina to the United States and the West Indies. Some of the areas occupied by the ants are due to introduction. Like other members of the subgenus, *fulva* is very fond of honeydew and can be found tending to aphids and other honeydew excreting insects. It is a house-infesting form with workers that show a decided preference for sweets."

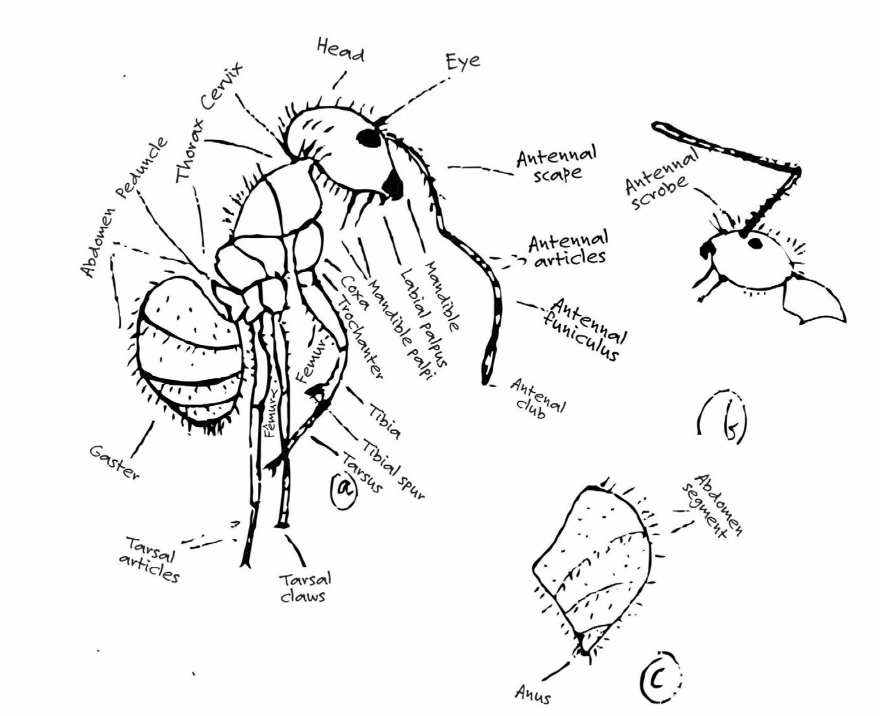

Figure 1: *Outer* Morphology, worker, *Paratrechina (Nylanderia) fulva* Mayr, drawn by the author.

a) lateral view; b) head and prothorax, lateral view; and c) gaster, lateral view.

In human dwellings, I have seen nests of *Paratrechina fulva* in cracks and hollows in floors and walls, and crevices near door frames.

Nests in these places are sometimes temporary – occupied for a few weeks or months. In vacant lots, especially those where garbage from residences is dumped, I have found colonies of this kind of ant, including sometimes winged forms, all of them single-gendered, under stones, tin plates, plastic sheets, paper, leather, bricks, tiles, and even old newspaper with pages all sticking together, gnawed and perforated by workers during their tenancy.

I have observed that colonies of *P. fulva* are generally of a small or moderate size – a few tens or hundreds of individuals – often with more than one queen. These features, according to Holldöbler and Wilson (1990), are prominent among opportunistic species, like *Paratrechina longicornis*, from the West Indies, that are usually the first to locate food sources and bring their nest-mates to them, but leave them on the arrival of more aggressive species. It has also been noted that ants in this genus have a somewhat nomadic disposition, and seldom remain in the same nest for a long time, and their nests, as pointed out above, in the case of *P. fulva*, are opportunistically established in places that already provide some natural protection against the elements.

In certain Spanish-speaking South American countries, such as Colombia, *P. fulva* and other species of *Paratrechina* ants are popularly known as *hormigas locas*, "crazy ants", given their habit of suddenly darting around aimlessly. I think it is an unfair name, from a psychological or ethological point of view, since it evokes connotations that are, as I will show, unwarranted. I believe there is a more acceptable explanation for this behaviour rather than mood: for instance, it may so happen that, especially on an overheated surface, this is a way to reduce to a minimum the contact of their tarsi with the surface, and prevent burns while they are exploring an area where some attraction has been found or signalled. In São Paulo, colder for most of the year, I have rarely witnessed this unmotivated racing around in *P. fulva* ants.

Afterwards, I deal with some points on the formulation of the issues initially raised, the path chosen for the research, methods of observation and record-taking, assessment criteria, prevailing viewpoints and opinions on the subject at the beginning of my inquiry; then, I provide a more accurate characterisation of the behavioural phenomena nature and causes of which this work is meant to determine, before proceeding to a more systematic exposition of the results. This research, as I have already mentioned, is heavily indebted to psychology, and this will certainly be found somewhat strange by most, if not all, biologically-oriented researchers devoted to myrmecology, as well as by a number of psychologists, including those who work with animals. For this reason I will return to this subject, and try to explain why this is so. It will be seen that this is so because there is a historical reason, related to events in the development of these sciences, not a logical or natural one, related to the species under study or any of these sciences. Hopefully, it will also be noticed how the investigation reported in this work could help both sciences get rid of some of the limitations they have burdened themselves with during their brief history.

3 INTRODUCTION: A COMPULSORY REFERENCE – THE PREVAILING INTERPRETATION, TO WHICH I OBJECT, OF THE SO-CALLED ALARM BEHAVIOUR

Before my inquiry, I outline the developments providing the basis for the almost unanimous interpretation of this phenomenon as adopted by the international scientific community, an interpretation that certainly has inspired most myrmecological studies now available or currently being undertaken. As the reader will see, this is necessary because I have adopted an independent outlook, and also because in the course of my interpretations and arguments, I will have to take this interpretation into account and point out where, in the light of my findings, I think it is incomplete or even totally mistaken.

When I started my investigation, in 1960, it was perhaps difficult to predict that the phenomenon that had triggered my interest in ants and come to be known in myrmecological literature as *alarm behaviour* would be considered by researchers – ethologists, biologists, and zoologists – especially in that decade, as, “beyond any doubt”, an automatic response to certain hormonal products released by ants in the environment, having among their primary, inborn functions, social communication.

In fact, as it is widely known (Cf. Dumpert, 1981, p. 64 ff.), as early as in the 1950s, some authors – Schneirla, Goetsch, Le Masne, and Stumper – had already suspected, based on the discovery of a number of exocrine glands in ants, that chemical communication among them could be even more important than communication through touch and sound (antennal tapping, tarsal contact, stroking of mandibles and nibbling, stridulations, etc.), as advocated by older authors (Wasmann and Forel, for instance). According to scholars, this proposition had proved correct. Soon a number of experiments were being undertaken to chemically analyse the products of exocrine glands and test their effects on ants as well as other insects.

Karlson and Lüscher (1959) proposed the term "pheromones" for these exocrine secretions used by insects in communication among individuals, replacing a previous term, "ectohormones", given by Bethe in 1932 to the substance originally discovered and defined by Starling. The authors distinguished pheromones according to their mode of reception, oral or olfactory, and Wilson and Bossert (1963) classified them as either "releasers" or "primers", depending on their effects. Releaser pheromones are generally olfactory and include chemical signals toward actions comprising "the classical responses to stimuli totally mediated by the central nervous system". On the other hand, primer pheromones (or, also, "inducers" or "preparers") are those that are orally received and cause physiological alterations in the endocrine and reproductive systems of the receptor. In this case, the organism is driven to new biological activity, and, in the presence of proper stimuli, starts to respond with a set of modified behaviours.

According to Hölldobler and Wilson (1990), researchers came to recognise twelve broad functions addressed by communicational signals, especially chemical signals, for any given species. These functions are alarm, simple attraction, recruiting, grooming, trophallaxis, exchange of solid food, recognition of mates and caste discrimination, recognition of wounded and dead individuals, induction or inhibition of growth in individuals of a given caste, control of reproductive females, marking of territory, home range, and surroundings, and, finally, sexual communication, which includes recognition of species and gender, synchronisation of sexual activity, and assessment during sexual competition. According to the authors, about 10 to 20 communicational signals, most of them chemical, are responsible for the social organisation of ant colonies in general.

The phenomena that first attracted my attention to ants fall under the first heading in the list above and are technically known as "alarm behaviour". According to Hölldobler and Wilson (1990, p. 260

ff.), however, this is the most difficult to characterise, since scholars have applied the term to all responses related to danger. According to them, broadly speaking, ants are said to be in a state of alarm when they, either calmly of frantically, flee from a potentially dangerous stimulus, or when they approach it in an aggressive way or simply roam around it in a state of increased alarm.

Another difficulty in characterizing it, according to them, comes from the fact that this kind of behaviour is frequently mixed with others, such as recruiting for defence, and defence itself. Dumpert (1981, ch. 5) adds to this picture an assortment of manifestations, differing according to species, including recruiting of larger workers or "soldiers" for inspecting and attacking the alien stimulus and, alternatively, flight of smaller workers, found in certain polymorphous species, reciprocating attack by workers, followed by disengagement after presumed recognition, in other species, and still, "playing dead", in others.

In 1978, the year Dumpert published his book, only one percent of known species had been investigated for alarm behaviour, and the number of patterns exhibited was already enormous and confusing. It was perhaps this that prompted him to say (Op. cit., p. 65) that we were probably in the early stages of an inquiry whose extent and meaning could not yet be discerned in detail.

However, Hölldobler and Wilson, in the work mentioned above, while recognising, as I pointed out, the difficulties in neatly characterising alarm behaviour, warned that each species had its own characteristic form of alarm behaviour, and this could, under proper inspection, be accurately described without reference to other species.

They also said that, whether in association with recruitment or not, alarm behaviour could be usefully classified into two broad categories, as proposed by Wilson and Regnier in 1971: *aggressive alarm* and *panic alarm*. In aggressive alarm, some members of the colony – generally larger workers or "soldiers" – are drawn to the threatening stimulus and attack it. In *panic alarm*, the colony as a whole flees the stimulus or starts running around in erratic patterns.

The behavioural phenomena I observed in an ant trail after the crushing of some of its members and first triggered my interest in ants, certainly fall under the second category. Given the term – "panic alarm" – chosen by Hölldobler and Wilson, it would not be impossible for them to consider – as I did – that these phenomena are of an emotional nature. However, it is clear that, following all biologically-oriented researchers, they would not describe them as instances of psychologically-determined behaviour, but rather of phylogenetically pre-programmed behaviour, automatically triggered, no doubt, by alarm pheromones. These substances – in combination, alone, or variously mixed, in proportions changing from species to species, from colony to colony, or even from individual to individual – had, according to them, been found in all ant species considered so far, and could often characterise phylogenetical relationships. Exocrine glands most commonly found to produce them are the mandibular, pygidial, Dufour's, and venom glands.

I do not know what secretions could be considered alarm pheromones in *Paratrechina (Nylanderia) fulva* Mayr, but, considering those found in related species, they must include undecane or some terpenoid in their composition and are probably excreted through the mandibular and, perhaps, the pygidial gland. These secretions would be released outside by ants in response to a strange object or sign of danger – such as a rival ant – in their environment or, presumably, as in my investigation, upon being crushed. However, I must say I have never seen ants lowering their abdomens or brushing their bodies with glands open against any substrate on being faced with crushed nest-mates or their remains.

4 A remark on certain peculiarities in the inquiry described in this chapter

Given the prevailing outlook, that alarm behaviour in ants is a response to alarm pheromones, I find it convenient, before presenting my findings in the first half of this book, and in order to avoid misunderstandings and objections, to warn the reader as to some peculiarities in my approach and the variety and range of the phenomena it considers.

First, I should stress that, when I crushed ants on or beside a trail, or in any other position, *I did not do it to obtain alarm pheromones.* Admittedly, if these substances really exist, there are more effective and accurate ways of collecting them. I did it instead to assess what the crushed individuals meant to live ants and how they would behave when faced with other interventions on a trail or in other pre-existing behaviour environment. And I did it not only to replicate the initial event that had triggered my interest, but also because I think this must be a fairly common occurrence in a natural environment, as, for instance, when a large animal tramples an ant trail.

These intentions are enough to grant my investigation a wider scope than the research on the action of alarm pheromones, which, as far as I know, has not included the role played in alarm behaviour by factors involved in the situation and by behaviour before the introduction of a modification. And this role, it will be seen, is of the utmost importance.

I suppose that many readers of texts on myrmecology might consider a major shortcoming my not having identified the substances generally supposed to act as alarm pheromones in each of the cases where I employed crushed ants. I must say, however, that even if all researchers of alarm behaviour had, without exception, worked only with pheromones and done so using only extracts accurately analysed for chemical composition, with all its elements thoroughly identified, synthesised, and employed in strictly specified amounts and conditions, I would not see any reason for doing the same. On the contrary, this would be instead reason enough for not doing the same and try what had been left untried. Anyway, I think I have the right to be judged for the things I have done rather than for things I have failed to do, an endless list including both reasonable procedures, like filmed evidence – at that time, not as easy and inexpensive as it is now – and identifying individuals with indelible and recognisable marks, and unreasonable procedures, such as frying croquettes in the fridge or flapping one's ears in order to fly.

Therefore, since I have not, for the above reasons, tried to isolate, analyse, synthesise, and employ substances generally considered to be alarm pheromones, I cannot, unless on the basis of deduction and inference, either subscribe to – as many researchers would certainly do –, or refute the claim that the effects observed in ants following the crushing of their nest-mates are elicited, at least in part, by the release of these substances out of their crushed bodies. However, I do believe that I can add to the findings of hormone researchers other major, though neglected factors determining alarm behaviour. I also point out that these factors, in cases where these hormonal products are thought or found to be functional, have important and unsuspected modulating effects. Generally speaking, the idea I want to convey is that, according to my findings on the behaviour of *Paratrechina (Nylanderia) fulva* Mayr, alarm pheromones are unnecessary and, sometimes, insufficient in eliciting alarm behaviour.

5 The beginning. First questions and remarks, and their role in the future course of this investigation

As already mentioned, I would remember for years to come the intriguing behaviour of ants on a trail upset by the remains of some crushed nest-mates. This was because the scene pricked my curiosity about the true nature of these phenomena. Could they really be emotional, as they seemed to be? Emotion, as it seemed to me then, was a too complex psychological phenomenon to be found in a creature as insignificant as that insect, and this increased my curiosity.

At that time I had neither the leisure (I worked during the day and went to college in the evening) nor a practical reason for trying to satisfy my curiosity.

Some years later, however, I would become an Assistant Professor of Psychology and finally have the opportunity to do so. In need of a break and some rest after a hard day working on a paper for a doctoral degree on “motive” and “motivation”, I went to my backyard and, on seeing an ant trail – apparently of the same species – I decided to resume my observations.

I was so excited by this renewed experience that it was really painful returning to work on the subject I had selected for my paper. Since that day – 17 June 1960 – my heart and my thoughts, even against my will, would be focused on ants. Since our first meetings were conducted on a clandestine basis – I did not have the courage to tell my supervisors in what strange ways I was shirking my duties – they seemed sinful in a certain way; even so, I could not turn my eyes away; I was like someone looking through a window, riveted by the sudden glimpse of a mystery scene.

After reporting my observations to my boss – it was easier than I had expected and met with encouragement – I secured her consent to change the object of my paper. Although time was scarce, I was enthusiastic and went through my work effortlessly. While with ants, time flew and my heart beat faster, and I was very sorry when, after only two months and a notebook full of records, questions, and hypotheses, I was forced to a halt and a one-year interregnum in the U.S, taking lectures on Experimental Psychology and preparing myself to lecture on the subject on my return to college. I returned and, all eagerness and pleasure, went back to my project.

Back to the beginning: I started my research on 17 June 1960, in an attempt to replicate the observation that, eight years before, had led me to consider the possibility of emotional phenomena in ants. My intention then was to verify the impressions I had had. On this subject, I take the opportunity to refer to those notes, given the importance they apparently had in guiding me along the solitary course of my investigation.

The reader will not fail to notice how naïve and even unprepared in myrmecology I was at the start. In retrospect, however, I do not see this as an unalloyed disadvantage, since lack of knowledge on the subject prevented me from basing my approach on established views and forced me instead to ground my opinions on observed facts. On the other hand, the text reveals, I think, a sort of sharpness and accuracy that may seem surprising in a beginner. After all, who would expect that out of the shell of a fresh graduate in Philosophy would emerge an ethologist, if not fully-fledged, endowed with at least a few feathers?

My first remarks were like this:

I have just made some observation, but need a better control of facts, with a list of specific issues, a record of results, etc. There was a trail of this kind of tiny (dark brown) ants near a wall, but on a cement floor; the trail went up a wall. I crushed two ants and waited to see what would happen.

Generally, even when 20 cm away from their dead nest-mates, ants halted, evinced agitation in hard and tense movements, and, some fell off the wall. Others hastily returned to where they had been coming from. Others still, after displaying 'agitation', would either go round the 'obstacle' or try a detour and fail most often than not; a 'good' mistake, because these attempts were not really random; it was clear they followed a curved path in relation the 'obstacle'; then, however, they returned to a point before the obstacle, and a new detour was tried, apparently. Apparently because it is possible the ants were simply exploring their surroundings, as they do when parts of their nests are destroyed.

Further ahead, on the floor and close to the wall, I crushed two more ants: the behaviour of the others was similar – a detour was taken either up the wall or along the floor. Some of them, after leaving the trail, would roam around, apparently unable to find it again.

It must be stressed that in both situations, the first ants to overcome or go round the 'obstacle' touched other ants; among these, some retraced their steps, while others evinced agitation or proceeded toward the 'obstacle' after a brief pause. Soon, the number of ants on the trail had decreased, as if some sort of communication had taken place, but I am not sure, for I did not observe it long enough.

I have observed that many ants, when on a trail, face all the accidents on their way without taking shortcuts ((ants are blind, I think))[2]; apparently, they are oriented towards a food source by their sense of smell, which must be highly developed; also, the trail must be a veritable olfactory path, with directions defined rather by ant smell than by the absence of obstacles ((a cement floor, for instance)). Once the trail is lost, they seem to have difficulties to find it again".

Having verified both the existence of the phenomena that had triggered my interest and the impression they had had on me, I formulated the first question I had to answer – a series of interconnected questions, in fact. Thus:

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[2] A mistaken impression, soon to be refuted. It should be observed that statements in double brackets have not been generally verified and demand more study.

"To ascertain whether the 'emotional response' mentioned above was really emotional and really evinced distress or fright at smelling a crushed nest-mate, or was only a response to an obstacle in the way, to interference in their orientation, or even an emotional reaction to something new ((certainly the smell because their behaviour was modified even when the 'obstacle' was a long way off)), I put a cotton wad dipped in kerosene on the floor, next to the wall, across the trail."

There is much naivety in this initial approach, for, of course, one should first determine what this emotion consisted of in order to devise a test for its detection. This reminds me of Plato's *Menon*, in which the philosopher tries to counter the Sophistic objection as to the possibility of attaining true knowledge. The Sophist argued that if philosophers were after truth, it was because they did not know it. Therefore, if they found it, how would they be able to recognise it?

I am with Plato in the belief that there is no other possibility of facing this claim unless we admit that we know the truth implied in a given concept, but cannot quite recall or figure out what it consists of, and that there is no other way of finding it out, but a thorough and systematic examination of reminiscences related to it. Our findings – the implications we may draw from these memories and test for agreement or harmony with our experience – will form the basis for the theory adopted.

At that time I certainly had some sort of intuition guiding my effort, but, after almost six decades and in the absence of any documents, it is difficult to convey with any precision what it consisted of. Apparently, since I conceived emotion as a complex psychological phenomenon, in which a memory of the past is used in a certain way to impart meaning to present events and project the near future, I wondered whether it could be involved in the catastrophic behaviour I had witnessed in ants. Perhaps the crushed nest-mates were an alteration in their environment with a greater likelihood of eliciting emotional, disorganised, behaviour than an alteration in a less socially relevant object, with a weaker connection with their ordinary lives; hence, the idea of comparing their behaviour under different forms of intervention in the trail. The reference to "something new" in these notes originated in an impression – that would prove correct – that ants, after repeatedly going along a trail, would become used to the path and/or its peculiarities, irregularities, and surroundings, and would reveal this by showing uneasiness before any unusual element in their environment – whatever “become used to” or “showing uneasiness” might mean. As to their feeling upset, this would – as I probably believed – indicate that, being of a shy and fearful nature, they would not only be suspicious before an unusual object, but also evince caution and fear.

Could there be a better start? Certainly, so would probably say those who explain this dramatic behaviour as an automatic, pre-programmed response to alarm pheromones. A better start should be to chemically analyse the composition of the substances released on the trail by the crushed ants and test them for their effects on the surviving ants. I felt tempted by this prospect and, as it will be shown, even started working on it, but subsequently preferred to follow the path pointed by my first observations. Anyway, I do not think an authorisation is required for entering unknown terrain – it was new, at least to me – and choose one’s own path. If one rebukes a fisherman for casting his nets in a neglected or untested area of a river, what better answer than the catch?

Thus, what I observed after placing the wad with kerosene on the trail:

“In this case, generally, the ants came within a shorter distance from the ‘obstacle’ than in the instance above [i.e., when ants were crushed], and showed agitation, shuddering, and flight to a lesser degree. Many of them returned, others tried a detour, unsuccessfully most of the time, or remained ‘in search of something strange’ or ‘exploring’. Again, they would touch each other, as they generally do in any situation, but, generally, new ants [or, rather, ‘newly arrived’] did not go back.

After that, I tried a cotton wad without kerosene on the trail. Now, ants would come closer, and exhibit the same behaviour, but to a lesser degree. None went over the cotton, but this was perhaps because the fibres would hinder their movement (Hard to accept, since none of them tried it). When ‘cornered’ between two wads, they would generally approach one, then the other, or try detours. When I included a leathern cigarette case, they went to the point of touching it; some went back, others tried a detour, and, after a while, some tried to go under it.

Although it is risky to talk about intelligence in ants, I think this is revealed by a certain behaviour; there are at least the detours; it is remarkable that I could not detect anything that might be considered a 'trial and error' procedure; in the circumstances, it is possible they were going round the obstacle without any reasoning or led by a change in stimulation, by an avoidance of the smell (if any; attempts at a detour were also observed in the presence of clean cotton)."[3]

Apparently recognising that it would be natural to expect signs of disturbed behaviour in ants faced with somewhat big and woolly and entangling obstacles as the cotton wads I had used, on the following day I decided to test their behaviour when facing less intrusive objects, that, on account of their size, could not be considered true physical obstacles to their march. So, I first set a match, with its head removed, across a trail formed on a cement floor, next to a wall.

In this case also, their behaviour was visibly upset. Typically, they would approach the match and, when close to it, hesitate – shaking from left to right and back – and then either hurry back, go over the obstacle, or take a detour before re-entering the trail. After hesitating for a while, some of them hurried under the obstacle, availing themselves of a small hollow on the floor that I had not noticed before; this behaviour seemed to clearly indicate a truly compulsive determination to not leave the olfactory path forming the trail, a compulsion they had already exhibited when faced with the cigarette case.

I moved the match to another point of the trail, without any hollows, and observed the ants for sixteen minutes, taking down a minute-by-minute account of their behaviour. Their behaviour was basically the same, except in that the apparent value of the match in inhibiting behaviour seemed to steadily decrease. Thirty nine ants were observed. Sixteen of them retreated, twelve went over the obstacle, and one – who found a tiny depression underneath, went under it. Two ants took detours and gradually distanced themselves from the match, one up the wall, the other along the floor. The four remaining ants took failed detours, that is, they tried to go round the object, but prematurely returned to the trail,

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[3] I would soon notice that an absence of smell was not the same thing for me and the ants.

before the point where the match was. What they did afterwards went unrecorded.

The same match was then dipped in kerosene and set across the ant trail again. I observed their behaviour for twelve minutes. ‘

Now, we could say the obstacle’s “apparent behaviour-modifying value” was easily discerned. No ant went over the object. Most of them returned when within a range of one half to five centimetres from the object. Six out of nine attempted detours failed. Generally speaking, I tried to record only their initial behaviour when first approaching a modified area in their environment. In this case, however, I wrote down that the record was faulty; within a space of 15-20cm, the same ants were observed coming and going, and then, as they failed to go ahead, attempting successive detours until finally succeeding in overcoming the ‘obstacle’.

The conclusions to be drawn from these initial observations seem quite clear. First, that the so-called *alarm behaviour* can be elicited in ants by other objects on the trail, other than their crushed nest-mates, and, therefore, alarm pheromones are not necessary for triggering this kind of behaviour, at least initially. This is well known among myrmecologists, by the way. In fact, they often remark that alarm pheromones are generally released on the trail only when some ant finds some major abnormal element in its way – an enemy ant, for instance. If this is so, the release of alarm pheromones may be one instance of alarm behaviour, not investigated as such because researchers are mainly concerned with the communicational phenomenon, pheromone release being an instrument for it.

A second conclusion was that, although not the only cause of alarm behaviour, a crushed nest-mate was, among the experimental alterations I introduced on the trail, the most effective, in the sense of being capable of eliciting clear alarm behaviour and a greater level of disorganisation on the trail. Would this conclusion hold under other forms of experimental alteration and different circumstances of observation? If so, could these frenzied changes in behaviour be caused by some property or substance found only among this species? Or could these be shared by other ant species? On the other hand, how could *P. fulva* and other species be compared as regards this kind of behaviour? Could a specific individual, on being crushed, not become a special kind of experimental alteration for its having been involved in a number of social activities in the colony?

6 THE OBSERVATION AND RECORD-TAKING METHOD

In order to observe and record their behaviour, I would generally adopt the following procedure. Armed with a notebook, a pen, a pencil, and a stopwatch, I sat down on a chair or even on the floor, within a convenient distance from the trail, taking care not to disturb them with my breathing. Then I selected a *space of observation:* an area of the trail previously chosen, given the impossibility of covering the whole trail while recording the different behaviours that might occur. Generally, this was an area bordered by some natural irregularities of the terrain (bumps, spots, gaps along the wall or floor traversed by the trail) or pencilled marks. Although, for recording purposes, I concentrated my attention on the events occurring within this area, I tried, whenever possible, to cover events occurring outside of it that might differ from those in the control phase.

Each observation session generally comprised two phases, and these were divided into units (usually of a minute or half a minute): a *control phase,* without any intervention by the observer, and an *experimental phase,* with some deliberate form of intervention (e.g., crushing an ant, placing an object or running a finger across the trail, etc.) in a point or area in the middle of the observation space. I called this intervention an *experimental alteration,* and the place where it took place an *alteration point.* The normal or control phase was meant as a point of reference for the next phase, and the division into units allowed for the analysis of modifications in the behaviour of ants over time. Departures or variations from the behaviour observed in the control phase were called *modifications in behaviour as against the standard of previously unchanged behaviour* or simply *behaviour modifications.*

Behaviour was recorded by means of pen on paper, using graphs, symbols, and, when convenient, ordinary text. Each ant was graphically represented by an arrow, the shape of its shaft being analogous to the way it moved (meandering, undulating, in a curved or straight line), and its head to the direction it took (up, down, left, right). Other symbols included a dot, standing for the *alteration point* in an ant's course, a short line, perpendicular to the shaft, for a jolt, a small circle over the shaft for a pause, and a curved extension of the shaft for a "sniffing" (the act of turning or lifting the head, then shaking the antennae, directed toward the point). Other events, such as disorientation, falls, etc., as well as distances in centimetres from other events (e.g., the beginning of a return) were indicated by abbreviations or numbers next to the symbols. Events such as raising the abdomen, opening the mandibles, acceleration, etc., although frequent, were in general incidentally recorded, and in ordinary text, the investigation focusing, for the most part, on modifications in behaviour as evinced by different kinds of motion, since they are more conspicuous and require less time for being recognised beyond any doubt. Figures 2 and 3 show how records were taken:

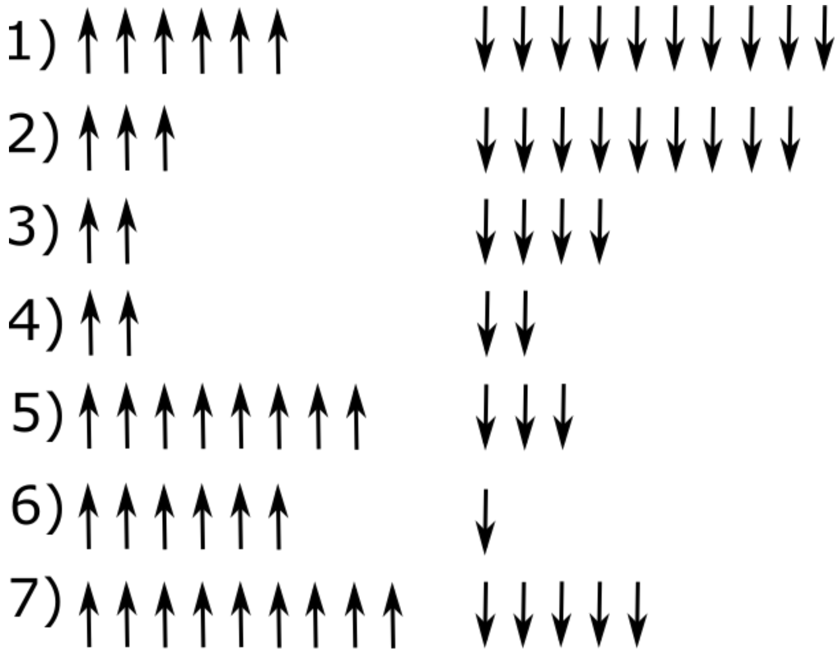

Figure 2: Graphic record of behaviour in *Paratrechina (Nylanderia) fulva* Mayr ants on a trail, in the first seven minutes of control phase in a randomly chosen observation session.

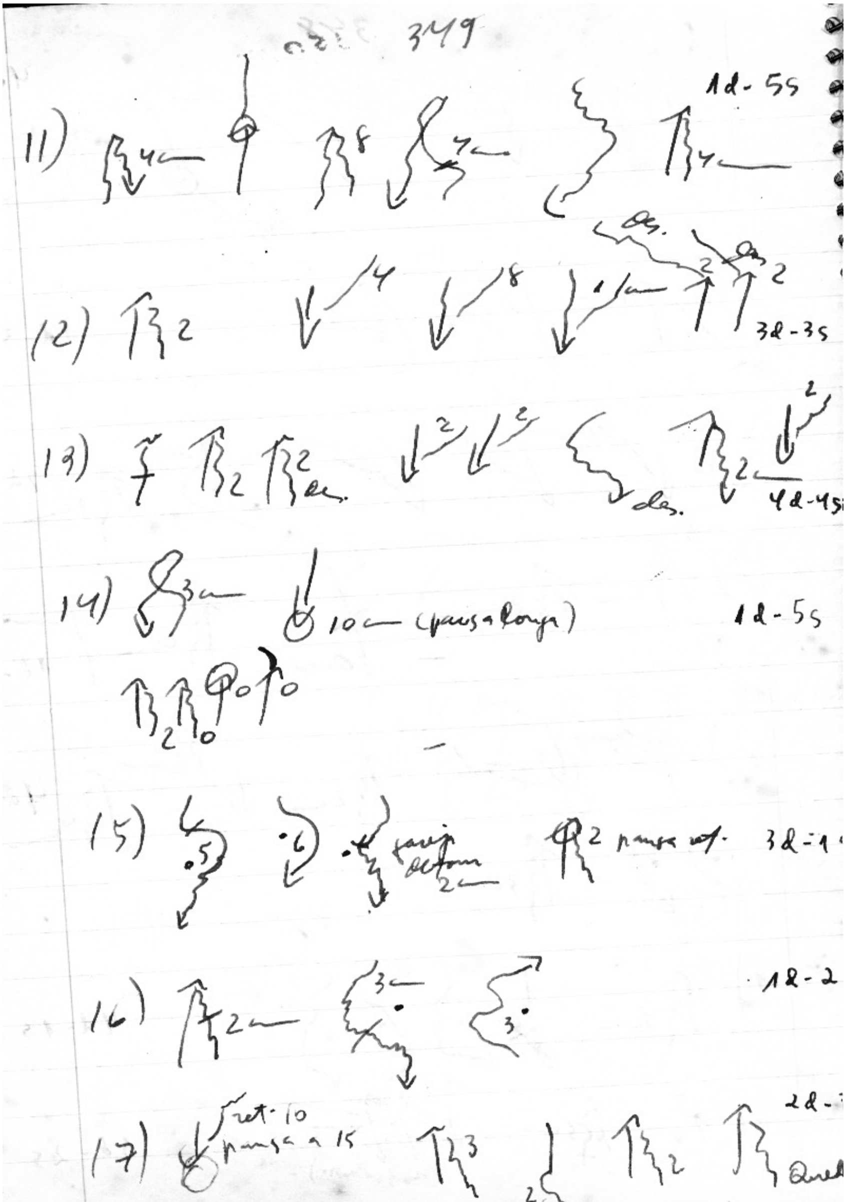

Figure 3: Record of behaviour of ants *(P. fulva)* on a vertical trail on a wall, starting after 10 minutes of an experimental phase in which four ants were crushed.

For greater clarity, I am going to describe how I represented the various kinds of behaviour modifications that used to or might occur in the experimental phase of the observations in this work, using as examples the representations in Figure 3 below. We indicate the position of each of these representations from left to right in a given line using numbers 1, 2, 3, etc. Lines are identified by numbers 11, 12, 13, 14, 15, 16, and 17, placed on the left of each line. Normal behaviour in its truest form is sometimes called "normal progress" (through the "observation space") and is indicated by a regular arrow, such as those In Figure 2, typically found in the control phase of various observations.

First, let us consider the behaviour modification represented by a *return*. Each drawing in positions 2 and 3, line 12, represent a simple return, that is, a reversal in direction exhibited by the descending ants. Numbers 2 and 4 on the simple line representing a return indicate the approximate distance of ants to the alteration point when the return occurred. It must be said that, in each return recorded, the angle formed by the line of return and the ant's original course does not indicate, unless otherwise stated, the precise distance at which the return was undertaken, in relation to the original displacement line of the ant. On the other hand, when the line representing a return has a circle or ring, as in drawing 1, line 14, this means that, after returning for a while along the substrate, the ant resumed its original course.

When a line representing displacement is indented, as in figures 1, 3, 5, and 6, Line 11, and a number of drawings in the following lines, this means that the displacement took the form of an *undulating march:* a sort of march where the ant seems to shiver, turning from left to right in succession, generally at a higher speed. This indentation or undulation in their march are a type of behaviour modification superimposed on another movement category (a return or detour, for instance).

Drawings 5, Line 11, 6, Line 13, 2 and 3, Line 13, 1, 2, and 3, Line 15, and 2 and 3, Line 16, stand for *detours* in relation to the alteration point.

A drawing where a line with the abbreviation "des." on the tip is added to the normal arrow means disorientation, which is marked by generally slow progress and frequent reorientation, and which I interpret as a start in trying to find the olfactory path underlying the trail.

A circle surrounding an arrowhead, as 1 and 5, Line 14, the last one in Line 15, and 1, Line 17, represent *pauses,* sometimes with text informing whether they were long or short. The number next to the circle is the distance between the alteration point and the point where the pause occurred, expressed in centimetres.

A short segment added to the shaft of the arrow, as in the last drawing in Line 14, and 3, Line 15, means an instance of "sniffing" in relation to the alteration point, that is, an ant bending the frontal part of its body and then waving its antennae, positioned like a V, in a front dorsal direction and then the opposite way. Here, "sniffing" also includes the action of waving the antennae as described above before bending the frontal part of the body to either left or right. The term "sniffing" was used by Karl Von Frisch in his classical work on the behaviour of bees; I have adopted it here to describe the same behaviour in ants (Cf. Frisch, 1950 e 1961).

Another category is indicated by Q (from "queda" which means *fall* in Portuguese) as in the last drawing, Line 17, the record of an ant that fell off the wall. It is either written in full or shortened to "Q" next to the representation of an ant's last displacement before falling.

Two types of behaviour modification expressed in motion do not occur among the drawings in Figure 3. The first one is *dislocated progress,* when an ant, at a certain distance from the alteration point, proceeds straight ahead, following a course parallel to the trail, either in an undulating march or not. It is represented either by a straight or wavy arrow beside a dot. The second one is *intermittent progress.* It is a march with brief stops at intervals, identified in writing, either in full or shortened form.

While these categories relate to motion, some refer to changes of posture in the ants, like *"huddling up"*, "*raising of the abdomen*" or *"lowered posture",* written in full.

7 THE CRITERIA ADOPTED IN COMPARING THE EFFECTS OF A NUMBER OF EXPERIMENTAL ALTERATIONS ON THE BEHAVIOUR OF ANTS

As the reader will see, this inquiry often entailed comparing the effects of certain experimental alterations on the behaviour of ants. This comparison was not very simple.

Apparently, it might be carried out by considering all categories of behaviour, one by one. However, this would not always be adequate, because it was evident that the data for some of these categories were interconnected.

Thus, for instance, the results for going back, taking a detour, evincing disorientation, and going through the obstacle, were mutually exclusive. On the other hand, falls frequently seemed to be the outcome of especially vigorous jolts and undulations. Also, what event should be considered more significant: a greater number of pauses, undulations, or "sniffing" motions? One might say perhaps that I should have not introduced any counterbalance and derived instead a final single index for change in behaviour in each phase of the observation phase. But then, how could one prevent mutual influences among different categories from accumulating differentially, thus introducing a natural counterbalance? In this connection, one has only to remember that a fall, for instance, would preclude other potential changes in behaviour, such as undulations, jolts, returns, etc., that might have occurred had the ants not fallen.

It seems, then, that the only index that could be used in isolation and in a direct comparison would be that of ants without any apparent change in behaviour – and this by definition, since the index would cover all cases in which behaviour were the same as in the control phase; of course, it would provide negative rather than positive information about the effects and nature of responses to experimental alterations; also, since not all changes would be taken down, it would not cover all ants with unaltered behaviour, only those with unaltered behaviour that had been previously recorded.

A proper comparison, therefore, would seem hardly feasible without a criterion for organising, albeit precariously, the data to be compared. In order to establish such a criterion I assumed that a thorough grasp of the issue was needed. Now, nobody who has read so far will fail to notice the obvious function of a "*behaviour-modifying obstacle*" such as the crushing of some individuals on an ant trail. In the absence of an experimental alteration, traffic flowed easily and in an orderly fashion; it was literally blocked sometimes, when an alteration was introduced; also, ants generally displayed modified activity, in the form of a previously unseen appearance, posture, and walking style.

Having stated in these terms the facts to be explained, the problem of comparing the effects of different experimental alterations seemed much simpler: they should inform us to what extent a given alteration has the "apparent nature of an obstacle or modifying repellent". Certain changes in behaviour – such as jolts, undulations (they seem to be caused by shudders all over their bodies or by wavering, light motions to left or right), rigidness, open mandibles, and raised abdomen – provided straightforward information about experimental alterations in inducing modifications; and, since they seemed independent, although somewhat coordinated, they could be said to be comparable in isolation. On the other hand, other types of modifications – such as dislocated progress, pauses, detours, disorientation, and returns, which, in our records, entailed mutual impacts – would fortunately provide us not only with information about the power of an experimental alteration in inducing changes in behaviour, but also about this alteration's apparent character as an obstacle, and in such a way as to clearly imply a gradation. Indeed, it was easy to see that a path, dislocated a few millimetres away from a point of alteration, before an experimental alteration of any kind, would turn out to have the apparent character as an obstacle or repellent to a lesser degree than a pause before the altered point; a pause, likewise, would present this character to an even lesser degree, the same being true for a detour, and successively, a return: for these phenomena seemed to extend over a gradient, starting with acceptance of or hesitation in accepting an altering object as part of the path, to partial or complete avoidance of this object, or even flight from it.

The suggestion, therefore, was that the problem of comparing the effects of different experimental alterations should be faced in the light of their character "as obstacles or as modifying repellents" in each instance of alteration. It must be understood that this character was but a tentative grasp, and as such, it could and should be corrected later. It must be really difficult for anyone who has seen how easily an ant can climb a rock or a wall or even go through a thin tuft of grass, to believe that a crushed nest--mate, who poses no hindrance to its progress, should prove a 'behaviour--modifying obstacle". However, I cannot deny that, under the conditions in which the initial facts in the observation were seen, experimental alterations had this *apparent* function. I would even suggest that another way of stating the opening issue in this work is saying that it is an attempt to explain why these alterations worked as if they did have this function. If they *do* have it, that is another matter: while stating the aim of an investigation and pointing to a series of facts to be considered, I cannot say what they truly are; if I did, there would be no real problem to solve. I must necessarily start by saying how I see them; and my intention of studying them entails the doubt as to whether they are what they seem to be. In every collection of external data, even in its most "neutral" form, involving physical data, it seems to be the case that, given the innermost nature of the perception process, there is always something like the beginning of an interpretation, subject to the logical categories of trueness and falseness.

CHAPTER II

AN ATTEMPT TO IDENTIFY THE CAUSES OF BEHAVIOUR MODIFICATIONS IN *PARATRECHINA (NYLANDERIA) FULVA* MAYR AFTER ALTERATIONS IN THEIR IMMEDIATE ENVIRONMENT

1 THE GENERAL AIM OF THIS CHAPTER

In this chapter I set out to present an inquiry into the nature and causes of the dramatic modifications observed in the behaviour of *Paratrechina (Nylanderia) fulva* Mayr as one or more individuals are suddenly crushed or when other intentional alteration is carried out on their trail.

In fact, the reader will see that as the investigation progressed, I was led to consider the effect of the alteration above and other alterations carried out on ant trails; other environments were considered, and attention was also paid to kinds of behaviour change and a series of behaviours deviating from the generally accepted definition of *alarm behaviour*, such as those having an exploratory or investigative, orientational, ingestive, or agonistic nature, among others.

2 GENERAL VIEW OF THE BEHAVIOUR OF *PARATRECHINA (NYLANDERIA) FULVA* MAYR ON A TRAIL ON SUDDENLY COMING ACROSS ONE OR MORE CRUSHED NEST-MATES

As already mentioned, dramatic changes occur on trails of *P. fulva* when one or more of them are suddenly crushed. The effect is always the same, whether visible remains of their bodies are left in the area or not, and this suggests that the phenomenon is, to a large extent (though not exclusively, as it will be seen), olfactorily mediated. A once orderly file is totally disorganised near the alteration point. The general impression is that their crushed nest-mates act as a powerful obstacle, repelling them, or disturbing their previous behaviour. The resulting behaviour, especially in the first few minutes after the alteration, and in the area adjoining this point, is very different from what it had been; it takes up the form of quick flight or avoidance of the area; many ants also hide in places offering some sort of protection such as crevices and cracks in the ground, their nests, or folds and holes in the food source to which they had been attracted. However, the resulting collective behaviour does not totally and irrevocably lose its character, that of a process of relating to the environment in the pursuit of some function required by the colony, such as foraging. Modifications or disturbances in behaviour gradually die down and exchanges with the environment generally become what they had been. Generally speaking, notwithstanding exceptions, which are mentioned below, it seems appropriate to follow the usual view, that many of the behaviours observed in this altered phase are alarm behaviours, although I think it would be more adequate to consider them as conflict situation behaviours.

It is important to mention that their ordinary way of behaving, of occupying themselves without hesitation or restraint with the usual aspects of their environment, is frequently replaced with suspicion and caution after an alteration occurs. For instance, I once observed that some ants, having gone past their dead nest-mates on their way to the nest, on facing a black raised spot on their way, would "either rear up, flee, or pass 'cautiously' by (hesitating only in this area…)". On many occasions, I observed that, after being repeatedly faced with the alteration posed by crushed nest-mates on the trail, ants evinced a sort of anxiety, as it were, at having to do it again. This manifested itself in an unusual delay in leaving the incentive, a certain reluctance to leave the floor and go up the wall, towards the lure on the top, and to follow the trail, in the intermediate area of which the crushed bodies lay. Other manifestation, probably of the same nature, was observed in some ants that, after leaving the floor, took a route of their own, totally independent from the collective one; they would often go astray on these occasions.

Under this topic, I intend to offer a more thorough and detailed picture of modified behaviours commonly brought about by this kind of alteration; determining and explaining the nature of these behaviours were the initial aims proposed for this inquiry. Soon, others were to follow, as it will be seen. This description will supplement the information on how behaviour categories were recorded, and it also serves as a kind of glossary, explaining and describing the categories of behaviour mentioned in this study.

Most ants respond to an alteration in their environment with a *return* – a reversal in direction. Ants returning to the nest now head toward the incentive, and vice-versa. This type (or category) of behaviour generally occurs all of a sudden, when ants are about 2cm to, exceptionally, 10cm or more from the alteration point, and, it usually takes the form of a quick pace and an undulating course. Frequently, when the ant flow was thin, I was able to follow single ants after their leaving the *observation space.* On these occasions, they would either return to their nests or to the incentive; in the latter case, they would sometimes go a little further, as if looking for an alternative path, independent from the trail, but then went in an inappropriate direction.

In some cases, this return is only partial: having returned for a while, the ant resumes its previous direction and faces again the altered area. In a number of cases, however, when the flow was *intense* – when the average number of ants on the trail was high in an observational *time unit* – I could not tell whether returns were complete or partial. This was because, in these cases, of course, only occasionally was there an opportunity of observing what happened outside the observation space.

The second most frequent kind of altered behaviour is usually that of taking a *detour* when in the face of an experimental alteration. In a *detour*, an ant leaves for a while the collective path and, without changing directions, goes past the alteration point before re-entering and proceeding along the trail. Sometimes, as already mentioned, this detour is *faulty*, that is, after leaving the collective path, the ant returns to a point of the trail before the altered area. In such cases, ants may try another detour, return, or go sideways, avoiding the area, and this, again, is generally done in haste.

Though less often, the altered point is overtaken not with a detour, as described above, but with *parallel displacement.* In this case, ants leave the trail before reaching the alteration point (this dislocation sometimes starts at either end of the path, the incentive and the nest), occasionally going past the alteration point in many tens of centimetres.

While attempting a detour or parallel displacement or simply darting away from the altered region, an ant sometimes leaves the trail and is disoriented. In instances of *disorientation,* ants seem to have lost their bearings, and this is generally evinced in a slow pace, frequently redirected to areas away from the trail.

All movements mentioned above may take up the form of an *undulating march,* especially at the start, that goes on for a variable distance. What we see in this behaviour is a slow marching away or, more often, a race with alternating changes to left and right, as if the ants were tremulous and hesitating as to what direction to take, which imparts to their course a wavy appearance. In other cases, however, distancing from the altered area may occur either in an ordinary march or in a sinuous march, a kind of march where oscillations to left or right occur at wider intervals, with wider bends, like the meanders of a river, than in an undulating march.

A kind of behaviour modification which is not as frequent as the other, though rather frequent sometimes, is what I call a jolt. It is a sudden shudder or lurch and may occur while ants are moving or after a sudden stop. When this occurs on a wall, it looks like an imminent fall. It is observed in larger ants, such as *Camponotus rufipes* Fabricius, 1775 – a very aggressive, hairy diurnal ant with a purplish colour – or in *Camponotus cupiens* Forel, 1908 – a glabrous nocturnal ant, with a black head and a yellowish, translucent abdomen. It looks like a sudden forward or backward thrust of the thorax, with legs tense, fixed to the substrate, and mandibles open, a movement resembling the recoil of a cannon. In *C. cupiens* this jolt is sometimes rather forceful: it can take the ant off its feet, and this is probably what T. C. Schneirla used to call a “nervous jump” in his works.

Sometimes, after a jolt or during another kind of displacement, a *fall* would take place – an ant would fall to the substrate. I must point out that, although I record falls together with other kinds of data, most of them are probably accidental events. I say "probably" because, in some cases, as when I catch an ant on a sheet of paper, the fall may be the outcome, or so it seems, of a deliberate jump. Indeed, there were occasions when I spent a considerable time alternating a notebook and a sheet of paper to gather ants that, having found out, after a chance fall, that they were away from the ground, engaged in a series of deliberate jumps. Anyway, it seems important to record these falls, since their occurrence, by removing the ants from the observation space, precludes the occurrence of other kinds of behaviour.

Another relatively common kind of behaviour is a pause or interruption of the march at any given point of the terrain. This pause frequently occurs as the ants face the alteration point and is followed by a *pre-sniffing posture:* a flexing of the head toward a given point in the terrain when the ant is moving parallel to it, or, when it lies ahead, by a dorsoventral flexing, together with a "stretching up" of the antennae into a "v" position – that is, with the funiculus and the scape set in a straight line –, and intensified movements of the same, both singly and in alternate motions. I call this apparently exploratory activity of their antennae "sniffing". The term was suggested, as already mentioned, by Karl von Frisch, who said the exploratory motions of the antennae in arthropods correspond to the sniffing motions of mammals.

Though less frequent, a behaviour worth mentioning is *abdomen rearing* – the raising of the abdomen, especially its back end. This kind of behaviour is commonly seen in *Solenopsis saevissima* Fr. Smith ants when they are upset and about to sting, something that does not occur among *P. fulva* and other ants in the Formicinae subfamily, which have no stinger, but, so it seems, can employ gaster rearing – or its opposite motion, the bending of the gaster underneath the thorax, a motion frequently seen in *Camponotus crassus* Mayr, 1862 – to spray formic acid, either defensively or offensively.

Immobility (at times for several seconds) may also be observed in *P. fulva*, and is caused especially by vibrations in the substrate, as when objects are dragged along a surface, or by the sudden projection of a shadow.

Given the description above, it can be seen that although behaviours brought about in ants *(P. fulva)* by crushing one or several of their nest-mates on a trail may, for the most part, fall under the heading of Hölldobler and Wilson's category of "panic alarm", they vary a little from individual to individual. Also, some behaviours definitely cannot be classified as such, but rather as instances of agonistic, investigative or exploratory behaviour. For this reason, I think it would be more appropriate to call them "disturbances or modifications of a previous behaviour taken as a base line" (in this case, a colony provisioning behaviour), or, simply, "disturbances, or modifications, in behaviour".

Even Figure 3, presented to show how record-taking was carried out during my observations, although randomly chosen and referring only to a small part of them, can be seen as an illustration of the diversity of behaviours mentioned above. Thus, for instance, consider the behaviour of ants in the very first period recorded, from the eleventh minute since the beginning of the experimental phase. Out of six ants, four returned to a distance of a few centimetres from the crushed ants, three of them in an undulating march, and one in ordinary march, but with a jolt. A fifth ant – last but one, left to right – turned away from the alteration point, also in an undulating march, and went on in the same direction it had been going. A sixth ant – second from left to right – went straight to the alteration point, paused over it, intensifying the motion of its antennae, and then proceeded on its way toward the incentive, without any undulations in its course.

The last behaviour mentioned is entirely different from the other and does not fit at all in the category of alarm behaviour, whereas the others might.

Another form of behaviour occasionally observed is worth mentioning here; though similar to the one mentioned above, it is even more intriguing and difficult to classify. It occurs as an ant, still many centimetres away from the alteration point, seems to suddenly sense the stimuli coming from its crushed nest-mates; instead of taking a detour and hurrying away from the trail or turning back, like most of its nest-mates, it speeds up its march toward the altered area; the impression is that it intends to go past it in a rush, but, instead, it halts and explores it with its antennae, and then, it either returns or goes on along its original path.

Going back to Fig. 3, I can affirm that the uncommented portions of the figure also illustrate this variability, since they include ants that were disoriented after taking a detour, ants that proceeded to "sniff" the altered area from its outward limits before entering it (for instance, the last but one, recorded in the fourteenth observation period unit), ants that fell, etc.

How could this diversity of individual behaviours be explained? Although it cannot be used to refute the presence and action of alarm pheromones, I think it does seem to go against the generally accepted interpretation, that of alarm behaviour as being automatically elicited by these substances. However, we could try to reconcile this incompatibility by assuming that this diversity might be caused by variations in the amount and quality of alarm pheromones presumably received by the ants, and then relate it to some random difference in distances, postures, position of the antennae, etc. One should notice, however, that, were this possibility to be accepted, one would probably be unable to account for the absence of alarm behaviour in those ants that, as shown in the figure mentioned above, paused at the very spot where their nest-mates had been crushed or came to "sniff" it at close quarters.

3 SOME INITIAL QUESTIONS RECONSIDERED. EXAMINATION OF THE EFFECT OF DIFFERENT SPECIES OF ANTS, WHEN USED AS A FORM OF EXPERIMENTAL ALTERATION, ON A TRAIL OF *P. FULVA*

Given the dramatic nature of behaviour modifications shown by *P. fulva* when some individuals on their trail are crushed, I set out to check whether they would be the same if ants of other species were used.

- *Observation 1 – Response of* (P. fulva) *ants on a trail to leafcutters put in their way.*

First, I selected for my consideration a 70cm stretch of an ant trail originating on the top of a wall and proceeding towards some refined sugar on the ground – a cement floor. In the middle portion of this area, I crushed three leafcutter ants, of a species popularly known in Brazil as "lemon leafcutters" (*Atta sexdens rubropilosa* Forel, 1908), because of the smell which is released when the heads of workers are crushed. I had to use an adhesive tape to fix them to the wall.

The behaviours observed after this arrangement did in no way look catastrophic. Especially in the first few minutes, the ants going up to the nest tended to halt near the crushed ants and then turn back, without, however, any acceleration or undulation in their march. Some ants, especially those coming down from the nest and toward the lure, tended to halt and pull at the fragments. In the sixth minute, the remains fell to the ground. In the eighth minute, workers had stopped gathering round the alteration point, even though a leafcutter's leg had remained attached to the wall and stayed there till the end of the observation period. Since the fall, returns, observed only among ants going to the nest, ceased. Later, I saw an ant walking towards the nest bearing a leafcutter's head.

After the first ten minutes, I observed the trail for further ten minutes. Almost all ants tended to slow down their steps or even halt in the altered location, and then, after some "sniffing" and even roaming round the area, they would proceed along their path. Detours were taken to a certain degree, but without undulation or acceleration in their march. Eventually, the trail seemed normal, with only a slight 0.5 cm sideway dislocation near the alteration point.

I observed on two other occasions the behaviour of ants on a trail upon suddenly finding leafcutters of the same species in their path.

On the first of these occasions, I put the fresh body of a large leafcutter across the trail. I noticed that ants tended to gather in the area. Some would go around the body and keep their course; others, however, remained. In the fifth minute, they started moving the body. In the sixth minute, the concentration of ants increased, and the leafcutter was slowly dragged toward their nest.

On another occasion, I crushed a leafcutter and fixed it to the wall with a strip of adhesive tape, secant to a trail that ran parallel to the junction of the wall and the cement floor. I paid special attention to differences in behaviour, as evinced in the direction of their march, in the ants faced with the crushed leafcutter. Their reaction was in no way catastrophic, but it was not indifferent, either. I did not see any return among the ants walking towards the incentive (fi.), a cotton wad dipped in a mixture of water and sugar, about 1m away, but saw one or two instances among the ants going toward the nest (fn). The reactions of fn seemed to be rather of bafflement and caution (they halted, withdrew, wavered; sometimes they raised their gasters, with a slight backward motion, a sort of light jolt, and then, took a detour and went on), while those of fi. evinced some curiosity, though without much interest: they would pause for a while, "sniff", take a detour, and go on, unruffled. In average, fn would pass by the leafcutter at a distance of 1cm or more, while fi at a distance of less than 0.5cm. Undulation in their march, when it occurred, was only perceptible in fn.

In short, considering these three observations, I think I can say that bodies of leafcutters, whether crushed or not, when set on a trail previously directed towards a food incentive, acted in different ways, depending on whether the ants *(P. fulva)* were going towards the incentive, or their nest. In the former case, it was as if the bodies themselves were a food incentive, or, at least, an object of interest, whereas, in the latter case, they were something obstructing or altering their path, preventing their reconnoitring, something strange and a little frightening. This difference in behaviour suggested, on its turn, that fi. had a more open attitude than fn. as to what might be found on the way, or, perhaps, were more focused on finding food, whereas fn. would pay more attention to details of the path itself. Incidentally, it seems to be of interest to mention that *P. fulva* ants, nicknamed "cuiabanas" in some areas, have been unsuccessfully used to fight leafcutters[4]. It also seems worth mentioning that, during one of the observations in which I tried to compare the distances at which ants gave signs of having sensed crushed nest-mates on the trail and suddenly started to return, this was considerably higher among fn., suggesting perhaps, that their attention was focused on the path itself, rather than on what it led to.

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[4] Cf. Carrera, M. *Entomologia para Você.* São Paulo: Edusp, 1963, p.267.

- *Observation 2 – Response of* (P. fulva) *ants on a trail to the remains of a crushed unidentified big black ant in their way.*

Since the bodies of leafcutter workers crushed on a trail of *P. fulva* ants seemed to be perceived as in some way a food incentive, I thought it could be of interest to observe how they would react to crushed workers of another species. So, later on, using the same trail I had used to observe their reaction to leafcutters, a few centimetres below the spot where I had crushed them, I crushed an unidentified big black ant, about 0.5cm long.[5]

The crushed body did not remain attached to the wall, but left a black spot on it. Upon being crushed, the ant let off a strong smell, similar to that of crushed *P. fulva* ants. For this reason, I expected dramatic modifications in their behaviour, but these did not happen.

I observed for fifteen minutes their behaviour when faced with this experimental alteration. Initially, both the ants going to the nest and those going to the incentive (white sugar on a cement floor), would stop at a distance of 2 or 3 cm from the spot, and most of them, generally after swinging to left and right, would go on, without any haste or undulation, and even walk over the spot. Some of them, eight out of sixty-four, returned, but only partially. Unfortunately, I did not consider direction of displacement when recording these returns.

Broadly speaking, the behaviour of the ants before this alteration did not seem to suggest either flight or avoidance, but, rather, something like momentary disorientation.

- *Observation 3 – Response of ants on a trail to a half-dead Camponotus cupiens* Forel, 1908 *worker laid on the ground near the colony.*

A certain evening, having observed for more than forty minutes the response of ants on a trail running along the edge of a washing tub to the crushing of 4 of their nest-mates, I decided to observe how they would react to a worker – a very big one if compared to those of *P. fulva.*

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[5] Given its aspect and later taxonomical research, I think it could be a small worker of the *Camponotus melanoticus* species – like *P. fulva,* a species in the Formicinae subfamily – therefore more closely related to them than leafcutters.

– of a species called *Camponotus cupiens* Forel, 1908[6]. This is, as already mentioned, a nocturnal ant with a black head and translucent abdomen that nests in hollows of rotten and dry trees; they are loved by hens, which fall greedily on them, and, because of their colour, are called "honey ants" in some areas of Minas Gerais, Brazil.

This worker was previously crushed, but was still moving when transferred to a spot near the floor – a cement floor – near the entrance of a nest, a cavity in the junction of wall and floor. The spot was certainly more than one metre away from the edge of the tub where some ants had been crushed earlier, but, very likely, the ants might still be somewhat upset when I started this new observation.

Generally speaking, the response to the intrusion was one of distress, with ants running around precipitously, going as far as 8 to 10cm away from the spot, although one of them approached and even touched the alien ant. Could the relatively increased distress of this episode, as compared with the previous ones – in which crushed ants of other species were used to alter a path – be explained by a greater familiarity with the terrain, traversed more often by the ants of that nest, the smell let off by the hurt body of an alien species, its lingering movements, some of these things together, or all of them combined? The observation protocols do not say how long this disturbance lasted, but do tell that, in the morning, the big ant and the crushed bodies of its nest-mates were no longer there.

In my observation and experiment protocols, I find only two other occasions where I had the opportunity of observing the behaviour of *P. fulva* workers in the face of still moving ants of other species. In both cases, it happened by chance, not as a deliberate action on my part. They are the subject of the following observations, which close this section.

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[6] Determined by Friar Walter Kempf. According to him (personal communication), this species, together with the very aggressive, black-coloured *C. fuchsae* Forel, 1908, were once considered subspecies of *Camponotus abdominalis (*Fabricius, 1804), though they are clearly independent species.

- *Observation 4 – Reaction of* P. fulva *ants in a trail to a big black ant that, although hurt, was still able to walk.*

In this observation, a big black worker, of an unidentified species, on which I accidentally stepped, limped around near a trail of *P. fulva.* It was found by one of the workers, which started running around it and then climbed on its body, paying special attention to its antennae; it stepped down again and, further ahead, repeated the same operations, and then went away. No other ants were affected by the event.

- *Observation 5 – Observation of the behaviour of* P. fulva *ants upon meeting enemy ants of another species on a shared trail towards a food lure.*

On another occasion, I had the opportunity of witnessing the response of *(P. fulva)* ants on a trail to the presence of *Solenopsis saevissima* Fr. Smith, 1855, a species of ant in which most workers[7] have approximately the same size of *P. fulva*. They are noticeably irritable, endowed with a stinger, and do not tolerate *P. fulva*.

In this observation, I came across a very strange trail, formed by workers of two different species, *Solenopsis saevissima* Fr. Smith, 1855, clearly in greater numbers, and a few *Paratrechina fulva*. The trail ran along the junction of a cement floor and a wall, and connected a lure, a cotton wad dipped in a mixture of sugar and water, to the entrances of two nests, one of them of *P. fulva*, located in the intermediate portion of the junction, and a second one, further ahead in the same junction, of *S. saevissima*. Both entrances were formed by cracks in the cement floor. Fig. 4 shows the position of the trail in the terrain.

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[7] *S. saevissima* has among its workers a caste of soldiers of variable size, distinctly larger than ordinary workers. This trail was formed only by this caste.

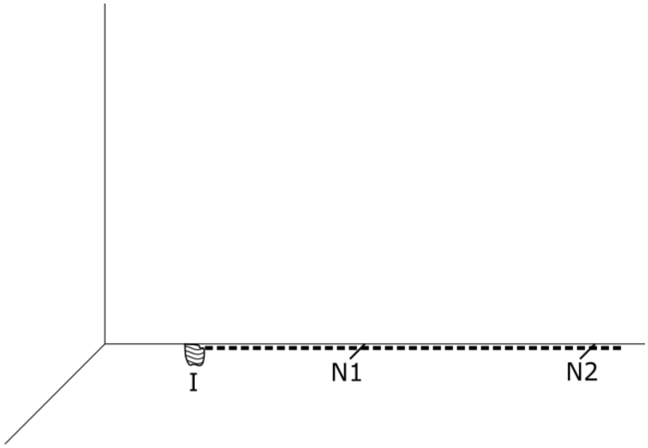

Figure 4: Trail running along the junction of a cement floor and a wall, formed by *Solenopsis saevissima* Fr. Smith, 1855, and *Paratrechina fulva.*

Dashed line: trail.
N1 and N2: cracks in the floor, access to nests
of, respectively, *P. fulva* and S. saevissima.
I: incentive (cotton wad dipped in a water and sugar mixture)

Since the trail was already there, I cannot say which species had started it. The only thing I know is that *P. fulva* ants used to form trails for a while along that junction. In this particular instance, the cotton wad was being visited by a large number of *S. saevissima*, and, surprisingly, since the two species are outright inimical, by a few *P. fulva* ants.

Being much more agile than their enemies, the *P. fulva* ants used the same path as the others, but in smaller numbers – not once did I see more than two workers at the same time on the lure. *P. fulva* ants would overtake *S. saevissima* ants in their march, usually with a motion resembling fright – a sudden and brief acceleration after coming across a strange ant on the trail – and then turn aside into a detour, either along the wall or the floor, in order to get past them. This apparent fright was clearly more intense when they came across *S. saevissima* ants head on than when they did it from the rear; it was also more noticeable in *P. fulva* ants returning to the nest than in ants heading towards the lure. In both cases, the ants would end up covering most of their course (about 2m) along the wall, only occasionally descending to the junction, which was clearly preferred as a route. As to the *S. saevissima* ants, they did not avoid encounters with *P. fulva* ants: they would face them instead, showing no signs, outside these encounters, of being "concerned" with the presence of intruders (that is, with no lingering signs of disturbance in their attitude originating from previous encounters).

I then provide a detailed report of my observations, because of their aptness in showing both the agility and opportunistic sense in the behaviour of *P. fulva* workers. Thus, for instance, I observed two *P. fulva* ants heading towards the lure. Practically side by side, both came upon one and, then, three *S. saevissima* ants, from behind. They went 1cm up the wall and on along, parallel to the trail on the junction of floor and wall, descending only occasionally to it. On coming face to face with a *S. saevissima*, they would suddenly dart in an undulating march one centimetre along the wall or two centimetres along the floor, and then go on, following a parallel course. I observed one fn (an ant returning from the lure toward the nest). After meeting a *S. Saevissima* frontally, it turned aside, with a sudden acceleration, and went on, in an undulating march, one centimetre up the wall, and followed this parallel course for a while; it came down again and met an fi. of its own species, and both seemed frightened: they moved as if about to turn aside – that is, they started doing so – in an undulating march; they then stopped and repeatedly stroke each other with their antennae; given their courses, they were deliberately searching for each other.

I observed another fn walking along the junction. After a frontal meeting with a *S. saevissima*, it took a detour, darting 3cm up the wall, and then went on in a course parallel to the junction, keeping a distance of 1cm from it.

I then observed one fi. It was going towards the lure, walking along the junction of wall and floor. On meeting one *S. saevissima* from behind, it went up the wall, evincing no sign of fright – that is, without any alteration in speed – for about one centimetre; with its greater speed, it overtook its rival, and returned to the junction, and went ahead on its course. Four centimetres away from the lure, it met another *S. saevissima* frontally; after a tremendous jolt, it went 3cm up the wall; then, it came down again, back to the junction, and continued towards the lure. I observed that, having climbed the lure, the ant, considering its relative immobility and the stillness of its antennae, did not pay as much attention to the presence of rivals as it had done along the junction; instead, its attention seemed totally absorbed in the food.

I saw another fi. that met two *S. saevissima* from behind near the lure; it overtook them by going 1cm up the wall, and then came down again, only to meet frontally another *S saevissima*, 1.5 cm away. After a vigorous jolt, it went back for 3cm, went 5cm up the wall, and then resumed its course towards the lure.

I saw another fi. which exhibited no undulation in its march nor jolts when walking alongside rival ants, but, on meeting frontally one of them, was overcome by a violent jolt and fell to the floor, whence it sped up in an undulating course; it then climbed up the wall and was soon back on its course towards the lure. I commented that "it is certainly the event of coming across another ant in its path that makes them more frightened", and that jolts and undulation during the march are observed in *Solenopsis saevissima* in the same cases.

I noticed that two *P. fulva* ants that approached *S. saevissima* ants from the flanks showed almost no sign of distress. I saw a *P. fulva* which, on being touched by a nest-mate from behind, sped up suddenly, and, on being touched a second time, turned around quickly and touched the other ant with its antennae. Had it recognized the touch of a nest-mate?

I saw that *S. saevissima*, as they reached the cotton wad, would stay round and underneath it, whereas *P. fulva* hesitated for quite a while: they would approach it and walk backwards, with raised, rapidly moving antennae; then, after going round the lure, they would choose a spot devoid of enemies, climb to the top and start sucking, antennae moving slowly and pointing forward. When they came across a *S. saevissima*, they withdrew, without acceleration, to the top of the wad, free from ants.

I noticed that some *P. fulva* would start circling – a sinuous, gyrating, meandering motion, continuously reoriented, as shown in Fig. 5, below – at a distance of 10cm or more from the lure. This behaviour, according to Cornetz's observations [8]of Algerian ants of the genera *Messor, Tapinoma, Myrmecocystus,* etc., which he called "Turner's circling", after

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[8] Cornetz, V. *Les Explorations et Voyages des Fourmis.* Paris: Flammarion, 1914.

the researcher who had first described it, would seem to indicate the operation of a "state of search" in the animal – in this case a state of search for the lure. If this understanding is correct, the fact would seem to indicate that the trail of *P. fulva* had preceded that of *Solenopsis* before being overcome by them, and that *P. fulva* had already adjusted to, or memorised, the distance to the provision.

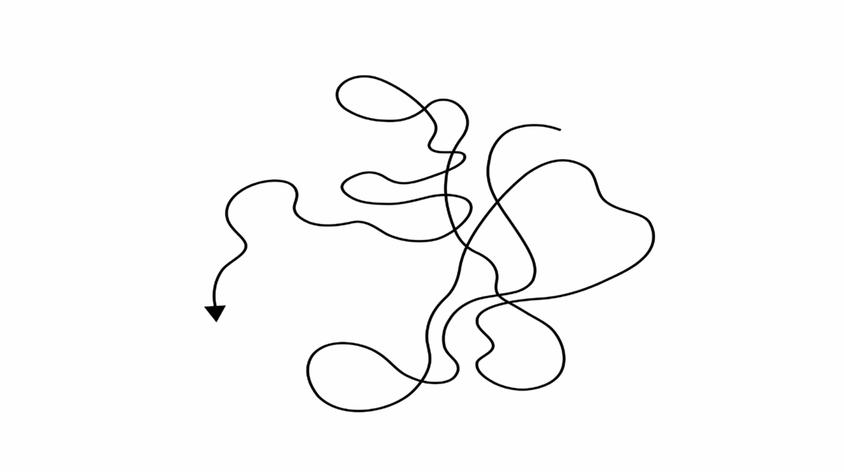


Figure 5: Illustration of the course of a circling *Paratrechina fulva* ant.

On coming across a *P. fulva* head on, one *S. Saevissima* halted, and then roamed around, as if searching for it.

Although sparse, the observations above seemed to leave no doubt as to what I was trying to find out: that the bodies of ants from other species, either crushed or whole, even if still moving, on a trail of *Paratrechina fulva*, if one considers the extent and duration of these disturbances, did not have the apparent nature of a behaviour-disturbing obstacle as dramatic as those of the crushed bodies of their nest-mates.

4 A FIRST ANALYSIS OF "ANTS OF THE SAME SPECIES" AS AN EXPERIMENTAL ALTERATION

The reason why the crushing of conspecifics on a trail of *P. fulva* is special for them, whereas the crushing of other species is not, is certainly the fact that they are *P. fulva* and, probably, part of the situation preceding the alteration, whereas the others are not. However, finding out what it means for the ants on a trail whether a crushed ant is a conspecific and part of a previous situation is certainly no easy task and entails a great deal of analysis and careful examination. But a possible starting point could be the following. It has already been mentioned that *(P. fulva)* ants sometimes exhibit modifications in behaviour of a catastrophic nature when in the presence of the crushed bodies of conspecifics on a trail from a distance of many centimetres. From this distance, they are probably responding to volatile substances released by their crushed bodies rather than to the actual sight of them. This assumption is supported by the fact that, in many observations, it was seen that the intensity of these behaviour modifications was not increased in the presence of remains of their bodies.

Having considered this, three questions occurred to me: 1) Could this substance be exclusive to some parts of the crushed bodies? 2) What effects would the crushing of a greater or a lesser number of ants have? And, finally, 3) How would ants on a trail respond to dead nest-mates with intact bodies laid close to or across the trail? I present bellow the observations I carried out in order to answer these questions.

4.1 OBSERVATIONS CARRIED OUT IN ORDER TO COMPARE THE EFFECTS, ON A TRAIL OF *(P. FULVA)* ANTS, OF THE CRUSHING OF SOME OF THEIR NEST-MATES, AND OF ANATOMICALLY DIFFERENTIATED PARTS OF THEM

A rough, but easily available, way of answering question (1) would be to compare the disturbances on a *P. fulva* trail by crushing whole ants and natural, easily separable parts of an ant, i.e., head, thorax, and abdomen.

In practice, however, I saw that there was a difficulty in using the thorax by itself as an experimental alteration, because this very dehydrated part of their bodies would not adhere to the wall, not even when crushed. Since I thought the presence, or the absence, of body fragments, considered as sources of emissions, could make a great difference, I decided to employ the thorax connected to its neighbouring parts, expecting to be able later on, by comparing effects, to determine their specific role in the ensuing responses. I should mention, however, that, even though they would not adhere to the wall, crushed thoraxes caused remarkable modifications in behaviour.

In order to effect this comparison, I relied on five observation sessions, all of them dealing with single, separate trails formed on different, though not widely separated occasions, by *Paratrechina fulva* ants from a single colony. All these trails ran along a cement floor and a brick wall and their ends were a nest in the soil and an incentive (refined sugar on a support on the wall).

Each observation session comprised two parts: a control phase and an experimental phase, each of them lasting for at least twenty minutes, controlled by a stop watch. In both phases, the ants' behaviour was recorded – basically, their course towards the nest or the lure, as well as other chance behaviours, such as a pause, return, or undulation in the march, occurring within the observation space.

In the following account, I omit, for the sake of simplicity, the description of control phases, which provide no relevant information, but I do add, in the table with the numerical outcomes of each session, the data regarding flow density in each of them. It would be obviously desirable that all basic features of these trails (speed, density – that is, the average number of ants moving during a single observation period – time spent in starting the trail, temperature, etc.), which might have any connection with the observed behaviours, were uniform, but, since this would not be feasible, uniformity of conditions was not attempted.

I provide below a summary account of these five observation sessions.

- *Observation 6 – Behaviour modifications in* P. fulva *following the crushing of 4 ants of the colony on their trail. (Duration: 60 1-minute periods).*

The quantitative results for this observation can be found in column A, Table 1, below: after Observation 10, since this table also presents results of other observations for comparative purposes. As regards quality, results are similar to those mentioned for observations of the same kind. Rather than describing them, I thought it preferable to present the original records for some initial and intermediate minutes in the observation, as shown in Figure 6. I should only add that, during the experimental phase, ants gathered near the lure and the beginning of the trail, on the wall, near the floor, and these ants seemed to hesitate before proceeding with their march. It was also observed that some ants, on coming across returning ants, tended to withdraw to a long distance – sometimes as far as one metre – from the alteration point. This fact reinforces the impression of the lure as having a low incentive value on this occasion.

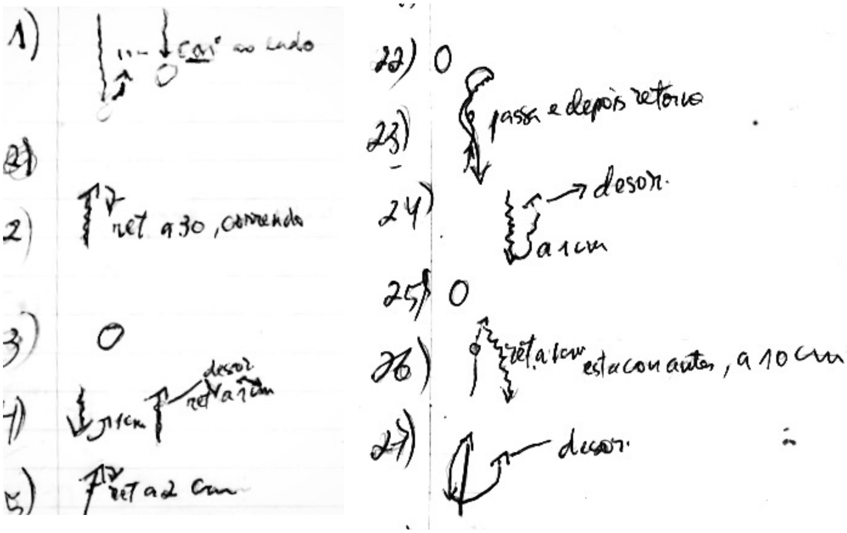


Figure 6: Sample of original record of behaviour of *P. fulva* ants on a trail, covering some initial and intermediate periods in the experimental phase of this observation, in which four workers were crushed on the trail.

- *Observation 7 – Modifications in the behaviour of ants on a trail following the crushing of the abdominal portion of eight ants on the trail (Duration: 20 1-minute periods).*

The operation released the typical, strong smell I had already noticed when crushing workers of the same species. Modifications in behaviour, more intense at first, relented a little near the end. Some ants paused for variable periods, and then either went ahead or returned, without any other apparent modifications. Other ants carried fragments of bodies.

The trail was gradually dislocated to the right of the alteration point; under these conditions, it was difficult to distinguish progress and detours, which makes the record less reliable in this aspect. The quantitative data for this phase are shown in column B, Table 1 below, and Figure 7 shows the original records for some of the initial and final periods of this observation. I believe they show a tendency to a gradual return to normal conditions.

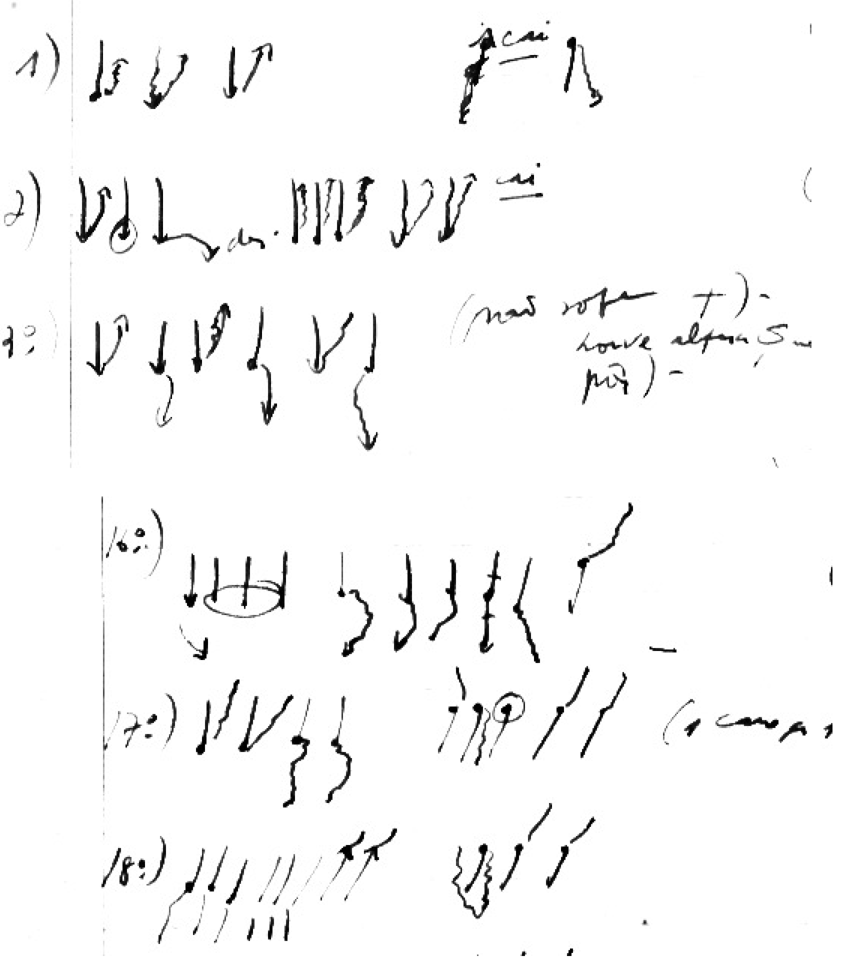
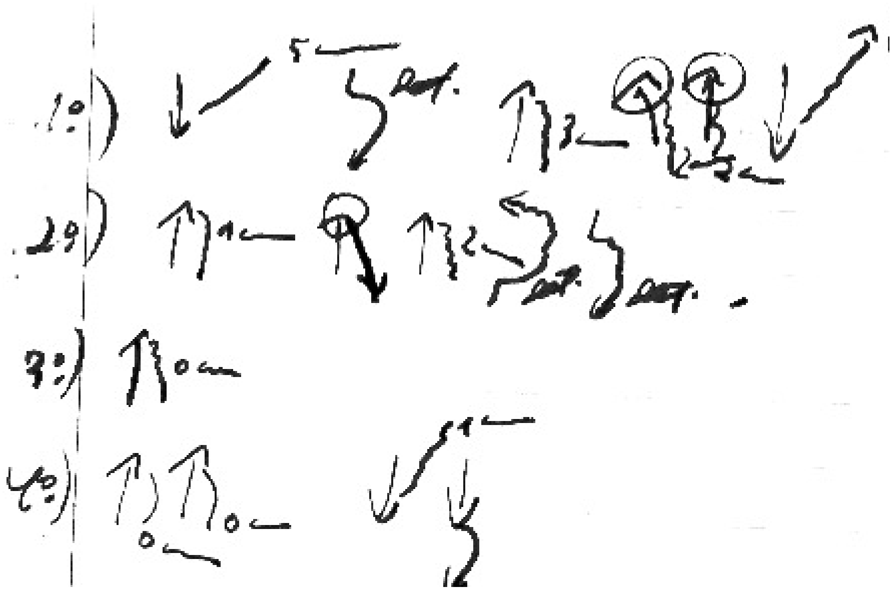


Figure 7: Sample of original record of behaviour of ants on a trail during some initial and final periods in an experimental phase, following the crushing of the abdominal portion of eight ants of the colony on the trail.

- *Observation no 8 – Modifications in the behaviour of* P. fulva *on a trail, following the crushing, on this same trail, of the thoracicoabdominal portion of eight ants of the colony (Duration: 20 1-minute units).*

As in the previous phase, the crushed bodies gave off a strong smell. Again, as in the previous phase, some of the ants, especially those ascending towards the lure, paused within the altered area itself. If, however, one of them undulated, a number of them would run and go on along their way. Two body fragments were carried to the nest. Column C, Table 1, below, shows the quantitative data for this observation, and Figure 8, below, the original records of behaviour change in ants on this trail during the initial and final minutes of this observation.



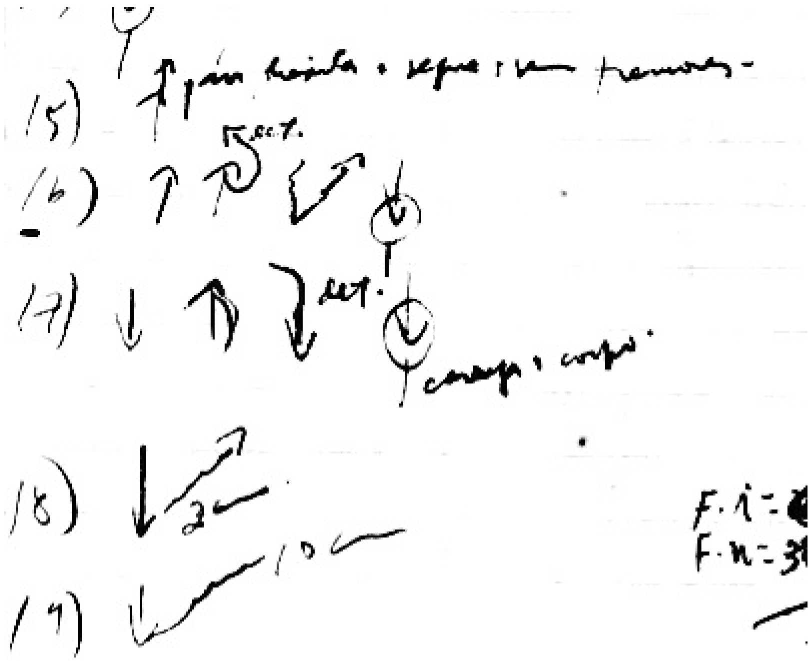


Figure 8: Sample of original record of the behaviour of ants on a trail during some initial and final periods of an experimental phase following the crushing of the thoracicoabdominal portion of eight ants of the colony on this trail.

- *Observation 9 – Behaviour modifications in* P. fulva *after the cephalothoracic portions of eight ants of the colony were crushed on their trail. (Duration: 20 1-minute periods).*

This time, the smell produced by the crushed bodies was almost imperceptible. Qualitatively, the results seemed similar to those in the previous phase. Three body fragments were carried to the nest during this phase, and the remaining ones within the next half-hour, during which, the trail, dislocated in about 3cm from its original course near the alteration point, was clearly recovering its normal aspect, except for the passage of some ants near that spot. Quantitative data for this observation are provided in column D, Table 1. Figure 9, below, shows the original records of the behaviour of the ants on this trail during some initial and final minutes in the observation.

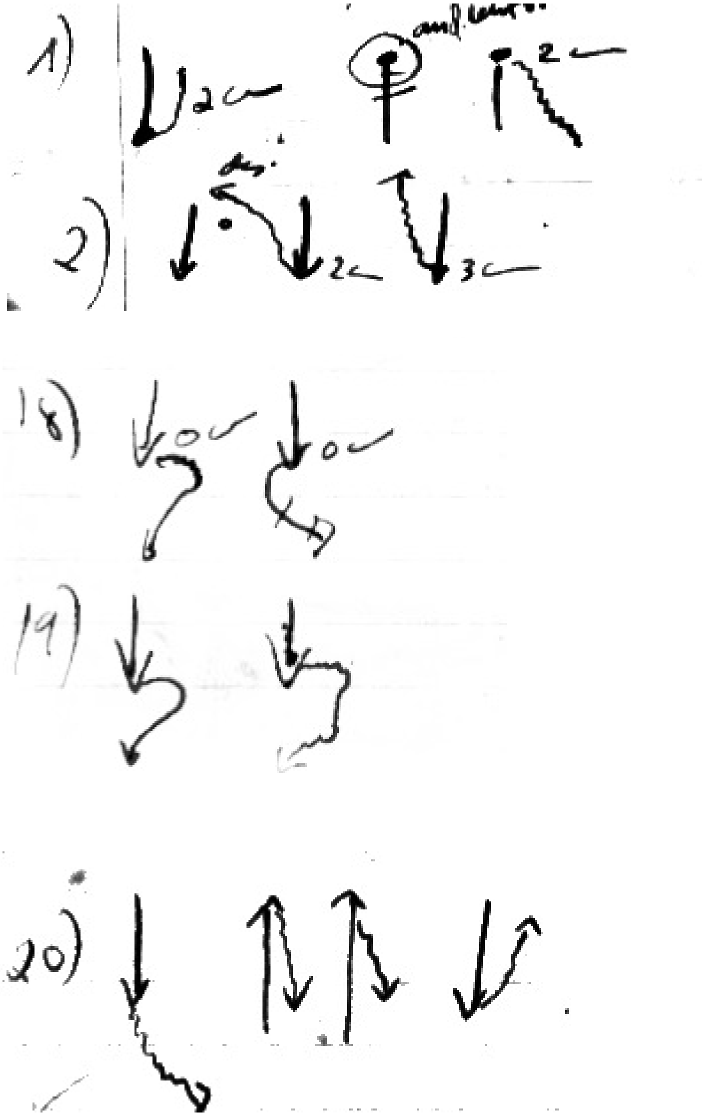
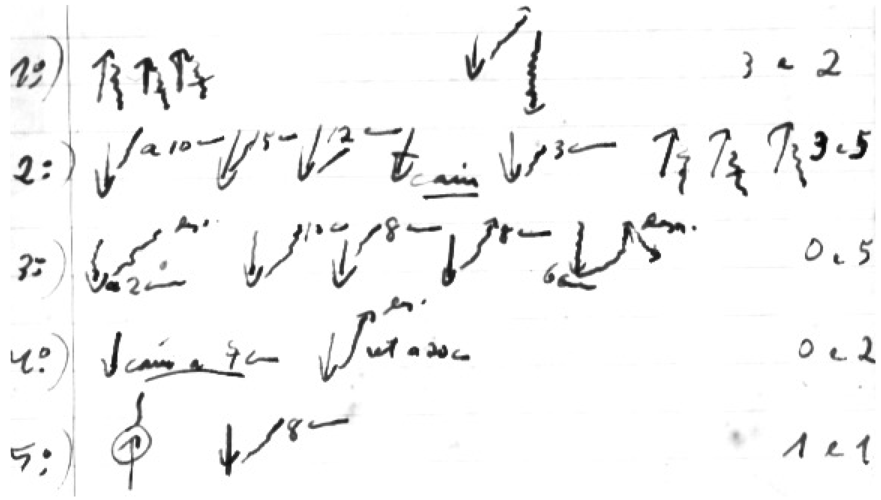


Figure 9: Sample of original record of ants on a trail during some initial and final periods of an experimental phase, following the crushing, on this same trail, of the cephalothoracic portion of 8 ants of the colony.

- *Observation no 10 – Modifications in the behaviour of* P. fulva *after the cephalic areas of eight ants of the colony were crushed on their trail (Duration: 30 1-minute periods).*

Seven heads stuck to the wall, but there was no noticeable smell. However, the modifications in behaviour seemed to me more intense than in the three previous phases, resembling those observed when whole ants had been crushed. In fact, undulations and jolts seemed more vigorous, accelerations more conspicuous, and, in the end, there were many stray ants on the wall, apparently disoriented. It is possible, however, that some of the modifications observed – especially the large number of falls – were due to the fact that the alteration point was in a particularly smooth area of the wall. Two head fragments were carried to the nest.

The quantitative data for this observation are shown in column E, Table 1. Figure 10, below, shows the original records of some initial and final minutes of the observation.



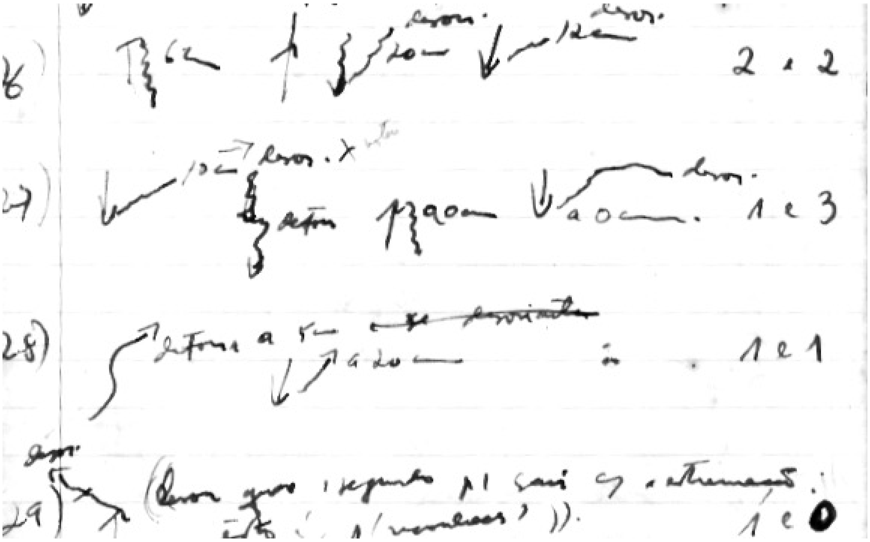


Figure 10: Sample of original record showing ants on a trail in some initial and final periods of an experimental phase, following the crushing of the cephalic area of eight ants of the colony on their trail.

Data modality	**A** **N = 60** **NA = 40**	**B** **N = 20** **NA = 191**	**C** **N = 20** **NA = 71**	**D** **N = 20** **NA = 78**	**E** **N = 30** **NA = 90**
F.D. Experimental phase	0.67	9.55	3.55	3.90	3.00
Diff. F.D. exp. phase and control	-1.06*	-9.70*	-3.15*	0.25	-3.00*
PERCENTAGE OF ANTS:					
Return	60	37	34	62	64
Undulation	70	48	37	69	74
Detour	10	10	17	17	20
Disorientation	23	5	2	8	14
Parallel progress	10	1	0	5	1

DATA MODALITY	**A** **N = 60** **NA = 40**	**B** **N = 20** **NA = 191**	**C** **N = 20** **NA = 71**	**D** **N = 20** **NA = 78**	**E** **N = 30** **NA = 90**
Pause	13	7	24	9	4
Jolt	30	5	2	17	16
Fall	3	1	0	0	8
Apparently undisturbed	0	34	21	1	2

Table 1: Data regarding the behaviour of *(P. fulva)* ants following the crushing on the trail of: A) 4 whole ants; B) abdomens; C) thoracicoabdominal areas; D) cephalothoracic areas, and E) heads of eight ants of the colony.

*Statistically significant at the level of $p \leq 0,5$ (Index: Fisher's t for small samples).
N = number of single observation periods (minutes).
NA = number of ants observed.
FD = average number of ants in a single observation period (minute).

DISCUSSION OF THE RESULTS OF OBSERVATIONS FOR THIS ITEM

Examining the results of the five observations in this topic – those in the graphic records, those described in the text, plus the quantitative data presented in Table 1 – I think I can affirm: (A) that all experimental alterations carried out under this topic brought about conspicuous, qualitatively similar, modifications in the behaviour of the ants on the trail; and (B) that, however, crushing the cephalic area caused more dramatic changes than the crushing of the abdominal area and, most likely, the thoracic area.

Given (A), I deduced there was no substance, exclusive to any of the three body parts, that could be considered responsible for the dramatic changes in behaviour observed when whole nest-mates were crushed on the trail. If any substance or combination of substances – for instance, one or more alarm pheromones – were responsible for these changes, they should be present in all three body parts, even if, considering (B), in larger concentrations, or more specifically, in the cephalic area. Indeed, one should ask: would it not be possible that a larger concentration of alarm substances, or an additional substance, might account for the greater effectiveness of a crushed head in bringing about the phenomenon under consideration?

This hypothesis seems especially attractive, for, as mentioned under item 2, mandibular glands are located in the head, and these are often considered by researchers to be one of the main sources of alarm pheromones in many ant species.

I must point out that, when I conjectured the possibility that crushing ants on a trail greatly disturbed their nest-mates because irritant and/or repellent substances were released in the surrounding area, I was not aware of the claim of biologically-oriented researchers, of pheromones as the most likely cause for this disturbance. My hypothesis, the existence of some irritant or repellent substance, was, however, related to their claim. It became more plausible to me when I found out, through readings and my own observations (of, for instance, the agonistic and defensive behaviour of *Camponotus crassus* Mayr*, Camponotus rufipes* Fabricius, and some species of *Craematogaster),* that many ant species – including the species considered here – emit liquid or viscous jets from the tip of their abdomens against intruders in the nest or wounds on the bodies of enemies.

In my readings I learned that, in many cases, these are said to contain formic or other kinds of acid, which may act as poison. Goetsch (1957), for instance, had affirmed that the formic acid in the poison gland in the stinger of some ants, on being released in the environment, would act as a danger signal to their nest-mates, who would run around in great distress; some would abduct their mandibles and raise their abdomens, through the tip of which they would frequently emit a drop of poison. Schneirla (1960), in his turn, reported modifications in the behaviour of ants, such as "nervous jumps" (jolts?), in a maze with "an excess of formic acid". For these reasons, I expected the crushing of the abdomen would bring about more modifications in behaviour, and these would be more dramatic than modifications caused when other body parts were used. To reinforce this opinion, there was also the fact that the strong, typical smell of the species is more intense when their abdomens are crushed, as compared to the other body parts. This expectation, as we have seen, was directly refuted by the results of these observations, which also revealed how the odour I thought was so characteristic of *Paratrechina fulva* could be, at least as regards the phenomenon under consideration, relatively irrelevant.

On second thoughts, however, it was not only this expectation that the outcomes of the observations seemed to refute in certain aspects, but also the hypothesis that these modifications in behaviour were caused by repellent or alarm substances. How could, indeed, the supposedly escape-inducing effect of these substances be reconciled with the fact that, during the observations, some ants would pause inside the modified area itself, "explore" fragments of crushed bodies with their antennae, and even hold, lift and carry them to their nest?

Perhaps the supposed existence and form of action of pheromones could be reconciled with this manipulation of body fragments by considering that the pheromones would have completely volatilised by then. According to Hölldobler and Wilson (1990), alarm pheromones in ants must have evolved a composition with effects limited to a few minutes, since their persistence would prevent ants from resuming the routine activities required by the colony. However, should this be so, a new difficulty would arise: Why did behaviour modifications denoting alarm persist, during observations with ants crushed on a trail, as in Observation A, till the end of a 60-minute period, and, probably, even further? It must be mentioned that, during my long series of observations, there was no evidence of behaviours indicating a renewal of alarm substances in the alteration point by the surviving ants.

In view of these facts, I think we must ask whether it is really necessary that we rely exclusively on alarm pheromones being supposedly released upon the crushing of bodies or body parts to explain the phenomenon of behaviour modification on an ant trail. In order to mitigate what Cornets (1914) very properly called "the natural voracity of a hypothesis", that is, its propensity to assimilate, once it is formulated, as many facts as possible in a given investigation, I think it is advisable, whenever possible, to set it against alternative hypotheses. In this case, it seems convenient to ask, with a view to future observations, whether the cause of these dramatic modifications in behaviour might not be, for instance, the interruption of the olfactory track underlying the trail, with its admittedly major role in orienting the marching of ants, or, still, in broader terms, the alteration of a situation of pre-existing behaviour, of which the whole bodies and usual behaviour of their nest-mates would be clearly a part, essential in keeping this behaviour unchanged.

Be that as it may, I intend to present in the course of this work a number of facts that seem to support these alternatives. There is one, however, that should be mentioned in this context: the apparent pre-eminence, in *P. fulva* ants, of the head, as compared to other body parts, in the social activities of the colony. Wherever two ants suddenly come across each other frontally, they generally explore each other with their antennae; often they exchange food through regurgitation. We should bear in mind that reciprocal regurgitation of saliva takes place since the larval stage in many ant species. Some authors, following Wheeler (1910), claim that this phenomenon, of reciprocal exchanges through regurgitation, technically known as *trophallaxis*, is the primary bond in the social life of ants and other insects, such as social wasps[9]. Could this pre-eminence, by itself or in conjunction with other factors, explain in some way why crushing an ant's head is more effective in inducing changes in behaviour than crushing its thorax or abdomen?

Before addressing these hypotheses, however, I should mention two other questions which I think are a natural development of the analysis presented in this item. One is the role played by the number of ants in behaviour modifications. The other one is ascertaining whether crushing is necessary to attain the effect observed.

4.2 COMPARING THE EFFECTS ON BEHAVIOUR IN *P. FULVA* ANTS EXPOSED TO VARYING NUMBERS OF CRUSHED ANTS OF THEIR COLONY ON THE TRAIL

A point that remains unclear in the observations reported so far is whether the number of crushed ants, or the total amount of body fragments involved, might play a role in the phenomenon of behaviour modification on ant trails.

This seemed unimportant to me, since, as seen in the previous item, the cephalic area of the ant was evidently much smaller than the other two body parts crushed on the trail; its impact on surviving nest-

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[9] See also, on this connection, Forel (1921, 1922), Warden et alii (1940), Michener , C. D. and M. Michener (1951), Schneirla, (s.d.), Morley (1954), Dumpert (1980), Hölldobler and Wilson (1990), etc.

-mates, however, was much stronger. Also, as already stressed, when whole ants were crushed on the trail, the presence or absence of body fragments on the substrate seemed not to affect in any way the severity of the resulting behaviour modifications.

On the other hand, as already pointed out, the response of individual ants occurred at highly variable distances, from 0 to 10cm or more from the alteration point. Those occurring further off suggested that ants were responding not to the sight or to a direct perception of the crushed bodies, but, rather, to volatile substances: as most, if not all, students of the so-called alarm behaviour in ants, would say, these were certainly the substances they call *alarm pheromones*, released when ants had been crushed. However, the question remained: could the amount of such substances, as nearby stimuli to which ants respond, not be proportional, or, at least, not evince a trend towards being proportional, to the amount of distant stimuli employed -- to the amount of crushed bodies or of those body parts (such as the cephalic area) having a more active, important role in the phenomenon?

In order not to preconceive an answer to this question, I decided to rely on an adequate experimental procedure.

To do so, I first selected two observation sessions, A and B, here collectively called Observation 11. It is reported below.

- *Observation 11 - The effect caused on ants on a trail by crushing a varying number of ants.*

In these two phases of the observation, I recorded the behaviour of ants of the same colony in two not widely separated occasions, during which they coincidentally formed two trails, laid out very similarly on the terrain. These trails, on both occasions, connected the nest to a lure; most of its course ran along the surface of a low brick wall, then to a ceramic mosaic floor, and, finally, after a short stretch up an adjacent wall, reached the nest, the entrance of which was a depression in the plaster, under a rainwater pipe. A 40-watt bulb, hanging near the wall, and two stronger bulbs further away, lighted the trail. Figure 11 shows the situation in its most immediate aspect.

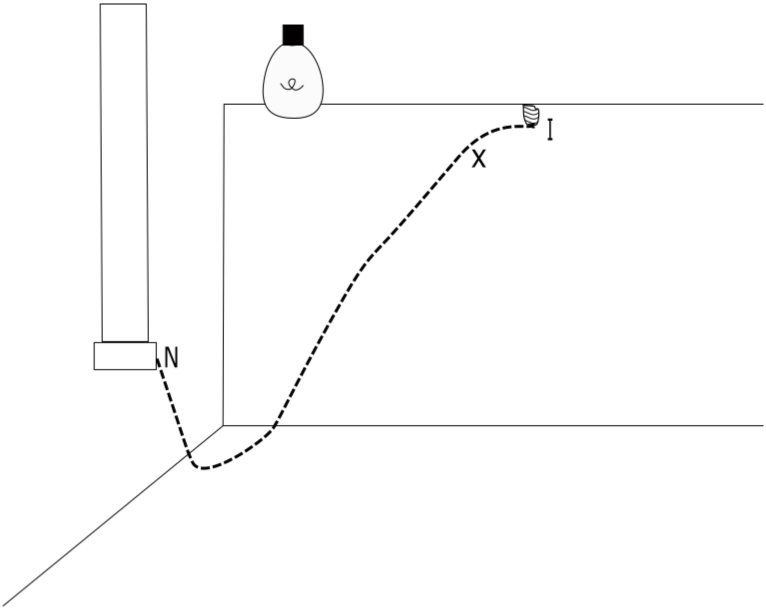


Figure 11: Sketch of the situation considered in Phases A and B, Observation 11.

The dashed line represents the trail on a low wall and a higher, adjacent wall, on two different occasions. **I** represents the incentive, **N** the nest under a rainwater pipe, and **X** the alteration point.

Each session comprised two observation phases: a control phase (with no alterations on the trail), of fifteen one-minute periods, and an experimental phase of forty one-minute periods for phase B, following the crushing of ten ants of the colony in Phase A, and one ant in Phase B. Here is a summary description of the two sessions.

In observation session A, I used as a lure two cotton wads dipped in a mixture of water and sugar, held together by a safety pin and placed under one of the rounded ceramic pieces topping the wall. The sugary mixture was twice renewed, the night before the observation and on the day of the observation.

Their sense of orientation proved impressive, for the trail ran slantwise along the wall, a course that tended to be the shortest route between the food source and the nest. However, an ant would occasionally go down the wall on its own in an almost vertical course, as if oriented by gravity or, perhaps, following a former route. Once in a while, one worker (sometimes two) of another species, unidentified in the records, bigger than *P. fulva* -- probably *Camponotus melanoticus* -- would visit the upper wad; no skirmishes or contact between the species were observed.

At 8:08 p.m., one hour before the control phase, I attached the 40-watt lamp to a window handle; it hung 18cm away from the wall, 1.05m above the ceramic floor, and 30cm away from the low wall. I turned it on. This was meant to supplement the light provided by the two stronger bulbs in the yard where the observation was taking place.

Unfortunately, at 8:20 p.m., it started to drizzle and then to rain. So, I opened an umbrella and mounted it on two rods with their ends resting on the window sill and the top of the low wall. I chose a spot where my eyes would be 75cm away from the trail. I put the stopwatch on the floor and sat down on some newspaper sheets and a fabric bag. Thanks to the eave above me, the rain missed the wall by at least one square metre, and also the rounded ceramic pieces covering the part of the low wall where the ant trail and the lure were. Soon the rain relented until there was only a light drizzle and no wind.

For the experimental phase of Session A, before the rain, between 8:20 p.m. and 8:25 p.m., ten ants were captured on the floor, one by one, as they were leaving the nest; they were kept in a glass container, and then transferred to a paper sheet, on which I immobilised them with a slight pressure of my forefinger; except for one of them, which managed to escape, they were all transferred to my forefinger and pressed against one of the ants on the trail going towards the nest.

The trail observed in Session B, carried out fifteen days after Session A, was laid out in basically the same way, including the odd ant on its own, going along a course almost parallel to the trail, and the chance visit, apparently tolerated or unnoticed, of an alien ant, of the same species observed in Session A. As in that session, another light bulb was added to the other two lighting the yard, an open umbrella was also mounted on rods, and I faced the trail in the same position as before; the session took place under drizzle and light and infrequent wind.

A cotton wad dipped in a mixture of water and sugar, in a 2 to 1 proportion -- unfortunately, I think, it was probably more concentrated than before -- was attached to the same safety pin about 5 and a half hours before the start of the observation. The early introduction of the lure and, probably, the greater concentration of sugar apparently attracted a larger number of ants and made the trail somewhat different from the one in Session A.

The sessions were also different in that, before Session B, I took a pencil and, right after the passage of some ants, marked with some short strokes the course they were taking before the control phase. I noticed that, for a few minutes, one or other ant, upon going over these marks, would go back or exhibit a jerking motion. After a while, however, the ants ceased to exhibit any change in behaviour when walking along the trail and over these marks.

The additional light bulb was turned on 2 hours before the start of the control phase. Soon, it seemed the number of ants heading towards the lure had increased. Could this new source of light, in its conspicuous heterogeneity as a stimulus near the trail and an easily available point of reference for the ants, account for this sudden increase in the number of ants?

In the experimental phase of Session B, a single ant on the trail, coming from the nest, was crushed. In both phases the results -- behaviours observed in ants nearing the alteration point on the trail -- were graphically recorded, with the aid of a stopwatch, and complemented by notes beside these marks, in successive one-minute periods, though often, unfortunately, given the number of ants, without precision or only by approximation.

In the ensuing assessment of results, the twenty final minutes of Session A were disregarded so as to make it more comparable with Session B, which had a total duration of only forty one-minute periods. The records were not always complete, and omissions and imprecision as to the side in which returns and detours were taken occurred especially when one or more ants started to exhibit modifications in behaviour before I had completed an ongoing record. Records for an undetermined number of ants were simply not taken. For this reason, the prevailing flow density for each experimental phase is not provided.

Unfortunately, observation sessions A and B were obviously different, not only as regards the variable in which I was interested -- the number of ants of the colony being crushed -- and the aspects mentioned in the previous paragraph, but others, beginning, probably, with the individual composition of each trail. Table 2 sums up all unplanned differences I was able to detect from my field notes.

CONDITIONS	**OBSERVATION A**	**OBSERVATION B**
Length of trail:	105 cm	102 cm
Beginning of observation:	09:30 p.m.	10:20 p.m.
Incentive:	Cotton wad dipped in water and sugar	Cotton wad dipped in water and sugar (more concentrated, apparently)
Time of exposure of the incentive before the beginning of the observation:	25 hours. Sugary solution renewed 8 hours before the observation.	5 hours and 40 minutes
Previous experience of the colony with this kind of experimental alteration:	None	Phase A, 20 days before
Persistence of the trail in the area before the experimental alteration:	One day and a half	8 hours
Flow density (average number of ants per single observation unit) during control phase:	5.87	9.2
Meteorological conditions during the observation:	Light rain; 21° C	Drizzle, light and infrequent wind; 19° C
Visible remains after experimental alteration:	3 groups of body fragments in an area 13 mm across inside a stain produced by the pressure of my finger	2 groups of body fragments 2.5 mm from each other, inside a stain produced by the pressure of my finger
Distance between experimental alteration and incentive:	46 cm	27 cm

Table 2: Summary of recorded differences between the conditions in Sessions A and B, Observation 11.

This table is meant as a reminder of variables with undetermined effects on behaviour and an indication of how difficult, perhaps impossible, it is to equalise desirable conditions during observations under natural or nearly natural conditions.

The qualitative results of these two sessions were similar to those already described for this modality of experimental alteration in other observations. That is, in the experimental phases of both sessions, there were behaviour changes and a disorganisation on the trail that might be described as dramatic. To illustrate this, I include below, Figs. 12 and 13, the first pages in the record of behaviours observed during the experimental phases of, respectively, Sessions A and B, and, Figs. 14 and 15, the final pages for these sessions. One can notice from these, quite easily, I think, how modifications in behaviour tend to abate over time, and, as instances of acceleration and undulating march tend to disappear and detours and parallel courses replace returns, how the trail gradually recovers the aspect it had during the control phase of these sessions.

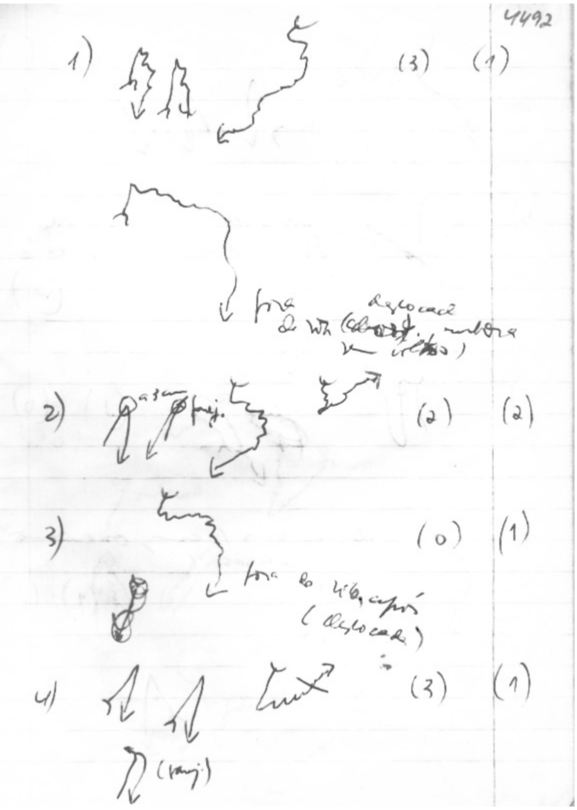


Figure 12: First page in the record of behaviour of *Paratrechina fulva* ants during the experimental phase of Session A, Observation 11, after 10 workers from the colony were crushed on the trail.

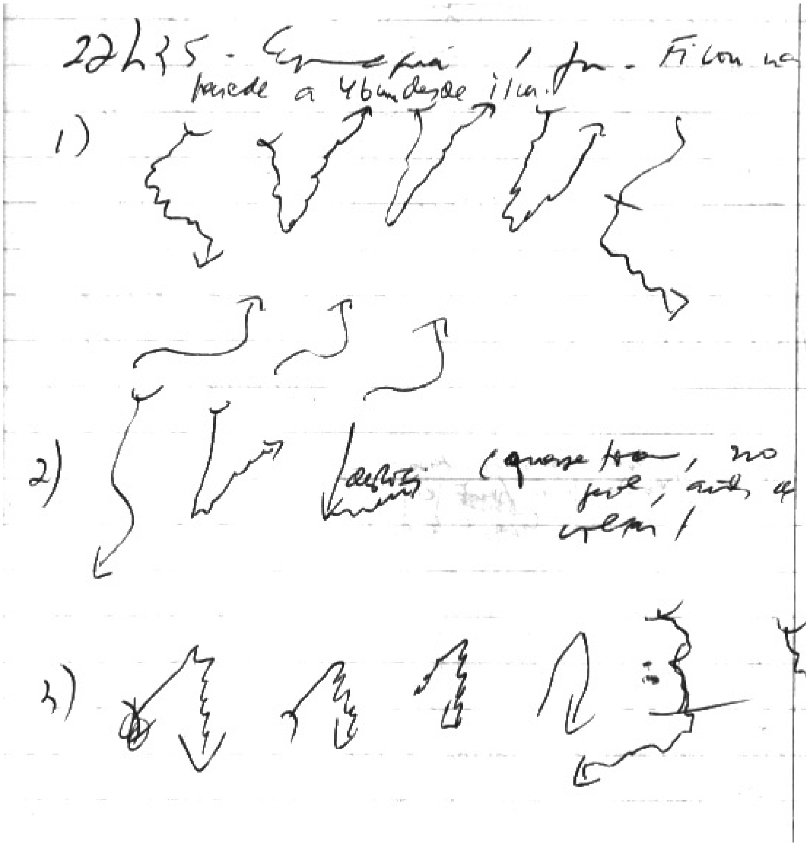
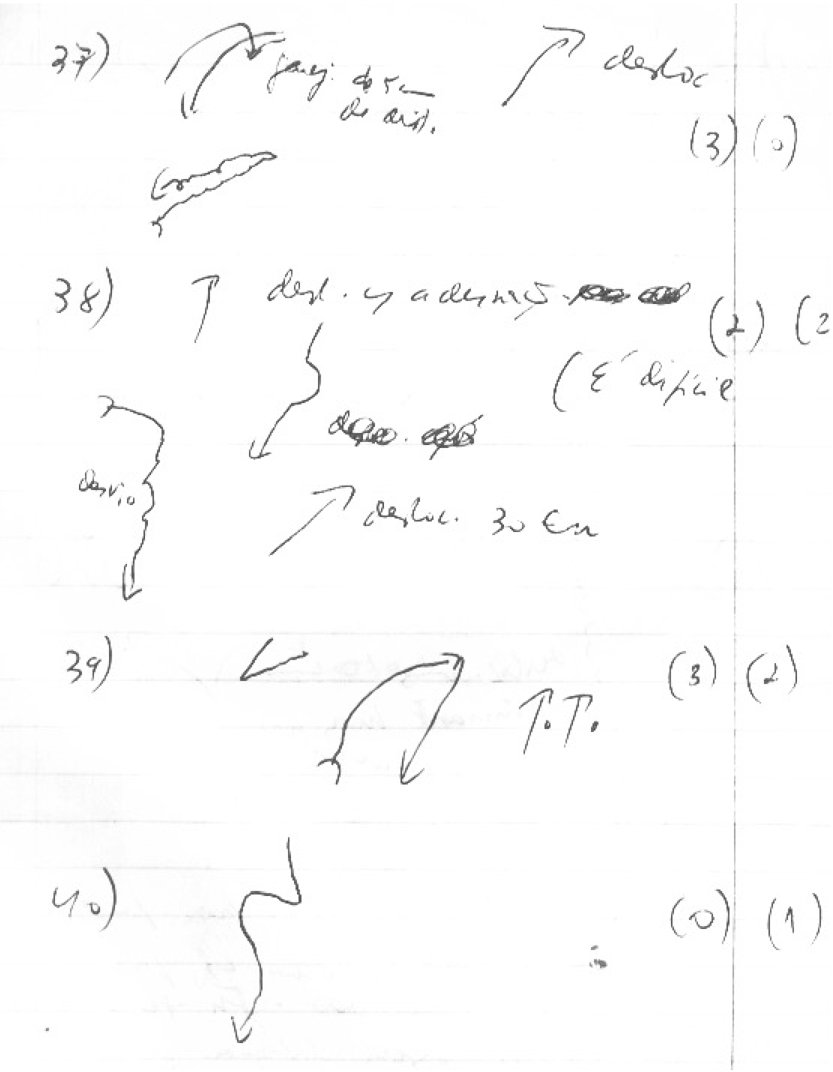


Figure 13: First page in the record of behaviour of *Paratrechina fulva* ants during the experimental phase of Session B, Observation 11, after 1 of the workers was crushed on the trail, while returning from the lure to the nest.



37)

desloc

(3) (0)

38)

(2) (2

desvio

desloc. 30 cm

39)

(3) (2)

T.T.

40)

(0) (1)

Figure14: Last page in the record of behaviour of *Paratrechina fulva* ants during the experimental phase of Session A, Observation 11, after 10 workers of the colony were crushed on the trail.

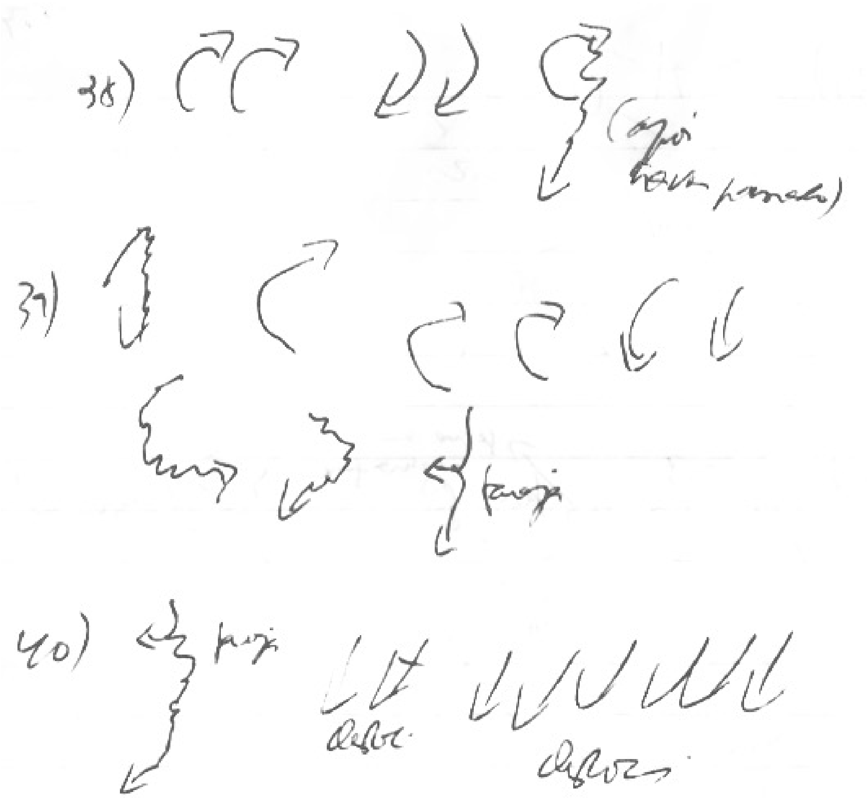


Figure 15: Last page in the record of behaviour of *Paratrechina fulva* ants during the experimental phase of Session B, Observation 11, after 1 of its workers was crushed on the trail while returning from the lure to the nest.

Qualitative results for the two sessions are provided in Table 3.

BEHAVIOUR CATEGORY	**SESSION A** **Number of ants: 81**	**SESSÃO B** **Number of ants: 234**
Progress over alteration point	0	0
Dislocated progress	20.0	23.5
Detour	19.7	23.5
Faulty detour	-	5.9
Return	58.0	52.9
Partial return	7.4	14.7
Disorientation	2.5	5.9

BEHAVIOUR CATEGORY	SESSION A Number of ants: 81	SESSÃO B Number of ants: 234
Undulating march	37.0	44.1
Jolt	4.9	35.3
Pause	2.5	17.6
Fall	-	5.9
Acceleration	44.4	8.8
No apparent modifications	-	-

Table 3: Percentages for the occurrence, on two different occasions, of each kind of behaviour, among those previously recorded, exhibited by *P. fulva* ants of the same colony, as ten (A) and then, a few days later, on a similar trail, one (B) of their nest-mates were crushed (Time covered by each observation: 40 1-minute periods).

DISCUSSION OF THE RESULTS OF OBSERVATION 11

Following the suggestions under Topic 6 in this chapter, one should ask, in the light of both qualitative and quantitative results in this observation, what conclusions might be drawn about the "apparent nature as an obstacle or behaviour-modifying repellent" of the experimental alterations employed in its two phases. If compared, first, in connection with their apparent function as an "obstacle or repellent", one notices there is not, either from a qualitative point of view, as expressed, for instance, in Figures 12, 13, 14, and 15, or from a quantitative one, as in Table 3, any differences that might point to a higher effectiveness of the experimental alteration in Session A -- ten ants crushed on the trail – over that used in Session B -- a single ant. In fact, if, on the one hand, there were more instances of full return and, especially, more acceleration in moving away from the altered area on the trail in Session A, different indexes point to the opposite conclusion. In effect, if one considers the percentages for parallel progress, pauses, disorientation, falls, and, as whole, the percentages for full and partial returns, and successful and faulty detours, the alteration caused by a single crushed ant proves even more effective, regarding this function, than that caused by ten crushed ants. And this notwithstanding the considerable difference in modifying mass – about 10 to 1 – of the alteration in Session A over that in Session B, and, again, notwithstanding the clearly lesser value of the lure used in this session as an incentive, which might lead one to expect, probably, a stronger deterring effect of the alteration.

If, afterwards, one compares the two sessions in connection with the categories in Table 3 that seem to provide more direct information on the apparent "modifying or disturbing function" of their experimental alterations, that is, undulations and jolts, since the others were not monitored, one notices that, surprisingly again, numbers for Session B are higher than those for Session A. The difference is especially noticeable regarding jolts, as it had previously been the case with acceleration, but in the opposite direction, which leads one to wonder whether these categories could not be the result of, in some way, mutually opposing conditions.

Therefore, taken as a whole, the results above seem to point to the conclusion that, as far as this comparison is concerned, the number of ants crushed on the trail or, which amounts to the same, the modifying mass represented by them, does not have an intensive effectiveness above a certain minimum or preliminary value.

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Considering, however, that the conclusion above had been supported by a very narrow observational basis, and, moreover, that it had been impossible to equalise many variables in the two observation sessions, the importance of which could not be determined, I decided to examine it in other ways. I thought it would be proper, among other possible procedures, to ascertain whether there was any connection between the number of ants crushed on the trail as an experimental alteration and the percentage of returns and undulation in the march among the surviving ants. These modalities of behaviour modification were chosen because, as it seemed to me, they expressed more readily and in the best possible way the apparent functions of an experimental alteration as, respectively, an obstacle or repellent, and a behaviour modifier or stressor.

To do so, I tried to select from my records only those observations meeting a number of the conditions required to make them strictly comparable. In fact, I found out there were observations in which crushed ants had been used as an experimental alteration, but, due to variations in procedures or the conditions in which they had been carried out, were not strictly comparable. So, for instance, in some cases the crushing had taken place beside rather than on the trail, and, as already pointed out, involving only body parts rather than whole bodies. In some cases, the crushing had been shortly preceded by other experimental alterations; in others, the trail was split or branched rather than single. Therefore, I decided to consider only observations of single-file trails where ants had been directly crushed, and the crushing had been a temporally isolated experimental alteration. For comparison purposes, consideration would be given to the percentage of ants exhibiting undulation in the march and that of returns in an arbitrarily fixed time span, as the first twenty minutes of the observation session – in order to somewhat control the fact that the frequency of behaviour changes tended to decrease over time. Returns were counted even when partial, that is, when reversed after a while.

In the end, I found in my records twelve observations amenable to the examination mentioned in (A) and thirteen for that in (B). Results are provided in Table 4 below.

Number of crushed ants	**A Percentage of ants exhibiting undulating march**	**B Percentage of ants exhibiting returns**
1	65.1	48.8
1	62.7	29.3
1	58.0	30.9
1	90.6	93.8
1	49.3	45.2
1	77.5	52.5
1	35.4	37.5
1	50.0	57.7
3	86.8	39.5
4	53,8	76.9
4	71.7	60.9
10	50.0	62.9
18	n/c	63.3
	M=62,58	**M=53.78**

Table 4: Data for the connection of number of ants crushed on the trail as an experimental alteration and the percentage of surviving ants exhibiting A) undulation in the march, and B) returns, in the first twenty minutes of each observation, consequent upon this alteration.

One first fact revealed by this table is the great variation in effects brought about by the experimental alterations. In these observations, the percentage of ants that returned or exhibited undulation in the march varied from a third to almost all of them. This seems to imply that the effect brought about by the stimuli originating from crushed ants on a trail is neither automatic nor absolute and is apparently modulated in some way by other factors, which vary from session to session.

In order to assess the relationship between the number of crushed ants as an experimental alteration during the various observations and the effect brought about by them – the percentages of ants exhibiting undulation or returns – Spearman's Rank Order Correlation Coefficient (Spearman's rho) was used.

This coefficient was equal to 0.219 for the correlation between the number of crushed ants and the percentage of ants exhibiting an undulating march in response to the alterations in the observations. Since, for the number of cases under consideration (N = 12)[10], the value required for this coefficient to be statistically significant at the 5% level is 0.506 or higher, one may conclude that the value obtained, though it indicates a slight, positive correlation, is not enough for refuting the null hypothesis - the absence of a relationship between the number of ants crushed on a trail and the percentage of ants responding to this alteration with an undulating course.

As for the rank order correlation between the number of ants crushed on a trail and the percentage of ants responding to this alteration with a return, or a reversal of direction in their course, the coefficient was of 0.582, which is, for the number of cases considered (N = 13), statistically significant at the 5% level. Given this result, one can claim that, in the observations under consideration, there was a trend towards a higher number of ants crushed on a trail being followed by a higher percentage of ants on the trail reversing the direction of their courses.

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[10] Cf. Guilford, 1965, capítulo 14 e p. 593

The results of the examinations in this item seem, therefore, contradictory, one of them pointing to some positive correlation between the number of crushed ants used as an experimental alteration on a trail of *P. fulva* ants and the resulting disturbance among the ants on the trail, while two other results point to an absence of this relationship. In the face of it, I thought it might be appropriate to undertake another examination, suggested by this reasoning: considering the experimental alteration of crushing ants from the colony on a trail, if its value as a deterrent, or apparent repelling obstacle, such as measured by the percentage of ants responding with a return, tended to increase as more ants were crushed, one might claim the same would happen as regards the distance at which these returns took place. Could this be true?

I found in my records eight observation sessions with estimates of the distances at which ants responded with returns upon coming across crushed nest-mates on the trail. Table 5, below, provides the data for these observations.

Direction of trail	**Number of crushed ants**	**Number of ants considered**	**Average distance of returns in centimetres**
Vertical	1	29	6.59
Vertical	2	40	2.32
Horizontal	3	71	2.57
Vertical	4	16	3.97
Vertical	4	72	3.29
Vertical	4	66	1.8
Horizontal	4	48	2.45
Vertical	18	52	8.81

Table 5: Data for the relationship between the number of ants crushed as an experimental alteration on trails running along a brick wall and the average distance at which returns occurred in 8 different observations.

In order to ascertain whether there was any relationship between the numbers in the second column and those in the fourth column, I calculated Spearman's rank order coefficient, and the result was 0.02, that is, practically null. This result, which contradicts the previous one, is surprising, since it implies the impossibility of rejecting the hypothesis for the absence of a relationship between the number of crushed ants employed to alter the trail and the value of this alteration as a repellent or deterrent, measured in terms of the distance at which it causes some ants nearing it to halt and then retrace their steps.

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Concluding, the examinations under this item, taken as a whole, provide very ambiguous results. Except for a single result, they suggest that, above a certain minimum value, there is not an intensive effectiveness for the alteration posed by crushed ants' bodies in a trail. If there is any correlation between the number of crushed ants and their apparent function as a behaviour-modifying obstacle or repellent, it is a very slight one and, so it seems, easily disguised or modulated by other factors, unidentified as yet. In my experience, these factors probably include very disparate things, such as the incentive value of a lure, the relative scarcity of food in the colony, the ants' familiarity or otherwise with their surroundings, the presence or not, beside the trail, of misleading olfactory tracks left by the passage of other nest-mates, or of features in the terrain that may help in their orientation, whether they had faced a previous alteration during the session, whether ants are going towards the nest or the lure, etc.

4.3 USE OF DEAD ANTS WITH INTACT BODIES AS AN EXPERIMENTAL ALTERATION ON A TRAIL

As we have seen, ants' body parts crushed on a trail are enough to trigger remarkable behaviour changes in *P. fulva*. Is the crushing, or some implied factor, a necessary condition for this effect? Or could their behaviour be substantially different if dead, but intact bodies were used as an experimental alteration on the trail?

The observation below was carried out in order to answer this question.

- *Observation 12 - Modifications in the behaviour of* P. fulva *before dead nest-mates with intact bodies on the trail.*

The trail in this observation ran along the junction of a rough cement floor and a brick wall. It connected a nest (a hole in the wall) to a lure (refined sugar under a cardboard box on the floor).

The observation comprised two phases with 20 one-minute periods each: a) a control phase, with no alterations to the trail, and b) an experimental phase, when 6 ants from the colony, previously killed and with their bodies intact, were laid on the trail with the aid of a sheet of paper. These ants had been killed by exposure to the vapours of a tiny cotton wad dipped in a solution of petrol and ethyl bromide introduced in the container they were in. After their death, which occurred almost immediately after exposure to the vapours, the container was left open until the following day, when the dead ants were transferred to a new container, where they were kept for some days before being used in the observation.

From a qualitative point of view, the following should be mentioned. During the control phase, as it might be expected, the usual behaviour found in foraging trails was observed. During the experimental phase, however, especially in the first minutes of observation, there were clear modifications in behaviour among most of the ants approaching the alteration point. Some of them would turn aside and go on along the floor or the wall, or pause to pick up and carry a dead ant. By the third minute of the phase, all dead ants had been carried away, three of them by ants returning to the nest and the other three by ants going toward the lure; five were taken to the nest, and one in the opposite direction, in a disoriented course (outside the trail), for a while, until it was finally taken to the nest around the sixth minute. After the start of this operation, modifications in behaviour were no longer visible, either among the ants carrying the bodies or those they came across along the trail. In the first few minutes, even after the removal of all bodies, some ants tended to pause near the alteration point and either take a detour or turn back, some of them in a clearly undulating march. After some time, however, modifications in behaviour gradually became less frequent and had almost ceased in the final minutes of this phase.

Qualitative results for this observation are provided in Table 6, below.

Categories	Control phase N = 20 F = 87	Experimental phase N = 20 F = 72
Percentage of ants engaging in:		
Return	1	11
Partial return	0	3
Detour	0	13
Disorientation	0	3
Pause	0	19
Undulation	0	15
Jolt	0	0
Acceleration	1	4
Progress over alteration point	98	47
No apparent modifications in behaviour	98	33

Table 6: Data for the behaviour of *(P. fulva)* ants on a trail during two observation phases: a control phase (no alterations on the trail), and an experimental phase, when six dead ants from their colony, with intact bodies, were laid at a point of the trail.

F = Number of ants considered.
N = Number of one-minute observation periods.

A comparison of the results for these two phases leaves no doubt as to the effectiveness of this experimental alteration, dead ants with intact bodies laid in the trail, in bringing about modifications in behaviour. The difference is such as to make a statistical significance test unnecessary.

On the other hand, however, a comparison of this table with, for instance, Table 3, shows that, conditions being the same, the use of crushed ants brings about more dramatic alterations in behaviour than dead ants with intact bodies. Crushing not only causes behaviour modifications in a greater number of ants, but can also be associated with a considerably higher frequency of those modifications which are more conspicuous such as returns, undulation, and jolts. A conspicuous difference between these two modalities of experimental alteration was that intact bodies were almost immediately picked up and carried to the nest, whereas when crushed body parts were used this occurred only exceptionally. In this case, most ants on the trail would simply get away from the alteration as fast as possible, as if suddenly overcome by panic. The *one* instance in which crushed parts were picked up and carried away was, as already mentioned, exceptional, but also enough to imply that the response to dead ants, whether crushed or not, is not automatic or pre-wired, but subject to some individual variation.

One fact that calls one's attention in this observation is the different responses of the ants on the trail to the intact bodies of their dead nest-mates. Some would readily pick up and carry the bodies to the nest, while others evidently avoided them, as if they were alien objects, to be observed from a distance, or even something they had to dodge and escape from.

How could these differences be accounted for? I suppose that some of the ants possibly sensed, first, an interruption of the path, an obstacle in the way, while others sensed a motionless nest-mate. In the former case, as already seen when a simple match was used as an obstacle in the trail, ants would tend to respond to the alteration by turning back, taking detours or, at best, by pausing to examine the object before exhibiting any other response. In the latter case, I suppose the immobility of a nest-mate, contrasting with the movement of the other ants, could be the reason for them to pick up and then carry the body to the nest.

In fact, some observations seem to support this interpretation. On some very rare occasions I had the opportunity of observing the behaviour of ants upon coming across a nest-mate that remained still for some seconds on the trail -- as, for instance, after regurgitating food in response to the request of a nest-mate coming along the trail. These ants would either take a quick detour and go back to the trail -- but then this could be triggered by a slight movement of the antennae, undetected by me -- or suddenly accelerate their march and, with one or more successive jolts, touch the motionless nest-mate. These observations might evidently provide more definite results as to what the ants would do if their nest-mate, in the interest of science, would only remain still. From what I observed in other circumstances, I believe the tendency would be for them to pick up and carry the still ant to the nest. In fact, there were some occasions in which I disturbed a nest and collected some earth with ants and brood and put them in a flower pot; as a rule, the ants, as soon as the pot was left alone, would start looking for a new shelter. They tended to gather eggs and larvae under some clod or leaf; then, some would stay with the brood, relatively still or cleaning their bodies and antennae, while others would inspect the surroundings, and go into cracks and holes in the wall and floor, apparently in search of a suitable place for the new nest. When these scouts had apparently found one, they would repeatedly return to the group of ants and immature individuals under their care and quickly pick up and transport them to the new location; first, immature individuals -- directly, when they were loose, or, if held by the mandibles of a ward, by grabbing and pulling them somewhat roughly, in a signal for the wards to let go, which they invariably did - and, finally, those ants who had failed to follow on their own initiative and stood still in the area[11].

Considering the hypotheses above, the reader will certainly ask whether this conjectured difference in perception – an altered path or a motionless nest-mate -- might not have its own causes. I also have conjectures about this. It is generally known that, among ants and other social insects, such as bees, workers perform successive functions as they grow old. First, they look after immature individuals, then they engage in cleaning the nest, which includes removing and disposing of dead nest--mates and waste produced by the colony, then in digging, building, and expanding the nest, until they finally become scouts and forage and provide for the colony. Therefore, it is not impossible that the tendency to pick up motionless nest-mates on the trail could be found among the youngest providers, new at this operation and still used to those performed inside the nest, such as looking after immature individuals. However, this conjecture will not be tested here.

Another curious fact in this observation was that modifications in behaviour continued for many minutes, even when the bodies were removed. This may have been caused by remnants of the vapour used to poison the ants, not totally volatilised, traces of incipient putrefaction left by their bodies on the ground, or, still, by the presence of tracks diver-

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[11] I have observed these events while working with *P. fulva*, *Camponotus crassus* and *Camponotus fuchsae*.

ging from the previous pattern, left by the ants which had responded to the bodies with alterations in their usual course. I suppose the hypothesis of diverging tracks is likelier than that of olfactory remnants, since the dead bodies, while being carried away, did not cause any behaviour alteration among the ants going past them -- this might also be explained, at least in part, by the fact that ants on a well established trail generally tend to march with their antennae pointing to the ground, as if they were primarily concerned with following the underlying track toward one of the usual destinations -- the nest or the lure.

4.4 THE USE OF ANTS IMMOBILISED BY MECHANICAL MEANS AS AN EXPERIMENTAL ALTERATION

On a certain occasion, while observing a trail that used to form every night along the junction of a ceramic mosaic floor and a brick wall, connecting a nest of *Paratrechina (Nylanderia) fulva* to the inside of a dust bin containing food scraps, I noticed ants crowding around a worker. I thought they had cornered an ant of a different species, but, on further examination, after blowing at the group to disperse them, I noticed the worker had two tiny threads attached to its back and one of its legs, and these were hindering its march. I thought the threads or the way the ant was walking caused the ants to touch it, as if they wanted to grab and carry it away.

Given this occurrence and having in mind the discussion under the preceding item, I thought it might be of interest to examine, on this and other occasions, the effects, on the behaviour of *P. fulva*, of a sudden encounter on the trail with an ant artificially immobilised or with its movements restricted for a while. This set of observations is identified here as Observation 13.

- *Observation 13 - The use of living ants, totally or partially immobilised by artificial means, as an experimental alteration in* P. fulva *trails.*

I found out that some kinds of mechanical stimulation, especially if repeated, could induce a state of immobility or thanatosis in this ant species. For instance, I could use my fingertips to titillate or gently and repeatedly press the ant against any surface, or gently rub it against the palm of my hand, or, still, put one or more ants in a container and shake it for a few minutes. Apparently, while trying to counteract this involuntary dislocation by tensing their legs and trying to hold onto the substrate, ants make too much effort and enter a cataleptic state for a while -- more than a minute, sometimes.

With this practical finding in mind, I undertook various observations, on different occasions, in order to find out what effects could be observed in ants when single individuals, with their mobility previously impaired by artificial means, were placed on their trail.

The first one to be laid on the trail, huddled up, motionless after being rubbed against the palm of my hand, was grabbed by the cervix before starting to move and then taken to the nest. Two ants in succession, after being given the same treatment, exhibited *staccato* motions, and looked as if crippled and seriously injured. The most common response of ants coming across them was to pause, “sniff” them and proceed on their march. Some, however, responded with an undulating march, detours, and, occasionally, a jolt.

Another ant, motionless, was laid on the trail; it then rolled on its side and halted in a crack on the floor; soon ants gathered round it, trying to touch or grab it by a leg or the thorax. It was eventually grabbed by the nape and carried away. I noticed on other occasions that as a small group of ants gather round an ant with reduced mobility they will generally lick it, which probably helps the ant to recover the typical odour of the trail and thus, on recovering its mobility, not to cause nest-mates on the trail to stop and inspect and touch them. In some cases, a worker, on coming across and approaching an immobilised ant, would rear its head, as if about to attack. On one of these occasions, I observed that the immobilised ant, perhaps misinterpreting the gesture, also tried to raise its head, as if in response to a regurgitation offer.

I noticed that this ant was carried between the legs, slanted, its front higher up and further ahead than the back, so as to prevent it from going against the substrate and hindering their progress.

Using a piece of fabric and a card instead of my hands to roll and immobilise the ants did not cause any difference in results. In this connection, it is worth mentioning that, on entering and leaving the dust bin, which was used every day, ants must have had their usual odour greatly altered, but this did not cause any behaviour modifications in the ants they came across -- perhaps this alteration had already become commonplace in their daily routine.

Flow density and trail width were clearly determining factors in the alterations caused by the presence of a motionless or nearly motionless ant. Once, as I set some ants I had rubbed into immobility on my hands on a trail with a flow rate of about 150-180 ants per minute and which, instead of being linear, had a varying width of one or two centimetres in their course over the floor, I noticed that only ants coming directly across the motionless ants responded to their presence, generally in the way already described. The vast majority that did not come across them head on, especially among a crowd of moving ants, seemed not to notice them. If one of the motionless ants started to move in jolts or ineffectually, especially if it had been laid across the trail, traffic would jam, rather because the ant was seen rather as a physical obstacle than an object of curiosity. Under these circumstances, perhaps because the great number of moving nest-mates acted as a distraction, its presence seemed to be hardly noticed.

Based on my observations, I concluded that it was motionlessness, total or noticeable, or irregularity of movement, that would prompt their nest-mates on the trail to carry them or to exhibit other major behaviour modifications. An unexpected event seemed to support this conclusion. It was as follows.

In one of the observations above, I chose one of three trails that had formed on a garage floor, the largest concentration of *P. fulva* I have ever seen. It was clearly the most linear in the trail system that had been forming for about seven hours towards a saucer containing a large cotton wad dipped in a solution of water and sugar. It was also the trail with the least flow density: about 35 ants per minute. There were three light bulbs hanging from two points in the garage ceiling; to enhance observation conditions, I set on the floor, some 15cm away from the trail, a 40-watt lamp, without a shade. Figure 16 illustrates the situation.

I noticed that, right after this further lamp was positioned on the floor, one or other ant would stop and rear up towards the light, as if "sniffing" it. Some left the trail and started roaming around the lamp and even touched its base, without, however, leaving the floor. After a few minutes, the disruption caused by the trail was amazing. The trail was linear until it was about 30 cm away from the lamp. At that distance, in the area surrounding the lamp, ants scattered and followed no trail. Once, I counted 31 ants roaming around the area.

Suddenly, I counted six of them carrying other ants, randomly. The impression was that they picked up and carried away their nearby nest-mates because they sensed them to be disoriented, given their erratic movement; however, they were themselves disoriented by the power and proximity of the lamp. So, in order to continue with the observation and restore the original order of the trail, I had to place the lamp higher up and further away towards the nest.

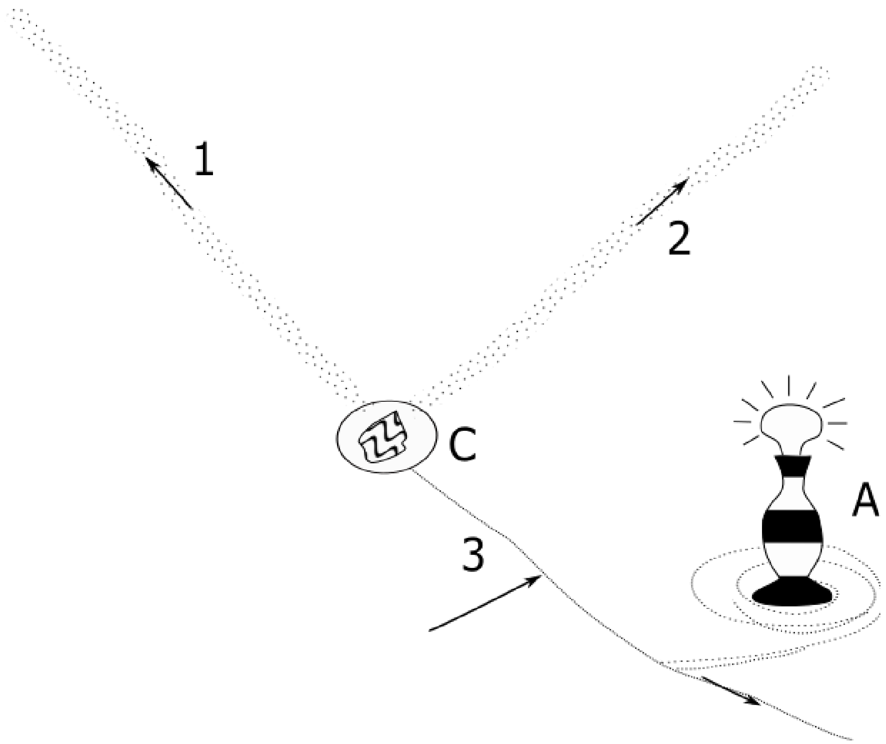

Figure 16: Sketch of circumstances in Observation 13, after a lamp was set 15cm away from one of three trails.

Legend:
A: 40-watt lamp without a shade.
C: Lure (a saucer with a cotton wad dipped in water and sugar).
1, 2, 3: Trails.
Long arrow: trail selected for observation.
Short arrows: direction of trails.
Dashes and dots: individual ants.

5 MODIFICATIONS IN BEHAVIOUR, A PHENOMENON GENERALLY ASSOCIATED WITH INTERFERENCES WITH AN OLFACTORY TRACK PRESUMABLY UNDERLYING THE TRAIL

It is widely known that many alterations carried out in connection with ant trails bring about conspicuous modifications in the behaviour of these insects.

The first to point out this phenomenon in myrmecological literature was possibly Bonnet who, as early as 1745, had already noticed that by simply rubbing a finger against their collective path one could make *Lasius* ants hesitate in their course (Cf. Piéron, 1912, and Warden, Jenkins, and Warner, 1940, p. 609).

According to Piéron *(Opus cit.,* tome II, pp. 230-239), Forel, who studied ants in the early 20th century, inferred there was olfactory path recognition among *Lasius* and *Formica* ants by observing disturbances in their behaviour when a piece of wood was used to block their path. Still according to Piéron (*opus cit.*), Bethe, while studying *Lasius* ants, had also prompted disturbances in their behaviour by blocking the path of a trail, changing its direction, and exposing the ants to smells foreign to the trail; and Ernst, after placing strips of water, alcohol, or petroleum in a collective path of brownish ants of the *Formica* genus had noticed these would generally act as obstacles and force them to take a detour, at least when alcohol and petroleum were used; finally, Piéron himself had observed some relatively mild modifications in behaviour (some hesitancy and brief stops) after removing a superficial layer of leaves, the substrate for a 25cm-wide trail (or, rather, a column) of *Formica truncicola*; also, upon scraping a 1cm strip of rock he had caused less intense disturbances in behaviour than those caused by the removal of a mere stem, a few millimetres thick, from a stretch of soil between two stones, or when a pebble or twig was set on the trail. Piéron also pointed out that “disturbances” in behaviour caused by an interruption of the trail were relatively short-lived, and, after one or two minutes of hesitancy, turning back, and searching, a number of individuals would go over the area until the trail was finally re-established.

Cornetz (1914, p.164-166) reported that by sweeping a 13 cm wide stretch of soil crossed by a *Tapinoma* trail he had forced the ants on both sides of the affected area to turn back; 4 minutes later, a first ant went over the area in a slanted course, after turning back for a while; 5 minutes later, four ants did the same in a relatively normal march; only after 16 or 18 minutes would ants go over the area without any hesitation. According to Cornetz, Fabre had carried out the same experiment using Amazon ants (*Polyergus rufescens).*

In these cases, the interventions directly altered the substrate on which the ants were walking. However, experimental alterations indirectly affecting a substrate where ants had apparently left an olfactory track to guide companions coming after them have the same effect. Thus Lubbock (1898, p. 234) reported he had hung brushes previously dipped in solutions of water and clove, water and peppermint, or "other strong-smelling substances", about 0.5cm above some strips of paper where some *Lasius flavus* ants were walking. He noticed that, whereas some ants would go on in their normal, unaltered march, others would pause, return for a short stretch, and then try again and finally cross the altered area; after doing this two or three times, they would no longer hesitate in their progress through the area. On the other hand, according to Warden *et al.* (1940, p.609), Turner is said to have prompted modifications in ant behaviour by suppressing the smell of xylol on a stretch of trail, and concluded that ants react to olfactory peculiarities in their path.

An important and frequently recognised fact to be mentioned in this connection is that interfering with a track brings about relatively mild behaviour modifications or no modifications at all, in species that, having good sight, only exceptionally or incidentally follow a collective path. This is what I observed in trails formed by ants from a colony of *Camponotus crassus* Mayr, 1862, established day after day along the same stretches of walls, the branches of a climber and even the wires of a clothesline, because they relied on the invariable location of their food sources (aphids and scale insects in the climber and other plants) rather than on olfactory cues left to guide them, even though these were certainly present. According to some authors (for instance, Warden *et al.,* 1940, p. 609, and Piéron, 1912, p. 238), this also happened when isolated individuals of some species would leave a trail and follow an independent path. In these cases, however, it seems no olfactory track had been left by the preceding ants, and the orientation of these individuals was based mainly on visual cues.

Generally speaking, however, the connection between alterations in the trail and behaviour modifications in ants with poor sight and relying on olfactory tracks for their orientation seems so compelling that Cornetz, for instance (Cf. 1914, p. 35 *et passim*), used to sweep or cover with sand the floor before an ant as a method to determine "with certainty", based on the presence or not of ensuing modifications in behaviour, whether it was, respectively, an ant following an olfactory track or a "pioneer" on the terrain, independently exploring a route. Schneirla (1956, p.396 ff.) also said he employed a "simple test" to ascertain whether the columns of army ants he was studying used olfactory tracks for orientation during their raids. The test consisted in moving a leaf or part of the surface on which the ants were moving and then see whether their course was interrupted as a result and so remained until the gap in the trail was progressively filled by newly arrived ants entering and leaving the altered area with increasing frequency.

The connection between interventions in the olfactory track presumably underlying a trail and behaviour modifications in ants with limited eyesight is so constant that it is no surprise that many authors – as well as those referred to above, Michener and Michener (1951, p. 17), and Goetsch (1957, p.103-105) – have ascribed all these modifications to a loss or impairment of orientation in these ants. Bethe (Cf. Wheeler, 1910, p. 533; Piéron, 1912, p. 232ff; and Warden et *alii*, 1940, p. 609ff) seems to have been the first to formulate this hypothesis. Bethe added to his hypothesis the assumption, later refuted[12], that trails were polarised paths formed by odoriferous tracks.

Like these authors, on many occasions I effected alterations in substrates of *P. fulva* ant trails to observe the effects they would have on their behaviour. For instance, relying on my memory[13] while working on a previous book of which this text is a thoroughly modified version, I frequently mentioned I had "cut" the course of a trail by rubbing a finger, a piece of wood, of sand paper, or a lump of camphor on it. When the width of this "cut" was small – from one to two centimetres –, "for about one minute, upon reaching the altered area, the ants would pause, 'sniff', and then proceed at a higher speed. Soon, however, all the ants were going over the area, and there was no noticeable difference between this and other parts of the trail".

A systematic examination of the records taken for instances in which the trail had not simply been "cut", but blocked by some object,

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[12] Piéron, for instance, in the work referred to, reports having prompted modifications in behaviour in *Lasius fuliginosus* specimens by removing a piece of bark from the tree on which they were walking; however – contrary to what might be predicted from Bethe's assumption -- there were no modifications when the piece of bark was simply replaced on the tree in a reversed position.

[13] Especially when starting this research I would often fail to record some of the observations.

either deliberately introduced in the trail or fallen on it by chance, reveals a paradoxical fact: small objects were more effective than sizeable ones in blocking the ants' march and disorganising their behaviour. We have already seen the effect of half a match or a cotton wad, either previously dipped in kerosene or not, on a trail of *P. fulva* ants. Other small objects introduced in the trail included a 1 cm piece of paper from the packaging of a soap bar, a short, narrow strip of sticking plaster or adhesive tape, a dead fly, a soft bread crumb, some tangled threads, a raw bean, a small glass container, etc. Generally speaking, the modifications observed suggested that these objects were sensed as curious, suspicious or even threatening.

However, when the object altering the trail was relatively large and covered a long stretch of it, the ants would simply concentrate in the blocked area and try to crawl under the obstruction, in a clear attempt to follow the olfactory track. This is what happened in the observation referred to above, when a leather cigarette case was placed on the trail. In other cases, not mentioned yet, other objects were placed on the trail, such as a 1m x 70cm sheet of cardboard and a large cardboard box. These cases and some of those already mentioned evinced a true compulsion to find the collective path again and confine their march to it.

The main point about these observations was that they refuted the assumption that the main factor in behaviour modification in those ants was difficulty in orientation caused by the suppression or modification of a stretch of the olfactory track underlying the trail. If it were so, covering long stretches of a trail would cause more disturbance than suppressing or altering a tiny spot in it. Clearly, a large object did not seem to be perceived by the ants as threatening or repelling, since, on coming across one, they seemed to be concerned only with the disappearance of the collective track. However, that the ants did not rely exclusively on this track for their orientation could be seen, for instance, in those cases in which a card was used to cover part of the trail: When they could not find an opening between the soil and the card and follow the collective track, they would stop at the edge of the card, "sniff" it, step on the card and hurry back, repeat the process a number of times at a fast pace, covering further distances in each of them and following a semicircular path, until they finally reached the other end of the card and found the trail again. This goes to show that, even when the collective track is lost, ants still retain a general sense of the direction to follow.

A comparison of behaviours prompted by the obstruction of a path by small or large objects seems to suggest that when ants cannot grasp the outline of an object with their antennae they will perceive it rather as a perceptual background than a figure. And that it is to a perceptual figure, seen as an obstacle and an inhibitor of their march, rather than to a gap in the trail, that they will respond. That a single crushed companion can disorganise so much the behaviour of the ants moving along the trail clearly shows that it is the nature of the object on the trail, rather than the suppression or modification of a stretch of it, the main cause for the dramatic behaviour modifications observed. However, as we soon shall see, this does not mean that whether there is an object on the trail, or whether the trail has been modified or not, does not have any bearing on ensuing modifications in behaviour.

Another point of interest in these observations was the difference in response between ants going toward the nest (fn.s) and those going toward the incentive (fi.s). When the trail had been recently established, some fi.s would occasionally pause for a while before an obstacle, move their antennae in an exploratory way or even climb it for a while before going ahead. This was observed when a raw bean, a dead fly, and a bread crumb were used, suggesting that perhaps these ants had not yet been to the lure, and tended to experiment with objects that seemed to be one. On the other hand, fn ants tended to go round the obstacle and hurry to the nest. When the trail had been there for long, fi.s would give up the path more often than fn.s. on coming across an obstruction or alteration. These, after turning back on meeting an alteration in the path, would sooner or later face it again until they could overtake it and return to the nest. The reduction, although temporary, in the number of ants moving along the trail after it was modified suggests that ants retain a memory of recent events. Later, using artificial nest boxes covered with glass sheets enabling an internal view of the device, I could observe that ants hindered by an obstacle, upon reaching the nest, would generally spend a long time performing certain movements called by myrmecological scholars "comfort movements" (basically, cleaning their antennae and legs and sometimes licking the tip of their gasters).

5.1 OBSERVATIONS OF THE BEHAVIOUR OF ANTS ON A TRAIL WHEN PRESENTED WITH ALTERATIONS IN THEIR ENVIRONMENT IN THE FORM OF SOUND, LIGHT, AND ALSO LIGHT AND THERMAL STIMULI, WHICH PROBABLY DO NOT DESTROY OR ALTER THE OLFACTORY TRACK PRESUMABLY UNDERLYING THE TRAIL

The preceding observations made it clear that modifications in the behaviour of ants caused by placing objects on their trail had more to do with the nature of the objects employed than with the length of trail that had been altered or suppressed. Small objects were more effective than large objects in their blocking or inhibiting effect. However, it was clear that these objects effectively suppressed or altered the existing substrate and the olfactory track probably left by the ants which had previously gone through the area. Therefore, we could wonder how ants on a trail would behave if their environment were altered by stimuli that would interfere with their collective path without altering its chemical composition, including the probable track mentioned above.

Bearing in mind these considerations, I had the Idea of exposing ants on a trail to sound and light stimuli and examine whether they would cause behaviour modifications, and, if so, of what nature. The observations carried out for this purpose are reported below.

- *Observation 14 – Behaviour modifications in* P. fulva *ants on a trail when exposed to sound stimuli.*

I did not observe any behaviour modifications in the ants on this trail when exposed to sustained sounds, such as those of speech. Sometimes, however, when presented with sudden noises, such as those of someone snapping fingers or a notebook falling on the floor, some of them would briefly display some agitation in the form of jolts and undulation and acceleration in their march. Whether these reactions were actually a response to vibrations in the air and, therefore, the expression of a true ability to perceive sounds, or to vibrations in the substrate on which they stood --- a frequently suggested possibility[14] -- is something I cannot say on the basis of this observation alone.

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[14] For instance, Lubbock, , 1898, p. 221ff; Wheeler, 1910, p. 512-514; Forel, 1921, V. II, p. 32ff.; Warden *et alii*, 1940, p. 649; Michener, C. D. e Michener, M. H., 1951, p. 13f; Goetsch, 1957, p. 98. More specialised

Observation 15 – Behaviour modifications in P. fulva *ants on a trail when presented with alterations in the form of light stimuli (sometimes thermal also).*

That *Paratrechina fulva* ants respond to light may be regularly observed during their nuptial flight, which generally occurs on warm nights during the rainy season. On these occasions, small swarms of fertile individuals can be easily found fluttering round light bulbs or roaming on lighted areas of walls; laymen commonly take these individuals, especially males, for "gnats". What I ignored, and could observe during Observation 13, reported above, was how workers of this species could be attracted to a strong light source, suddenly placed near their trail. As we have seen, its attractiveness prompted many of the workers to leave the trail to approach the light source, and was strong enough to cause disorientation.

Paratrechina fulva ants have eyes; however, the fact that they frequently form trails, both at night and during the day, suggests that sight is not as important for their lives as smell. In order to ascertain whether, when on a trail, their behaviour would be affected by variations in the lighting of their trails, I carried out the following interventions:

A) One night I turned on a light bulb inside a small room, in which an ant trail ran along one of the walls; I repeatedly turned it on and off, and noticed no differences in their behaviour.

B) Then I had the idea of projecting on the trail a light beam contrasting with the lighting around it. There were two possible alternatives: I could use a thin beam and keep the room in the dark, and, in this case, I would have to confine my observation to the limits of this focus, or, I could keep the environment in partial darkness, and project a beam that would be relatively stronger than the surrounding light.

   Having chosen the latter course, I took a torch and directed the light through a small hole in a sheet of carbon paper and onto a length of the trail on the wall; I could adjust the size of the focus, from a dot to a circular, 4cm-across luminous patch. Under these circumstances, I

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works on the perception of sound and vibration by ants by Markl, Autrum, among others, are summed up by Dumpert (1981), and Höldobler and Wilson (1990).

observed that, when this spot or luminous patch contrasted with the surroundings, many ants halted before it and changed their courses.

C) On another occasion, I chose a trail of *P. fulva* ants extending between a nest in the yard and a lure (a cotton wad dipped in a mixture of water and sugar) placed inside a small room. The trail ran along the edge of a ceramic floor, parallel to an adjacent wall, and then under a door and into the room.

On the following day, I entered the room while smoking and turned on the light. The trail had practically disappeared, with only two ants left. Both were heading toward the nest. Probably the smoke, together with the light and air from the outside, affected their behaviour, since they moved their antennae while walking and turned back before heading again to the nest. The sun came through the half-closed door, projecting a strip of intense light on the floor and the wall. The strip was secant to the trail and 1 cm wide and 20 cm long – 10 cm on the floor and 10 cm on the wall – as shown in Figure 17, below.

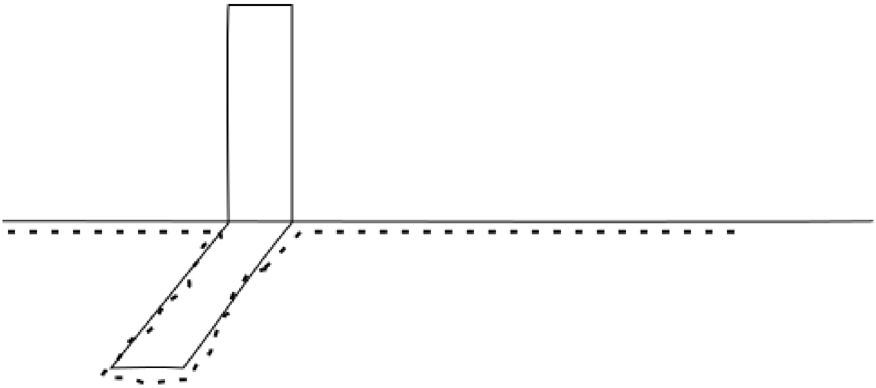


Figure 17: Schematic illustration of one of the situations considered in Observation 15.

Legend:
Solid line: junction of floor and wall.
V shape: strip of sunlight on wall and floor.
Dashed line: path followed by ants returning to a distant nest, on left of the strip of sunlight.

When they were 1 cm away from the strip, each of the ants paused, "sniffed" the now warm sunlit area, and slowly approached the border of the strip; then, they withdrew for a while, came back and went on along the floor and the wall, bordering the strip, sometimes entering and leaving the sunlit area, until they finally went past it in a highly oscillating march. From that point on, they followed their way without hesitation.

In these cases, the warming caused by exposure to sunlight, as well as the light itself, could be involved in the behaviour modifications observed.

D) Throughout these two previous observations, a relatively motionless beam was projected on the trail; another observation, actually done before these, could provide the answer to a question that would certainly arise from the examination of the results mentioned above: how would the ants respond to a moving focus? In this observation I used a candle, placed 20 cm away from the trail, and a lens to collect its light, 50 cm away from the trail, in an almost totally dark room. The light from the candle was enough to light a good part of the trail. The flame was very unstable, since there was a draught coming through the door (parallel to the trail, which ran along the floor, near the junction with a wall), and so the focus was mobile and changeable in size. By simultaneously moving the candle and the lens I was able to produce a focus surrounded by a ring of shade and project this either in front or behind a particular ant and follow its course.

Under these circumstances, a number of ants exhibited modifications in their usual behaviour. Some of them, especially after their first "contact" (that is, after being first hit by the light), would pause and "sniff" both the focus and the surrounding ring of shade; some reared their gasters, while others, simply by being pursued by the beam, could even be induced to turn back or even leave the trail and move away from the lure: it was as though they were trying to escape from it. After some "contacts", many ants seemed to avoid entering or coming near the area on which the beam and the ring of shade were projected.

DISCUSSION OF THE RESULTS OF OBSERVATIONS NO. 14 AND NO. 15, ABOVE

The results of these two observations demonstrated that, under certain conditions, alterations in the environment such as noises or luminous stimuli could prompt modifications in the behaviour of *P. fulva* ants on a trail. These modifications ranged from mere halts and probing motions of the antennae, sometimes in a state resembling watchfulness, to flight and escape responses. They also showed that it was not necessary to chemically alter a trail for behaviour modifications to happen. However, one might say that, for them to happen, it was important that the alteration in the environment could be located as something bounded, especially a mobile alteration – as in the case of light stimuli --, on the ant trail; and it is not unlikely that the same might be the case with sound stimuli, such as the sound of snapping fingers. It would be interesting to find out whether these sounds might be less effective if the ants were not following a trail; unfortunately, however, I have not carried out any observations to this effect. In order to be effective in behaviour modification, sound and light stimuli – in some cases, thermal stimuli also – apparently have to meet certain conditions. Sound stimuli should be sudden and intense; light stimuli (sometimes also thermal), besides these characteristics, should also be bounded, or mobile, and placed on the path being used.

6 A COMPARISON OF THE DIFFERENT EFFECTS ON ANTS ON A TRAIL UPON COMING ACROSS CRUSHED NEST-MATES IN THEIR COLLECTIVE PATH OR WITHIN A SHORT DISTANCE OF IT

We have seen that virtually every alteration effected on a *Paratrechina (Nylanderia) fulva* Mayr trail was associated, to a greater or lesser degree, with behavioural modifications. Considering these results, one could naturally ask whether the trail itself could not be involved in these phenomena, and, if so, in what way. Every alteration with a modifying effect on their behaviour, especially ants crushed on the trail, acted as if with the apparent function of a "behaviour-modifying obstacle", and an obstacle, as such, is something lying in the way or interfering with a movement or a process. How different would these modifications be if an experimental alteration were carried out outside the trail, leaving it unobstructed? And how would ants not following a trail behave when faced with an alteration in their immediate environment?

I report below some observations regarding these questions.

- *Observation 16 – Behavioural modifications in* P. fulva *on a trail when faced with crushed nest-mates; first, beside the trail, and then, on the trail.*

This observation focused on a 1.90m long trail, formed on a kitchen ceiling. It ran parallel to the junction of the ceiling and a tiled wall, at a distance of 2 or 3 mm. The trail connected two orifices, here identified as O1 and O2, which, I assumed, were, respectively, the access to a path under the tiles, leading to a food source, and the entrance to a hidden nest. The assumption was based on the fact that 90% of the ants moving from O1 to O2 had swollen gasters, with conspicuous yellow bands, a condition generally observed after the ingestion of food, whereas the ants coming from O2 to O1 were thinner and darker, with small and opaque gasters. The ants seemed to prefer walking on the ceiling, and this was probably because it had been plastered and provided a firmer hold to their tarsal claws and a lower likelihood of falls than the smooth surface of the tiles. Figure 18, below, illustrates this situation.

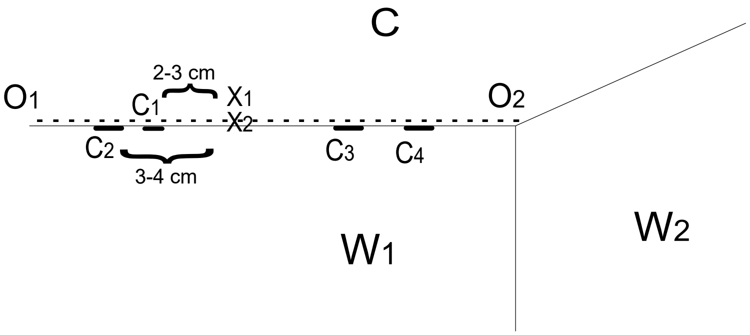


Figure 18: Conditions in Observation16.

Legend:
Whole lines: junctions of ceiling, C, with two tiled walls, W_1 and W_2.
Dotted line: trail.
O_1 and O_2: orifices in the junction of ceiling and walls.
c_1, c_2, c_3 and c_4: narrow crevices in the junction of ceiling and wall.
A slight, barely visible crack runs along the junction.
X_1 and X_2: areas of the ceiling where, on two different occasions, four ants of the colony were crushed.

I observed the ants from the top of a ladder, while taking down notes on a notebook placed on the top of a steel locker attached to one of the tiled walls.

I also placed a stopwatch on the locker. The trail was observed from a distance of 50 cm (distance between my eyes and the alteration point). My breath, since it was directed downwards, seemed not to affect in any way their behaviour. Sunlight came through a long lateral window and a glass door opposite. The colour of the tiles (ivory) and the ceiling (white) made observation quite easy.

This observation comprised the three phases described below.

PHASE A: *Control*, or, without alterations in the trail.

In this phase, records were taken for the behaviour of the ants on an intermediary stretch of the trail, selected to undergo the experimental alterations of the ensuing phases. It lasted for twenty half-a-minute observation periods, as marked by the stopwatch. During odd-numbered periods records were taken for the behaviour of ants going from orifice 2 to orifice 1 (presumably, *fi.s)* and, during even-numbered periods, ants going the opposite way (presumably, *fn.s)*. Apart from behaviours seen in ant trails flowing under ordinary conditions, nothing unusual was observed. In this phase, the average number of ants marching in both directions per minute was 13.9; of presumed *fi.s*, 15.4, and of presumed *fn.s,* 13.4. One may conclude from these numbers that an already high flow density was on the increase from the start of the observation.

PHASE B: *1st. Experimental phase*, when four ants of the colony were crushed beside the trail.

I captured four ants of the colony and held them between my thumb and forefinger. Then, with the tip of my forefinger, I pressed and rubbed the already half-crushed ants against an area of the ceiling near the intermediate stretch of the trail. This procedure left a stain of about 0.5 square cm and tiny fragments on the ceiling, at a distance of about 1.2-1.7 cm from the trail.

This intervention, carried out in a heavy-flow trail, immediately caused nearby ants to run around in disarray. I waited for about one minute for the turmoil to abate in order to be able to follow individual courses and start recording behaviours. Even so, given the large number of ants, I missed most of them. Figure 19, below, shows the records I was able to take for some of the ants on the trail, regardless of the direction they were going, during the first four minutes of record-taking, that is, from the second to the fifth minute since the ants were crushed.

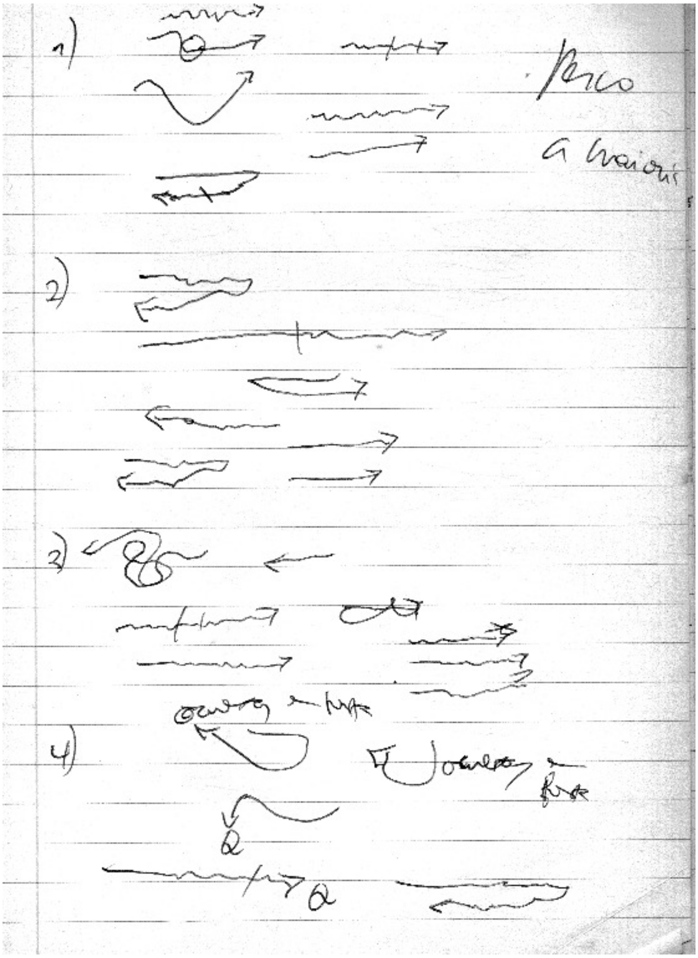


Figure 19: Graphic record of behaviours exhibited by *(P. fulva)* ants during the first four minutes of a period starting one minute after the crushing of four ants of the colony at a distance of 1.2 and 1.7 cm from the trail.

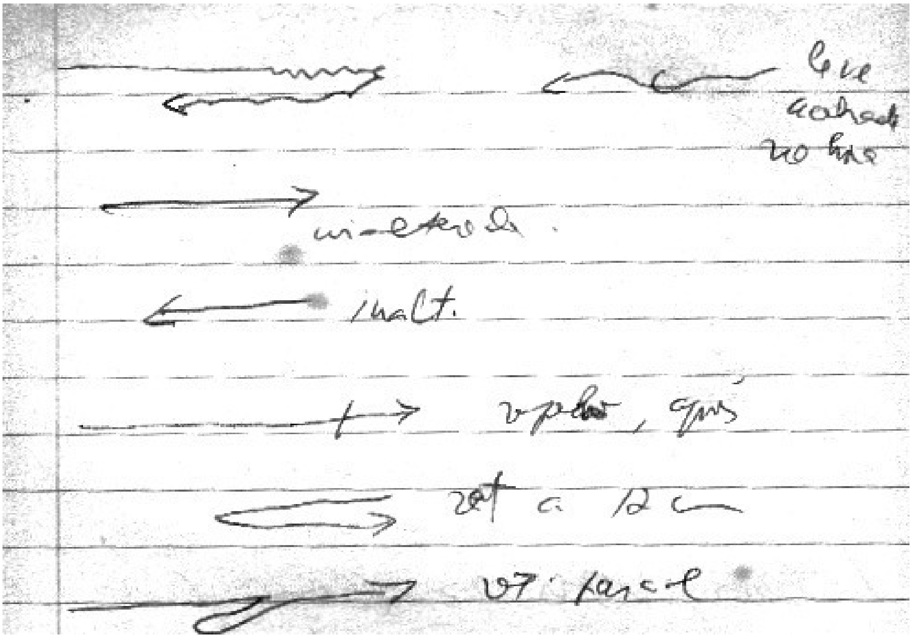
A few words are needed for a correct interpretation of these graphic representations. During the first minute, only behaviours exhibited by *fn.s*, that is, of ants coming from O1 to O2, were recorded. By examining the individual records, one notices that, except for the last one, all the ants went past the altered area: the first, third, and fifth in an undulating march, the second with a partial return, the third with two jolts, and the fourth with a return along the wall that took it further away from the dead ants than its nest-mates on the trail; the last ant observed during this period, turned back in an undulating march and exhibited a jolt. I must point out that returns were recorded as U- or V-shaped arrows simply for my convenience, since they do not necessarily imply a return outside the trail and may simply stand for a reversal of direction in their march.

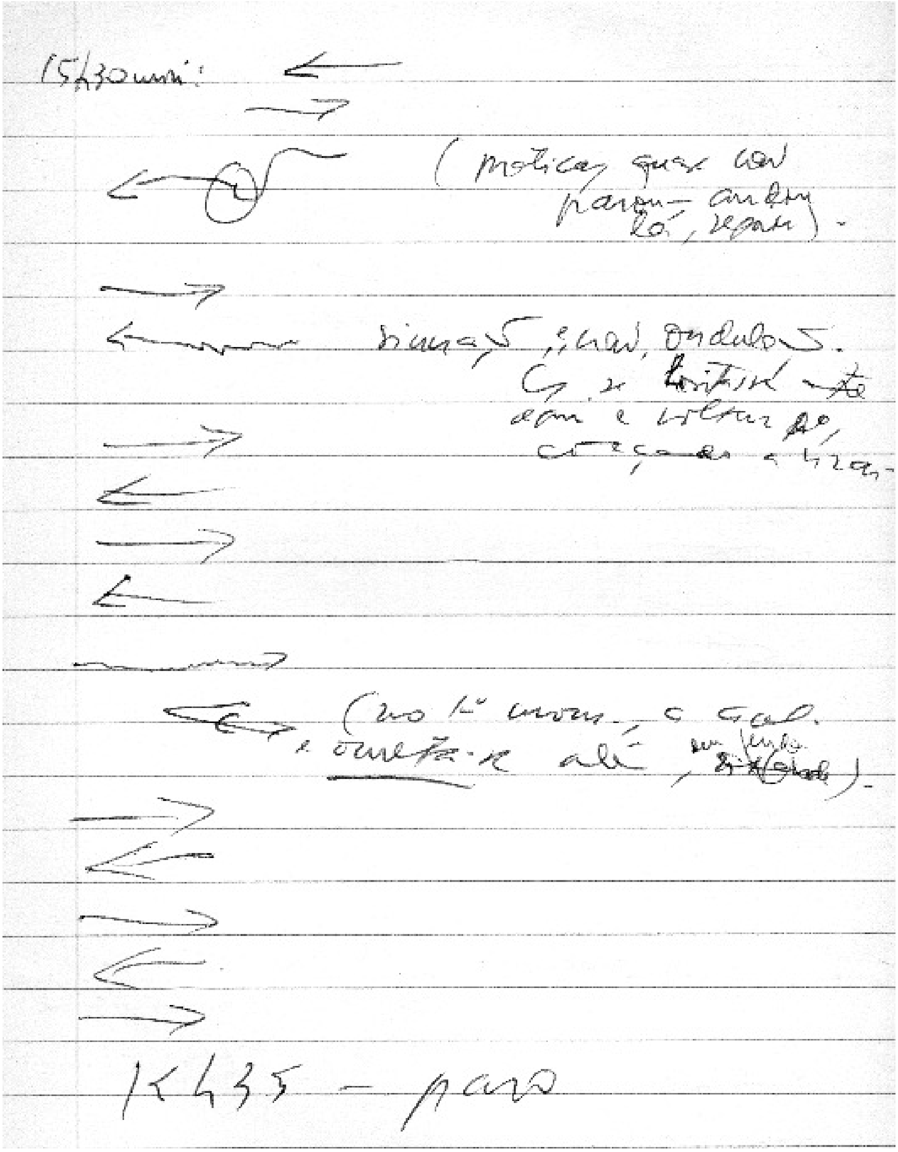
In the record for the second period, there is already a representation of the behaviour of *fn.s*, as well as those of two *fi.s*: one ant that went back without undulation in the march, and another that went on along the trail in an undulating march. As for the behaviour of the other ants, I do not think the way they were recorded poses any difficulty to interpretation.

As for the third period, I call attention to the records of three ants, which might be misunderstood without an explanation: from left to right, top to bottom, records for the first, fourth, and fifth ants. The first ant went round the altered area of the trail a few times; the fourth, having gone along the trail and past the alteration point, turned back towards O2, bent the front part of its body, "sniffed", facing the direction of the stain left by the dead ants, and then continued its reversed course. The fifth ant went over the alteration itself in an undulating march.

Finally, in the fourth minute, I highlight a few differences. The first ant to have its behaviour recorded, after halting on its march towards O2 and turning back, crawled into a narrow crevice under the trail and remained half-hidden for a while. The second ant, an *fi*, after going slightly off the trail near the altered area, also hid in a narrow crevice in the junction of the wall and the ceiling. It should be mentioned that, were it not for these events, I would not have noticed there were crevices in and near the path. If I had, I would certainly have selected another point for the experimental alteration. Returning to the records: the third ant fell to the floor after turning away from its course, which it probably did at a higher speed (unfortunately, instances of acceleration were not recorded) near the altered area. The fourth ant, having gone past the alteration point, fell to the floor after a vigorous jolt.

By the eighth minute of record-taking, I decided for a different procedure. I put the stopwatch aside, and started to alternate the ants observed, now an *fi*, then an *fn*, and see what they did – whatever it might be – in the vicinity of the alteration point, and record it. Records were taken for further fifty-five minutes, until their behaviour had practically gone back to normality, that is, when it was similar to the behaviour observed during the control phase. Figure 20, below, top, shows some of the records taken for the first few minutes using this new procedure, and, bottom, those taken for the final minutes.





15h30min:

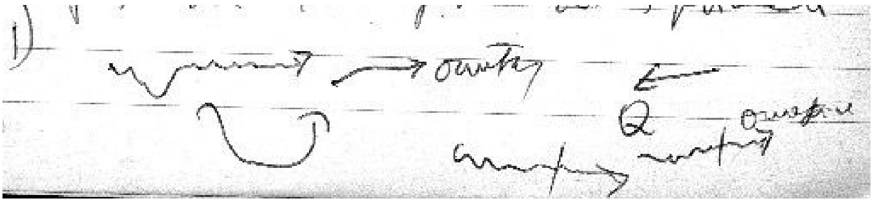
15h35 – paro

Figure 20: Records of behaviour alternating fn.s and fi.s, taken during final minutes of a 55-minute observation period, starting 8 minutes after the first experimental alteration.

PHASE C – The third and last experimental phase, when four ants of the colony were crushed beside the first alteration, but right on the trail.

This phase started twenty-five minutes after the end of the preceding record. As in the preceding phase, four ants from the colony were crushed, but now on the trail, in a spot adjoining the area where the previous alteration had taken place. Some fragments stuck to the ceiling, while others fell to the floor.

The intervention caused turmoil at once, and this still persisted one minute later, when I tried, as I had done in the previous phase, to record the behaviour of those ants I could observe, and then, again, as I had previously done to make the comparison of the two experimental phases easier, to successively alternate the observation of one *fi* and one *fn*. However, two minutes were enough to show that the first form of record-taking could not be sustained. Upon approaching the altered area, the ants would fall off, exhibit dramatic undulation in their march, go back, approach it again, turn aside, hide in crevices before reaching the altered area or, more often, while returning. So, I decided to wait for eight minutes before record-taking, and started to alternate records for pairs of ants coming from different directions, provided each of them had been closely observed. Figure 21, below, shows the records taken using the first method, during the two minutes following the first minute of confusion. It is provided for comparison with Figure 19. Figure 22, below, like Figure 20, to which it is to be compared, is divided into two parts, and presents the records taken using the second method.



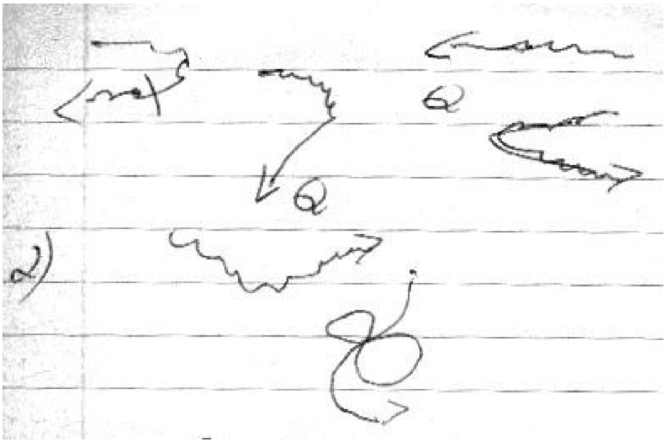
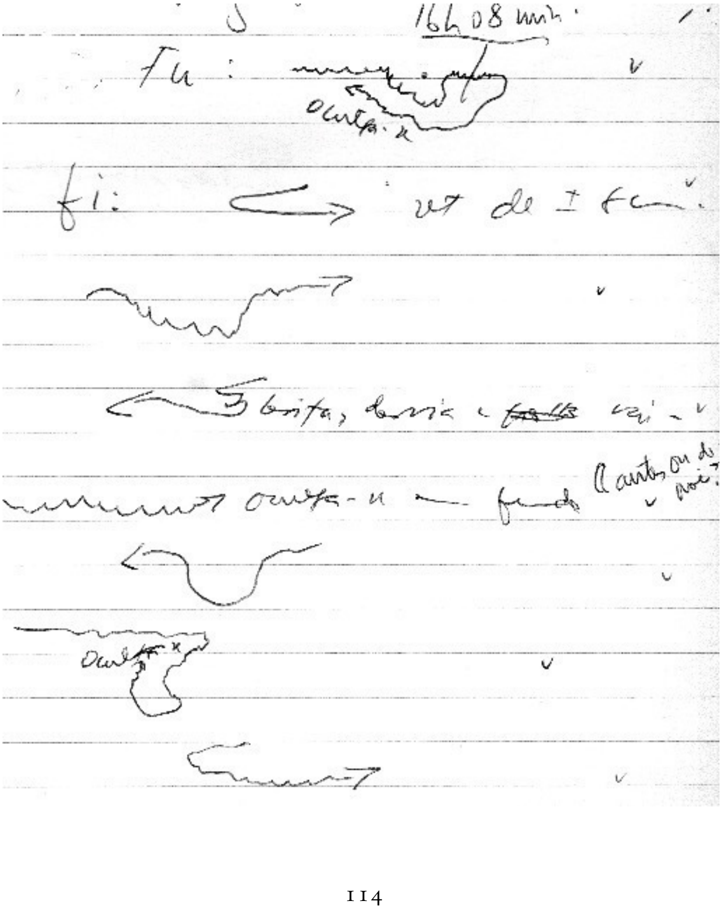
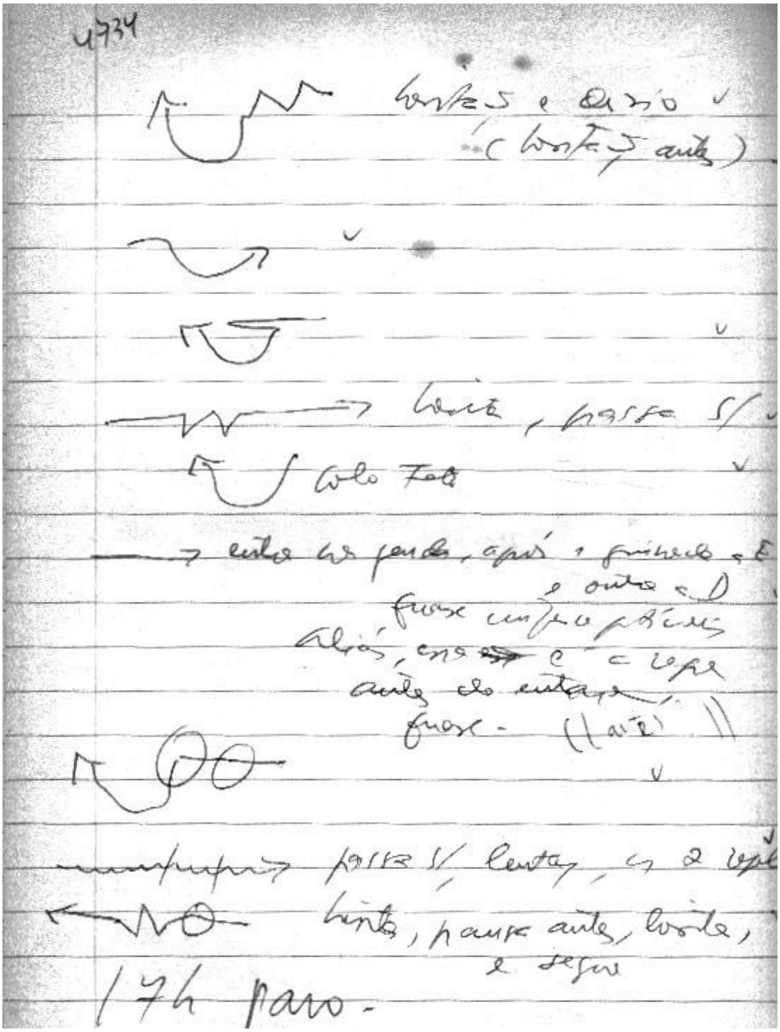


Figure 21: Graphic record of the behaviours observed during the first two minutes of an observation period starting one minute after the second experimental alteration.





4734

174 paro.

Figure 22: Record of behaviours alternating fn.s and fi.s, taken down during: the final minutes of a 52-minute observation period starting 8 minutes after the second experimental alteration.

Table 7, below, provides the quantitative results for the two experimental phases in this observation.

Percentage of ants:	**A** **F1=72**	**B** **F2=96**
Return	1.4	34.4
Partial return	2.8	5.2
Detour	1.4	30.2
Disorientation	0	0
Pause	4.2	14.6
Undulating march	18	29.2
Hesitancy	2.8	7,3
March in blocks	0	1
Jolt	15.3	19.8
Fall	1.4	0
Concealment or attempted concealment in crevices	8.3	24
Exploration of alteration	4.2	1
“Sniffing” at alteration	1.4	0
No apparent modifications in behaviour	47.2	0

Table 7: Data for the behaviour of *(P. fulva)* ants on a trail on a kitchen ceiling in the presence of A) four ants of the colony crushed 1.2-1.7cm away from the trail; and B) four ants of the colony crushed on the trail, beside the first alteration. Duration of A: 55 minutes. Duration of B: 52 minutes.

F1 and F2: total number of ants with their behaviour graphically recorded during, respectively, the first and the second experimental alterations.

DISCUSSION OF THE RESULTS OF OBSERVATION16

One can see from these results how the same experimental alteration, the crushing of some nest-mates, if carried out at a short distance from their collective path rather than on the trail, had much less dramatic effects on the behaviour of ants on a trail. This difference can be seen both in the disorganisation of the trail and the time it took to recover its original, orderly aspect. It seemed almost unbelievable that the same kind of alteration had been employed in both cases.

An objection that might be made against this conclusion is the absence of controls to account for a possible repercussion of the effects of the first alteration on the second alteration. One such control could be secured, for instance, by carrying out the two alterations simultaneously in two different spots of the trail and then recording their effects – let us say, by two observers or two film cameras – during the brief time span spent by the ants at one spot to reach the other. Since I was working on my own and did not have the equipment, I did as described above. However, it should be pointed out that this repercussion, should it exist – which is not unlikely – would have the effect of reducing or intensifying behaviour modifications caused by the second alteration. In the first case, the conclusion allowed by the results reported above, of a greater turmoil in response to the second alteration, would only be reinforced. In the second case, however, the objection would be justified.

To face this objection, I suppose I could compare the effects of these two kinds of experimental alteration by carrying them out on different trails. And this is exactly what we have if we compare, for instance, the results of the first alteration in this observation with those in Observation 6, reported earlier in this work. In their qualitative aspect, the results of both kinds of alteration – four crushed ants placed at a distance of 0.7-1.2 cm from the trail, and four crushed ants placed directly on the trail – may be assessed by comparing Figures no. 19 and no. 20, above, with Figure 6. As for the quantitative aspect, the assessment could be made by comparing the data in Column A, in the table above, with Column A in Table I. These comparisons will confirm, beyond any doubt, that modifications are more dramatic when ants are crushed on the trail rather than in its vicinity. However, another objection might be raised: the variable represented by the inequality of a number of the features involved, probably related to the greater or lesser intensity caused by a given experimental alteration.

I must admit that the features and circumstances of each trail do seem to have an influence on the behaviour modifications exhibited by ants on a trail when suddenly faced with an alteration in it. Factors that seem important in this connection include the shape of the trail, which may be thin or broad, the length of time since it has been established, flow density, the attractiveness of the lure, the presence, or absence, of material features supporting the orientation of the ants, etc. For example, the fact that there are no instances of disorientation in the present observation (Observation 16) seems to arise from the presence of a heterogeneous source of stimulation, the junction of ceiling and wall, in an otherwise relatively homogeneous environment. The junction probably served as an aid to orientation, since the trail moved next to it whenever possible.

Given the objections above, I found it advisable, even running the risk of being somewhat redundant, to report other observations in order to solve the issue. These include Observation 17, regarding the effects caused by the crushing of one ant of the colony outside the trail, and a set of observations collectively named Observation 18, in which an alteration was similarly placed, but using different body parts of nest-mates. The results of these observations should be compared with those of observations already reported in which similar alterations were carried out on the trail.

- *Observation 17 – Regarding behaviour modifications exhibited by* (P. fulva) *ants on a vertical trail on a brick wall when coming across a crushed nest-mate at a distance of 0.5-1cm from the trail.*

This time I observed a trail about 4m long, marching on a brick wall in a vertical course, from the entrance of a nest in the soil to the branches of a grapevine growing on a raised area in a neighbouring yard. Since the ants going up the wall were thin and those coming down had swollen abdomens, I assumed the lure they were visiting was on the other side of the wall and might well be the sweet secretions of aphids and coccids parasitizing the grapevine. Initially, the trail went straight down the apparently homogeneous surface of the wall for about 2.5m; lower down, it bordered the wall of a brick staircase. Sitting on a chair on the upper landing of the staircase, I could see a stretch of the upper part of the trail from a distance of about 50cm and record their behaviour in a notebook placed on the top of the wall. The trail was lit by two bulbs, 2.5m and 9m away. The ivory colour of the wall made for good visibility. For convenience's sake, a stretch starting 1.60m and ending 2.10m above the soil was selected as an observation space. Figure 23, below, illustrates the situation.

The observation was carried out in the early evening and comprised two discrete phases: a 12 one-minute period *control phase*, with no alterations on the trail, and a 39 one-minute period experimental phase, following the crushing of a worker of the colony in the middle of the observation space, at a distance of 0.5-1cm from the trail.

During the control phase, the passage of 34 ants was recorded, 15 going towards the grapevine and 19 towards the nest. This relatively low, not highly variable density flow (an average of 2.8 ants per minute, with standard deviation of 1.3) was conducive to very precise record-taking. Except for an ant with a sinuous march (moving 0.5cm to one side and then 0.5cm to the other) and an ant with a *careening march* (a brief oscillation, with lowered body, as if the ant were searching for olfactory cues underlying the trail),

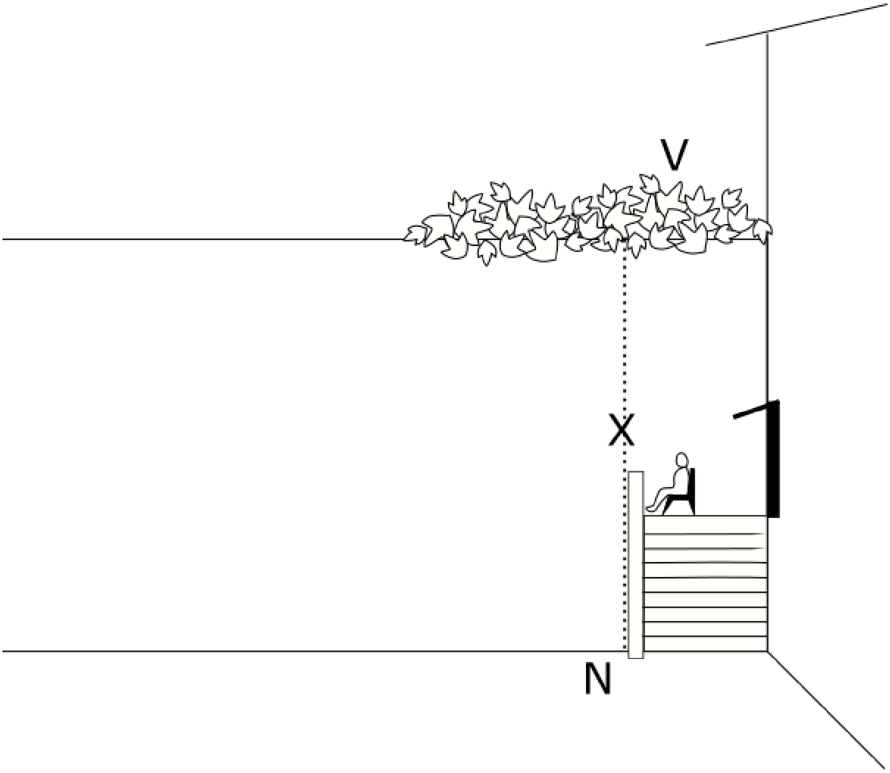


Figure 23: Schematic illustration of the situation prevailing during the observation of ants on a trail on a brick wall, connecting a nest in the soil and an incentive (probably, excretions of aphids and coccids on a grapevine) on a neighbouring raised plot.

Dotted line: trail.
X: alteration point.
N: nest.
V: branches of a grapevine.

Perhaps because of the wind, hitting first the trail and then me, all the ants moved in the usual way in the observation space.

The experimental phase began at 8:00 p.m., with the crushing of an ant found on the staircase wall, which apparently had not fed yet. I placed the ant on the tip of my right forefinger and rubbed it against the wall in an area 0.5-1cm from the trail, where it remained in one single piece with its head facing the trail.

The alteration, except in a few cases (including the first ant to come across it!) acted as an apparent behaviour-modifying obstacle until the end of the phase, even though this effect was mitigated towards the end. Figure 24, below, provides the records taken down during the initial minutes of this phase. Table 8 shows quantitative results for this Observation. By comparing this figure and table with, respectively, Figure 13 and Column B in Table 3, one can see how the use of a single ant as an experimental alteration caused more dramatic effects when the ant was crushed on, rather than outside the trail. Although we cannot say which of the trails had more favourable conditions for dramatic behaviour modifications, we can see at least that the differences favoured the expectation that crushing ants on the trail causes more behaviour modifications than crushing them outside.

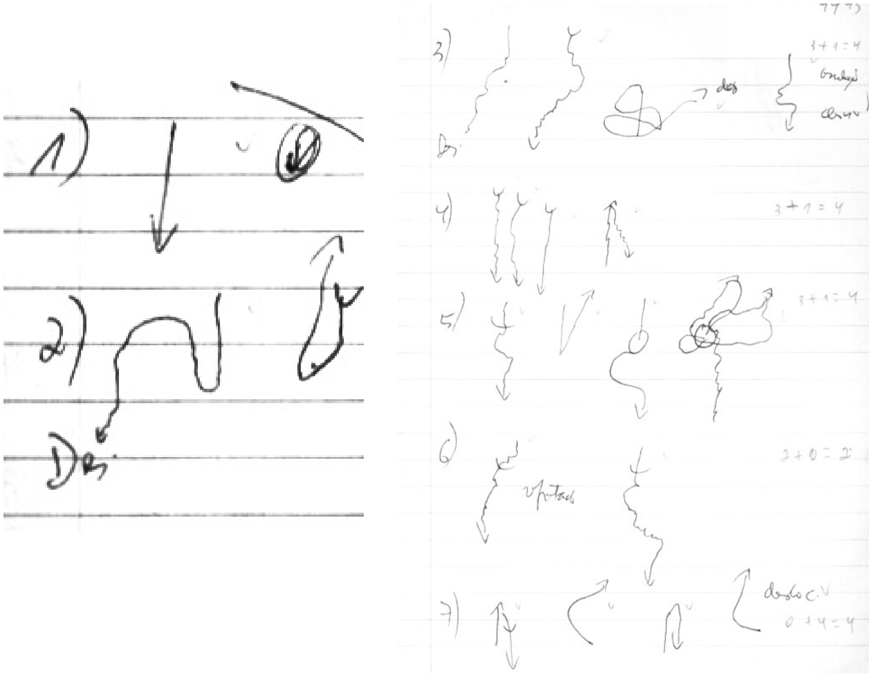


Figure 24: Record for the first seven minutes in an observation of behaviours exhibited by *P. fulva* ants in a trail when faced with a companion that had been crushed and rubbed against the substrate at a distance of 0.5-1cm from the trail.

CATEGORIES	**Percentage of ants:**
Return	25.7
Partial return	9.5
Detour	32.5
Dislocated progress	14.9
Disorientation	6.8
Deflected march	4.1
Undulating march	27
Acceleration	27
Drifting march	4
Sinuous march	4.1
Pause	8.1
Jolt	4.1

CATEGORIES	Percentage of ants:
“Sniffing” at alteration	1.4
Entering the altered area	2.7
No apparent behaviour modifications	6.8

Table 8: Data regarding the behaviour of *P. fulva* on a vertical trail on a wall, extending from a nest in the soil to a food source (probably exuded by aphids and coccids on a grapevine), when faced with a nest-mate crushed and rubbed against the wall, at a distance of 0.5-1cm from the trail (Total number of ants: 74).

I will now proceed to the last observation selected for the question under consideration. It was originally carried out as an attempt to explain the problem considered under 9.1, in this text, when anatomically discrete body parts of ants from the colony were used as experimental alterations. In this case, these body parts were crushed beside the trail by chance, since, on the occasion, I was not aware that by placing them this way, rather than straight onto their collective path, behaviour would be differently affected.

- *Observation 18 – Behaviour modifications in* P. fulva *on a trail when faced with anatomically distinct body parts of nest-mates crushed beside their collective path.*

This observation regards an almost vertical trail marching on a rough plastered wall, between the floor and a strip of adhesive tape holding some sugar. It comprised three experimental phases: phases A and B were both preceded by a control phase, during which we would focus on another stretch of the trail, rather than on the one being observed in the previous phase. For brevity’s sake and since nothing unusual occurred during the control phases, their description has been omitted. Phase C, on the other hand, was carried out right after Phase B. In all its three phases, the experimental alteration was the crushing of body parts of ants killed by petrol fumes two days before and exposed to the air before use. I describe below the qualitative aspect of each phase. Table 9, below, provides quantitative results of the categories systematically recorded.

CATEGORIES	PHASE A F=145	PHASE B F=157	PHASE C F=139
Return	9	5	1
Detour	37	3	2
Disorientation	7	3	1
Undulating march	47	10	5
Jolt	3	2	0
Fall	1	0	0
Entering the experimental alteration	4	2	5
“Sniffing” experimental alteration	0	0	19
Without any of the behaviour modifications above	35	82	90

Table 9: Data for behaviour modifications exhibited by *P. fulva* ants exposed to body parts of some crushed nest-mates outside the trail. The parts used were: A) 10 cephalothoraxes, 0.5 cm - 1 cm away from the trail; B) 6 heads, 1 – 1.5 cm away; and C) 6 abdomens, 1 cm away.*

* F = Number of ants observed.
Duration of each phase: 20 1-minute periods.

PHASE A – CRUSHING OF THE CEPHALOTHORAXES OF 10 *P. FULVA* ANTS AT A DISTANCE OF 0.5-1CM FROM THE TRAIL (DURATION: 20 1-MINUTE PERIODS)

After the parts were crushed, the behaviour of all ants nearing the alteration was clearly modified. They walked slowly and would sometimes pause or lightly turn their heads towards the altered area.

PHASE B – CRUSHING OF THE HEADS OF 6 *P. FULVA* ANTS AT A DISTANCE OF 1-1.5CM FROM THE TRAIL (DURATION: 20 1-MINUTE PERIODS)

As the heads were crushed, a few ants above and below the alteration point ran away. No fragment stuck to the wall. Some ants, generally only those heading towards the lure, tended to pause briefly, make “sniffing” motions and then turn lightly aside, in the opposite direction of the alteration point. Behaviour modifications were more intense in the beginning of the phase, and the trail gradually altered its course, moving away from the alteration point.

PHASE C – CRUSHING OF THE ABDOMENS OF 6 *P. FULVA* ANTS AT A DISTANCE OF 1-1.5CM FROM THE TRAIL (DURATION: 20 1-MINUTE PERIODS)

A number of ants halted near the alteration point, leaned towards it, "sniffed" it, and then went ahead. Some left the trail, entered the altered area, and then either resumed their march or went back. In the ninth minute, a body fragment pulled by an ant fell to the ground. Instances of undulation were few and generally of low intensity.

The data in the three columns of this table (columns A, B, and C), when compared with, respectively, the data in columns C, E, and B, Table 1, item 9.1, in this work confirmed the impression I had in Observations no. 16 and no. 17, reported above, that an experimental alteration, made up of whole bodies or of different body parts of *Paratrechina fulva*, is more effective when these are crushed on the trail rather than at a short distance from the trail. The difference, found in all observations, is so flagrant that there is no need to present statistical significance tests.

DISCUSSION AND FINAL CONCLUSIONS OF THE OBSERVATIONS UNDER THE PRESENT ITEM

Some of the conclusions to be drawn from these results are very clear.

First, all the results in this item seem to demonstrate beyond any doubt that crushing whole nest-mates or body parts of their nest-mates at a short distance from the trail, or parallel to it, reduces the intensity of behaviour modifications observed when they are crushed on the trail.

Second, these results also refute the assumption that would probably be made by researchers of the so-called alarm-pheromone in ants, that behavioural modifications observed in ants on a trail when some of their nest-mates are crushed are automatic responses to these substances. If they were, responses to ants crushed on the trail or in the vicinity of the trail should not be different, since alarm pheromones, allegedly volatile, would quickly spread in the air surrounding the area. And one cannot claim that the emanations from ants crushed near the trail would not reach their nest-mates as fully as if they had been crushed on the trail. In fact, some ants, on being faced with an alteration outside the trail would turn towards it, occasionally approach and even walk on the affected area. The very fact that when ants were crushed on the trail their nest-mates would exhibit alarm behaviour at a distance of 10cm or more would be enough to challenge the assumption, since it was clear that the ants that came across the alteration at a distance of 0.5-1cm were stimulated by it, as evinced by their subsequent behaviour.

Things being as described in the previous paragraph, a third conclusion seems inescapable: if it were true that these behaviour modifications are caused by alarm pheromones, one should admit that their effects are crucially *modulated* or even *annulled* by factors that have not been considered by alarm pheromone researchers. These factors include the fact that ants can probably determine whether an alteration in their environment has occurred in or outside their path and, accordingly, will exhibit less dramatic responses in the latter case. Or, perhaps, the more commonplace fact of a possibly synergic action of stimuli from an alteration outside the trail and a disorganisation of the olfactory track underlying the trail. In fact, I think the results do not allow us to determine if what really matters in causing the behaviour modifications under consideration is (a) the integrity of the olfactory track underlying the trail, (b) the position of the alteration in relation to the orientation of the ants, c) both, or, perhaps, d) some other as yet unidentified factor or factors. However, I have found in my records some observations, carried out on different occasions, with results that seem to shed light on these issues.

7 BEHAVIOUR MODIFICATIONS IN ANTS NOT FOLLOWING A TRAIL WHEN SUDDENLY FACED WITH THE ALTERATION OF THEIR IMMEDIATE ENVIRONMENT POSED BY CRUSHED NEST-MATES

A question that seems to be entailed by the findings described in the preceding item is how ants not following a trail would react to an alteration in their immediate environment, especially if it involved stimuli originating in some crushed nest-mates. In such a case, these ants would not be facing the alteration of a previously known and perhaps habitual path or olfactory track, and this fact might make a difference in their response. The observations described below, collectively called Observation 19, were undertaken as an attempt to answer this question.

- *Observation 19 – Behaviour modifications exhibited by ants moving in the absence of a trail.*

On a certain occasion, with a view to ascertaining how *P. fulva* workers roaming around an area without any discernible trail would react to stimuli originating from crushed nest-mates, I went to a certain spot in my yard constantly visited by ants. It was a cement stand, a support for the waste bin with the daily load of leftovers and kitchen waste. First, using my right forefinger, I crushed two *P. fulva* ants. Having ensured that, except for some humidity and the smell of crushed ants, no remains were left on my finger, I placed it in front of a number of individual ants. They would stop and sometimes rear up, and then return in a quick undulating march, some of them only for a while, others for longer stretches, but the course to their final destination was not observed. When a clean finger was placed before the ants, they would stop at a distance of 0.5cm, come closer, touch it, and then go on in any direction. The same results were observed among ants walking on the ground, next to an avocado tree.

On another occasion, I placed two *P. fulva* workers, one by one, on top of a wooden chest in my office. While they roamed on the chest, I placed before them the finger I had used to crush one of their nest-mates, at a distance of 1-2cm. In both cases, the ants reversed their course, and hurried away in a wide semicircular path. The operation was repeated a few times, eliciting milder behavioural modifications.

The same stimulation was used with two other ants walking on a wall where I had never seen ants before. One of them paused to "sniff" my finger and went on, while the other turned away from the "obstacle" and went on, somewhat hurriedly.

On another occasion, with the idea that it might be of interest to undertake the same observation with ants unmistakably walking on their own, in the absence of a trail or tracks left by nest-mates, I went to my yard after a heavy shower, and there I observed two ants walking on a four-metre wide ceramic mosaic floor, by then almost completely dry. The ants moved along a straight line, acting probably as "explorers" or "scouts", without the aid of a trail or olfactory tracks left by other ants.

The first ant came from a shed and headed to the walls of the house. I placed my clean finger before it. The ant halted at a short distance, "sniffed" my finger, and, moving slightly aside, resumed its march. When it was about 2-3 m away from the shed, I placed my forefinger, which I had used to crush one of its nest-mates, some 2 or 3 cm ahead of it. The ant turned back and returned in a quick undulating march, following a semicircular path until it reached the spot I had touched with my crushed-ant-scented finger; there, it moved again in a circle and resumed its return. When the ant was about one metre from the shed, I placed my finger before it again. Once again, the ant reversed its course, in a quick undulating march, following a semicircular, 30cm-radius path, and then resumed its retreat. The same happened further ahead, when the same alteration was introduced for the third time. Finally, the ant crawled under some crates with empty bottles in the shed. Its repeated changes in direction, invariably followed by a resumption of its previous reversed course, suggested it was a "scout", walking away from the nest until being forced back by the stimuli coming from the first alteration. Figure 25, part A, below, illustrates the course taken by the ant during the observation.

The second ant was walking beside the shed, towards a low wall bordering my neighbour's yard. As I had done before, I placed a clean finger before the ant. It halted, "sniffed" my finger from a very short distance (1.5 cm or less), turned aside and went ahead. I repeated the operation, now with the finger I had used to crush one of its nest-mates. Initially, it turned back in a hasty undulating march, in a 20 cm-radius path, but, differently from the first ant, it ended up by taking the same general direction it had been following. The same alteration was three times repeated, and the response was the same. The ant followed its original course and then crawled into a crevice between the floor and the wall (Cf. Figure 25, part B). Its persistence in following its original course after a brief return led me to assume that it was, from the start, returning to its nest.

The observations were interrupted by another shower.

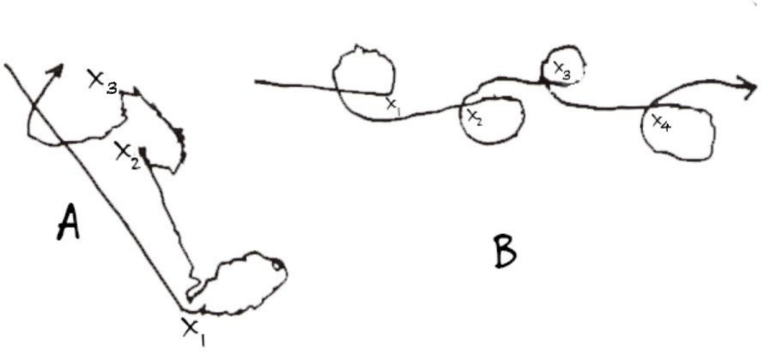


Figure 25: Representation of the course taken by two *P. fulva* “scouts” repeatedly faced (at points X_1, X_2, …) with the finger I had used to crush one of their nest-mates.

Discussion of the results in this topic

The results from these observations show, I believe, two different things. First, that the presence of a trail is not essential for the occurrence of the behaviour modifications of Figure25. flight and escape triggered by stimuli originating from crushed nest-mates. And, second, that the modifications exhibited – a reversal, or otherwise, in the direction taken by the ants when fleeing the alteration – are not independent from what the ants had been doing before (going towards a lure or returning to a nest, for instance). The latter point, by the way, is an important indication that, at a certain point, it will be necessary to describe the behaviour that had been exhibited before an alteration in the environment was carried out, since the nature of this behaviour seems to be related to some characteristics of the behaviour modifications to be presented.

8 AN EXPERIMENT WITH A DOUBLY-BIFURCATING TRAIL. NEW EVIDENCE THAT ALARM PHEROMONES, WHICH HAVE BEEN SHOWN NOT TO BE NECESSARY TO TRIGGER ALARM BEHAVIOUR, IF PRESENT AT ALL IN THE CRUSHED BODIES OF ANTS ON A TRAIL, WOULD NOT BE SUFFICIENT TO DO SO

A question raised at the end of item 7 was why, for the ants on a trail, the crushing of one or more of their nest-mates, or parts of them, would have a much more dramatic effect on their behaviour when carried out straight on the trail rather than in its vicinity. Could it be because, in the former case, the alteration had been effected straight on, and, in the latter case, outside their path? Or could it be because, in the former case, to the effects of the crushing would be added those of altering the olfactory track underlying the trail, while this would not be so in the latter case?

I found in my records an observation, one of the oldest I keep[15], that was carried out in order to answer the first question above and that, on second thoughts, also concerns this last question. Although the observation has not been reported as yet, given the logical sequence I have adopted, it was carried out only two and half months after the start of my research and a few days before I had to interrupt it and, as requested by my Chair at the University, travel to the United States with my wife and daughter – only three and a half years old at the time – to attend post-graduate lectures on Experimental Psychology. I mention this in order that the reader may see how my investigation, initially guided by an intuition that these phenomena were of an emotional and psychological nature, would lead me into paths that have been neglected by mainstream investigation in the area.

The observation took place at the house where I then lived and it happened by chance, when I came across a trail marching on a brick wall, which, by some sort of accident during its formation, had split into two branches that joined again further ahead. The trail was formed in such a way that, either going up the wall towards the lure, or down the wall, back to the nest, a number of ants would join one branch, while their nest-mates joined the other. My strategy for this observation can be found in my records: *"I am going to observe a trail that bifurcates (...) taking down*

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[15] Observation on 2 August 1960, reported in 2nd Notebook of Observations and Experiments, pp. 132-41.

separate notes for each branch; then, I am going to choose a branch and crush ants on an area lying at the same distance from both the other branch and the point where the trail splits. By doing so, I will ascertain whether what is important [for the intensity of their responses] is the disturbance that occurs on "my" trail [from an ant's perspective] or elsewhere... Hypothesis: if this is so, the ants taking the branch to be disturbed will return and be more upset than the ants choosing the other branch". On the occasion, I did not anticipate that the behaviour exhibited by the ants near the area where the branches came together again and those near the alteration point, on any of the branches, would lead to even more important conclusions.

This observation and the strategy adopted are described below as Observation 20.

- *Observation 20 – Behaviour modifications in* P. fulva *when faced with three crushed nest-mates on the branch with lighter traffic in a doubly bifurcating trail situated on a brick wall.*

This observation regards a trail laid out in the following way: initially, on a horizontal plane, starting at the entrance of a nest – a crevice next to the junction of a rough cement floor and a roughcast wall – and extending to the right along this junction for about 30cm; at this point, it went up the wall for about 20cm, and then split into two branches that initially diverged from each other, then took practically parallel courses, at a distance of about 10-12 cm, then converged and, 50 cm above the point where they had separated, came together again and, as a single unified trail, marched on for further 8 cm to a lure – moist white sugar on the edge of a washing tub next to the wall.

Figure 26, below, is an approximate representation of the upper part of the twice-split trail, taken here as an observation space. The traffic was less intense in the left branch, L, than in the right branch, R; as already mentioned, traffic in these branches flowed both up the wall, towards the incentive, I, and down the wall, towards the nest.

I started taking records at 8:00 p.m., sitting at a distance of about 70-80 cm from the trail, under artificial light, coming from my right. There was some wind, irregular both in direction and frequency, but usually blowing past me and towards the wall. This situation, especially in the beginning of the observation, apparently prompted behaviour modifications (especially as regards acceleration and undulation in the march) in a few ants on the trail and caused others to hastily leave the lure. For this reason, I decided to wait for 8-10 minutes until their behaviour became normal again, and then started the observation.

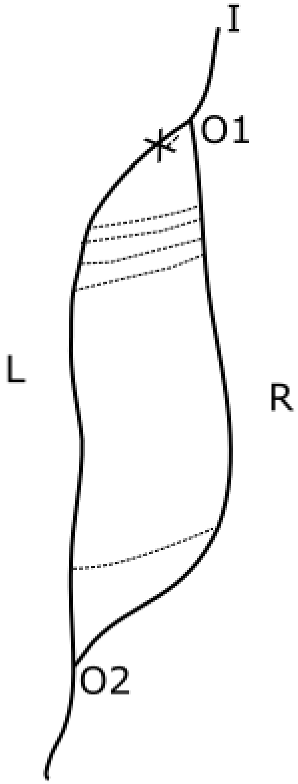


Figure 26: Upper part of a doubly bifurcating trail, considered as an observation space.

Legend: L: left branch, less traffic;
R: right branch, more traffic;
I: incentive (lure);
X: alteration point;
O1 and O2: bifurcation points.
.... Dotted lines: some transposition routes.

CATEGORIES OF BEHAVIOUR	LEFT BRANCH	RIGHT BRANCH
Flow density – 1st half of the phase	0.98	3.1
Flow density – 2nd half of the phase	0.63	3.22
Total flow density	1.62	6.32
Difference of total F.D. in relation to control phase	-1.73	0.22
% of ants showing:		
Progress	4	99
Parallel progress	0	0
Detour	5	0
Return	29	0.5
Partial return	10	0
Disorientation	4	0.5
Undulation	38	5.5
Jolt	4	0.5
Pause	0	0
Fall	1	0
Transposition	59	0.5
None of the modifications above	1	94

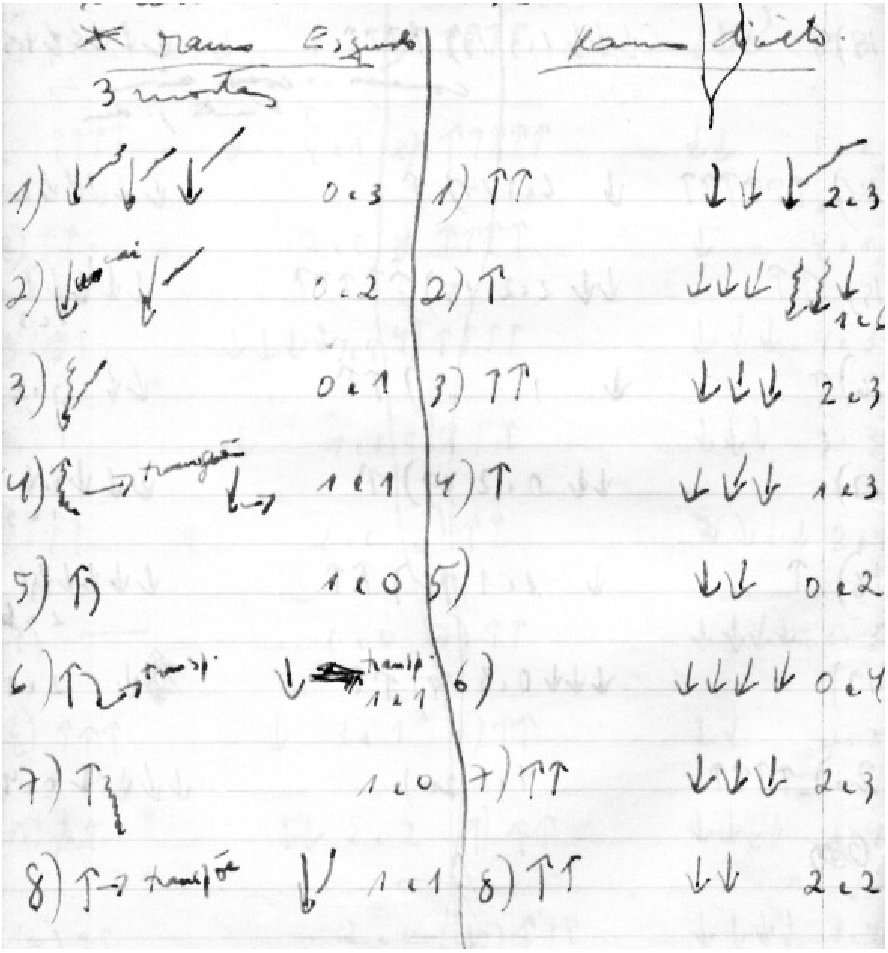
Table 10: Data for the behaviour of *Paratrechina (Nylanderia) fulva* Mayr ants in two branches of a doubly bifurcating trail, after three of their nest-mates were crushed on the left branch at a distance of 4 cm both from the other branch and the point up the wall where the branches came together again.

Fortunately, the ants on this trail walked at a slow, regular pace, and this made precise record-taking much easier. Records were graphic and complemented by comments, and comprised two phases: a 20 1-minute period *control* phase, in which no alteration was introduced; and a 60 1-minute period *experimental phase*, after 3 ants were crushed at a spot (x) on the left branch of the trail at a distance of 4 cm from the other branch and the upper bifurcation point (O1).

The results of this observation, in their quantitative aspect, are collected in Table 10, below, but only for its second phase, since the ants' march was normal during the first phase. The events following the experimental alteration, in their qualitative aspect, are reported below. For a better understanding, four figures are provided: the original records of behaviours exhibited during the first 8 minutes of the control phase, without interventions (Figure 27), the first 8 minutes of the experimental phase (Figure 28), the following 8 minutes, that is, from the 30th to the 37th minute of the experimental phase (Figure 29), and finally the last 8 minutes, from the 53rd to the 60th minute of the experimental phase (Figure 30).

Left branch			Right branch		
1) ↑↑↑↑	↓	4 e 1	1) ↑↑↑↑	↓↓	4 e 2
2) ↑↑↑↑	↓	4 e 1	2) ↑↑↑↑↑	↓↓	5 e 2
3) ↑↑		2 e 0	3) ↑↑↑↑	↓	4 e 1
4) ↑	↓↓↓↓	1 e 4	4) ↑↑↑↑	↓↓↓	4 e 3
5) ↑	↓	1 e 1	5) ↑↑↑	↓↓↓	3 e 3
6) ↑↑		2 e 0	6) ↑↑	↓↓↓↓	2 e 4
7)		0 e 0	7) ↑↑	↓↓↓↓	2 e 4
8) ↑↑↑	↓	3 e 1	8) ↑↑	↓↓	2 e 2

Figure 27: Original record of behaviours exhibited during the first 8 minutes of the control phase in Observation 20, regarding a doubly bifurcating trail.



* Ramo Esquerdo
3 mortas

Ramo direito

1)	↓ ↓ ↓	0 e 3	1) ↑↑	↓↓↓	2 e 3
2)	↓ cai ↓	0 e 2	2) ↑	↓↓↓ ↓↓	1 e 2
3)	↓	0 e 1	3) ↑↑	↓↓↓	2 e 3
4)	→ transporte ↓→	1 e 1	4) ↑	↓↓↓	1 e 3
5)	↑	1 e 0	5)	↓↓	0 e 2
6)	↑→ transp ↓→ transp	1 e 1	6)	↓↓↓↓	0 e 4
7)	↑	1 e 0	7) ↑↑	↓↓↓	2 e 3
8)	↑→ transporte ↓	1 e 1	8) ↑↑	↓↓	2 e 2

Figure 28: Original record of behaviours observed during the first 8 minutes of the experimental phase in Observation 20, regarding a doubly bifurcating trail. Left column: obstructed branch; right column: free branch.

Figure 29: Original record of behaviours observed during the first 8 minutes in the second half of Observation 20. Left column: altered branch; right column, free branch.

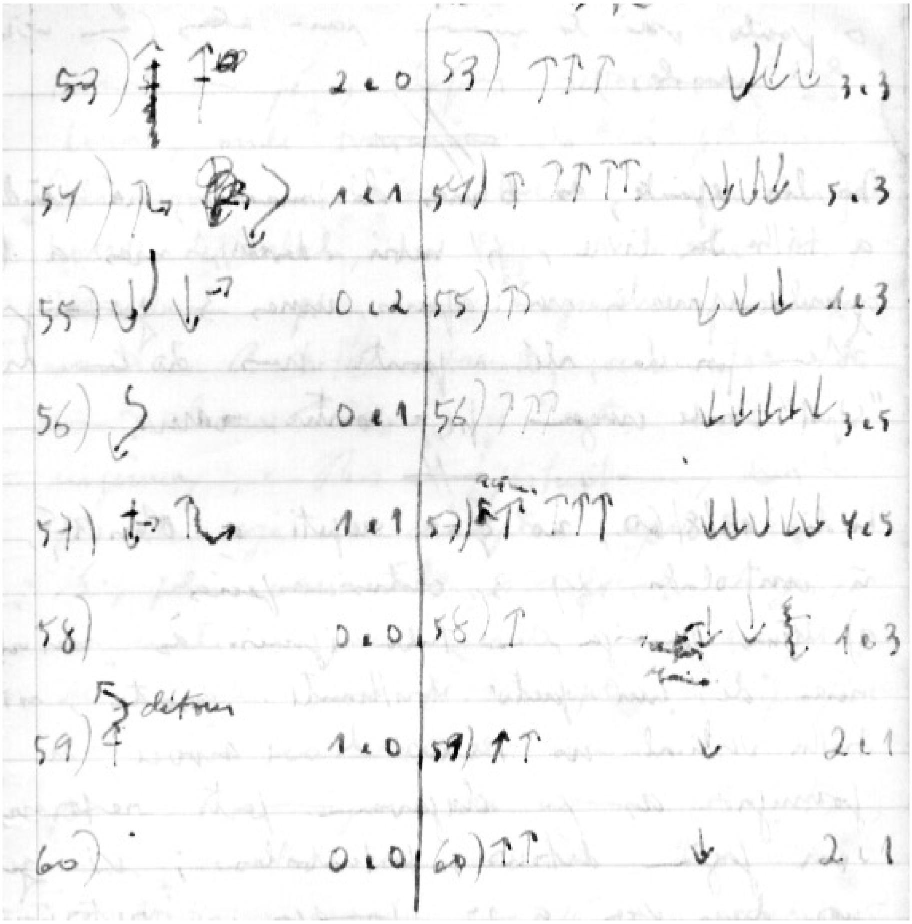


Figure 30: Original records of behaviours observed in the final 8 minutes of the experimental phase (comprising 60 1-minute periods) of *Observation 20.Left column: altered branch; right column: free branch.*

As regards the qualitative aspect, only a few ants on the unaltered right branch, especially those going down towards the nest, exhibited behaviour modifications, especially undulation in the march; most of them, however, both going up towards the lure, and down towards the nest, marched on without any modification. The opposite was the case in the altered, or "obstructed", left branch. In both cases, undulation occurred especially when a stronger gust of wind reached the trail. More important, however, was the occurrence of a new kind of behaviour modification, which I call here "transposition"; this phenomenon, observed in most of the ants going up and down the left branch, comprised the following sequence: first, the ants, at a certain distance from the alteration point, soon after taking the left branch, if they were going down, or 1 to 20 cm ahead, if going up, turned to their right, if going up, or to their left, if going down, suddenly positioned themselves secant to the trail; then, they started walking towards the other branch, with or without undulation in their march. Upon reaching the other branch, they entered the trail and, without any apparent modification, resumed their course, in the same direction they had been following on the other branch. Transposition routes tended to be somewhat slanted: downwards in the case of ants going down to the nest, and upwards in that of ants going up, as approximately illustrated by the dotted lines in Figure 27. Some ants, however, returned for a while before setting out towards the "unobstructed" branch of the trail. Among the ants in this branch, only two – one going down, the other going up – carried out this move, though only after going past the level of the alteration area.

Other facts in this observation are worth mentioning. About 10% of the ants coming down tended, upon reaching the upper bifurcation (O2 in Figure 27), to raise the front part of their bodies (especially their heads) and their antennae, make "sniffing" motions from side to side, and then, invariably decide for the "unobstructed branch" (R); some ants, upon leaving the edge of the tub or reaching the junction of border and wall, tended to return to the vicinity of the lure and remain there for a while, before attempting again to leave the tub.

By the end of the observation, the left branch had almost disappeared. The following day, at 6 a.m., the "free" branch was still there, but the other had apparently disappeared. During a number of minutes only three ants followed it, until reaching a point some 20 cm away from the experimental alteration, and then traversing the space to the other branch.

DISCUSSION OF THE RESULTS IN OBSERVATION 20

A) A comparison of the two phases – control and experimental – in this observation reveals that one of the effects of the experimental alteration employed was to cause, quantitatively and qualitatively, much stronger behaviour modifications in the "obstructed" L branch than in the "free" R branch. It also reveals that, even in the branch where these modifications were more conspicuous, they were much less intense than those caused by a similar alteration in a simple, linear trail. This can be confirmed, for instance, by comparing the percentages of behaviour modifications in column A, Table 1, with those found in the first column of Table 10.

It must also be stressed that the modifications observed in branch R were probably reinforced by other factors, extraneous to the experimental alteration employed. In fact, some of the behaviour modifications observed, especially instances of undulating march, were clearly related to stronger gusts of wind, coming from behind me towards the wall on which the trail was located. It is true that these gusts also occurred during the control phase, but with practically no discernible effects. This, however, does not preclude their occurrence during the experimental phase, when the ants, given the stimuli coming from their crushed nest-mates, were apparently more "excitable".

Is it possible that the differences in behaviour modifications in the ants of these two branches were an indication that crushed nest-mates were not perceived when placed beside the trail, at a distance of 4 cm? Or that, positioned like this, although perceived, they did not provide stimulation enough to cause the other ants to interrupt what they had been doing, which was marching towards the incentive and back to the nest, and other activities to provision the colony? The data collected in this observation seem to indicate this alternative as the likeliest one. A further piece of evidence is the fact that some ants, upon reaching the upper bifurcation point (O2, Figure 26) on their way back from the lure, on being faced with their crushed nest-mates, only 4 cm ahead, did not exhibit the dramatic modifications usually found in similar circumstances in a non-bifurcating trail; they simply moved to the "free" branch. All these facts suggest that what is really decisive in causing dramatic behaviour modifications is not simply whether there is an interfering object on the trail, but, rather, whether this object lies ahead of the ants, and, if so, whether there is an available alternative path.

The same facts seem to suggest some other conclusions. One of them is that, as far as *Paratrechina (Nylanderia) fulva* Mayr, the subject of our observation, is concerned, *it is either untrue that, upon the crushing of ants, volatile substances, claimed to have been found by zoologists and named by them as alarm pheromones, are released in the surrounding area, or, if this is so, it is untrue that their sensorial reception by ants on a trail would automatically trigger the reactions known in myrmecological literature as "alarm behaviour".* I need to say that, based on my inquiry into the behaviour of *P. fulva* ants, it is hard not to wonder whether the substance being discussed is not a fabrication by zoologists in a haste to explain a phenomenon that, if properly considered, could be seen as related to a number of interferences that may be carried out on a trail, a fabrication perhaps inspired by the actual discovery, in many insect species, of a whole class of pheromones with proven biological functions. And also to wonder whether this substance, if real, is not secondary, something evolved in order that ants could profit from a skill they already had: being able to see the difference between things normally found in their environment and things suddenly perceived and related to extraneous interference. The function of such a substance would be to make this perception easier, and this perception would lead to a state of alertness before the new situation. This issue will be considered later on.

B) During the experimental phase of the observation, the flow density of the two branches taken together was reduced to 84% of what it had been during the control phase. This difference, however, is not statistically significant.[16] This might lead us to think that in this observation, in contrast with others, the experimental alteration effected did not cause any appreciable change in the characteristics of the flow. However, a comparison of flow density in each branch during the two phases shows that this is not the case.

In fact, after an experimental alteration was effected, there was a 3.5% increase in the number of ants walking along branch R, and a 50%

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[16] t = 0.803.

decrease in branch L. The first difference is not statistically significant, but the second one is.[17] It must be added that flow density in branch L was increasing during the control phase (flow density of 1.55 in the first half and 1.80 in the second half), and decreasing during the experimental phase, whereas, correspondingly, branch R went from a stable figure (3.05 in each half of the control phase) to progressively higher ones. The difference in distribution between the two parts of the experimental phase and the whole control phase, as assessed by a chi square test, is also statistically significant.[18] All this leads to the assumption that the experimental alteration affected at least one of the branches, causing a decrease in density and a trend towards extinction – confirmed during the observation undertaken nine hours later.

If the "obstructed" branch had been the only one to exhibit a flow decrease (to about half of what it had been during the control phase), one might think that only the ants marching along this branch would be detained before the bifurcations, or by the lure or in the nest, or that they would also proceed at a lower speed – in short, that they would exhibit modifications leading to lower flow density. However, I do not think this was the case. In fact, a comparison of flow density in the two branches during the first ten minutes of the experimental phase shows that both were affected approximately in the same proportion. One might say then that if, finally, only branch R remained stable, this was due to the fact that it was chosen by ants that would normally have taken the other branch, in numbers that were enough to make up for the decrease observed before.

In fact, as pointed out in the description of the results, about 10% of the ants going down from the lure towards the nest wavered at the upper bifurcation point, assumed a posture preparatory to "sniffing", then "sniffed" and took the "free" branch".[19] However, this percentage of redirected courses does not seem enough to make up for the 25% decrease in the number of ants going down branch R during the first ten minutes of the experimental phase. Apparently, then, some ants that had not hesitated at the bifurcation point had also redirected their course to this branch, though not in the same proportion as the ants that did exhibit them. As to the

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[17] $p < 0.01$.

[18] $p < 0.01$.

[19] This seems to confirm the exploratory function previously attributed to this behaviour category.

ants going up towards the lure, there was a decrease in flow density in both branches in the first 10 minutes, and since, in the end, traffic in branch R was the same as in the control phase, it seems clear that a good number of ants that would have gone up branch L had redirected their course at the lower bifurcation point. This fact is less easily accounted for than in the case of the ants going up, since the alteration point was now much further away (about 0.5m) to be perceptible. It seems more easily grasped if one imagines that the option for the "free" branch may have occurred in this case (and, in part, in the case of ants going down) by their encountering more altered nest-mates or more incongruent tracks (due perhaps to some undulation or tremor in the march) than those found in previous journeys, or more "alarm" substances (causing alertness rather than alarm behaviour), etc., in the "obstructed" route (where more behaviour modifications occurred) than in the "free" route. Should this be so, the ants might prefer this branch for its better preserving of previous features. Some of the ants on those stretches before the bifurcation, some of those already at the lure (as shown in the description of the results), perhaps even some still in the nest, might hesitate longer in setting out for the bifurcating area for having encountered altered nest-mates or other signs of a modified route. However it was, if one considers transposition, *which,* it should be noted, *did not influence the figures for flow density,* one would have to admit that, at the same time ants were leaving branch L in response to the experimental alteration, this traffic was being absorbed by branch R. This was undoubtedly a remarkable effect on the flow. One might say that the availability of alternative routes in the environment allowed the ants, on being faced with an experimental alteration that would normally lead to a drastic reduction in numbers, to redirect their progress, without any apparent difference in flow density.

C) Let us now consider the phenomenon of *transposition*. It is apparently a new form of behaviour modification, not found in the observations reported so far. The only phenomena superficially similar to this were those of disorientation and of taking a detour. However, I can show that they are not the same.

One might see transposition merely as an instance of disorientation in which, as in this case, the course of disoriented ants is interrupted by a chance encounter with a new trail crossing their route. However, there is actually a distinction between disorientation and transposition, and this can be shown by the following facts:

1. Disorientation usually involves small numbers. Transposition, however, was exhibited in this case by more than half of the ants moving along the "obstructed" branch.
2. Disorientation is usually slow-paced, and often interrupted by pauses for reorientation. Transpositions, in this case, were a continuous, consistently oriented march.
3. Disorientation usually spreads indifferently to both left and right of the trail and movements may be oriented sideways, backwards and forwards; on the other hand, the vast majority of transposition instances was from the "obstructed" to the "unobstructed" branch, and most of them were progressive, that is, there was actual forward progress in relation to their prior position.[20] The unlikelihood of these phenomena being instances of disorientation is increased if we consider that orientation towards the other branch was carried out by their turning their bodies either to the left, in the case of ants going down to the nest, or to the right, in the case of ants going up to the incentive.

This precision in choosing the right direction to the alternative, unobstructed branch of the trail might lead us to think that the ants, when carrying out a transposition, were doing so as a direct response to stimuli coming from this other route. Some considerations, however, are enough to preclude this possibility. For instance, it has already been pointed out how difficult it is for *P. fulva* workers to find a trail only 3 or 4 cm to their sides. Therefore, it is unlikely that transposition had been triggered by stimuli from the alternative route, at least in the case of ants that had been coming from the nest and taken the "obstructed" branch, since this route would then be about 10 cm away. Also, these ants followed a course parallel to the alternative route and, therefore, their position was not as favourable to perception as if they had been frontally oriented towards the source of stimulation (this is, at least, what is suggested by the fact that ants assume this orientation as a preparatory posture to "sniffing", when they seem about to inspect an object beside them). Anyway, I do not think

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[20] Four ants in Observation 20 exhibited phenomena identical to those previously called "disorientation"; two to the right, two to the left of the obstructed branch; two of them progressively, two regressively.

that the mere reception of stimuli from the trail would be enough to ensure a transposition. It did not occur during the control phase and, in the experimental phase, it would sometimes happen when ants were as far as 20 cm from the experimental alteration, therefore, on a "free" stretch of the left branch, just ahead and certainly more easily perceived than the right one, further ahead. Also, during transposition, *P. fulva* ants had to give up the trail ahead and enter a relatively homogeneous space, not previously traversed, stretching from the wall to the other branch of the trail. Now, as already mentioned, *P. fulva* ants generally seem compulsively inclined to not leave the trail they are following. The perception of the alteration could certainly induce them to do so. However, it must be pointed out that some ants coming from the lure, on arriving at the upper bifurcation point, only 4 cm away from their crushed nest-mates on the left branch, entered it, and, after a little while, left it for the other, unobstructed branch – suggesting that this sort of experimental alteration, when placed laterally to the ants' course, even if at a short distance, was only lightly perceived. Therefore, it is not impossible that the ants going up the left branch were prompted to a transposition to the other branch of the trail by the perception, even from a distance, of an obstruction in the other branch – crushed nest-mates, an alteration to which ants of this species are particularly susceptible, as shown by other evidence. This very fact, however, would reduce even more the possibility of their properly distinguishing the sources of simultaneously perceived stimuli, coming from both the experimental alteration and the olfactory track of the other branch, which was not only distant, but also in a strictly lateral orientation in relation to the course the ants had been following. All these reasons point to the conclusion that the behaviour exhibited by the ants in this observation were not only a response to stimuli effectively perceived, but also to aspects not actually working as sources of stimulation, to an assumption originating in their previous individual experiences of aspects and events in their environment which had impressed them in some way and been incorporated.

It should be pointed out, however, that not all instances of transposition entailed an ability for mnemic assumption. Ants arriving somewhat later to the vicinity of the altered area, especially, might have found traces of the new routes taken by nest-mates preceding them and would certainly have less difficulty in effecting a transposition. There were effectively 11% more instances of transposition in the second half than in the first half of the experimental phase of this observation. This difference, however, proved not to be statistically significant. It should also be mentioned that the starting points of a transposition varied considerably from ant to ant during all the observation, and that it was only after a considerable time that a preference for a certain spot could be detected, a fact already reported in the context of transpositions observed one day after the experimental alteration.

Another point of interest already mentioned, raised by the occurrence of transposition, refers to an apparent compulsiveness of *Paratrechina fulva* ants in sticking to trails. Why did ants prefer not to walk on the space between the two branches of the trail? Is it not an indication that these ants have difficulty to find their bearings in a space devoid of reference points, or that they prefer, whenever possible, to find their way based on physical reference points? Why, then, should they venture into the "empty" space between the two branches? This might be seen as a compromise between two opposing trends: to follow a clearly defined trail, or to avoid, either an alteration perceived as a threat in that specific situation, or a route apparently perceived as diverging from the one usually followed before.

D) The influence of an alternative route on behaviour modifications in *P. fulva* can be seen by comparing the data for the left branch of the trail in Observation 20, Table 10 (with three crushed ants as an experimental alteration), with those in Column A, Table 1, Observation 6, for behaviour modifications resulting from a similar alteration (four crushed ants) on a trail with only one branch. The different number of ants crushed in each observation is irrelevant, since it is not possible to predict how severe behaviour modifications will be based on this number alone. This comparison shows that:

1. As compared to the control phase, traffic was considerably reduced along the "obstructed" path in both observations. On this basis, therefore, and considering flow density alone, the availability, or otherwise,

of an alternative route does not seem to prevent crushed ants from being perceived as an apparent obstacle by their nest-mates.

2. If, however, one considers the percentages of ants exhibiting behaviour modifications indicating the apparent function of the experimental alteration as a disturbing obstacle, it can be noticed that, for all of them, transpositions excepted, the number of ants in Observation 8 was higher – sometimes twice as much – than that in the left branch of Observation 20. In the latter case, the lower percentage of behaviour modifications leading to disorganisation of the march along the trail was certainly due to the fact that most ants effected a transposition to a nearby branch of the trail – a possibility not available in Observation 8. On this basis, it might be said that the availability of an alternative route enabled most of the ants in branch L to adopt a more efficient behaviour, in that it enabled a better continuation of a previous interchange between the colony and its environment, as well as more efficiency in orientation. It certainly cannot be said on this basis that the alteration lost its nature as a behaviour-modifying obstacle, generally present on single-line trails; so much so that the ants kept avoiding it, even more than on a single-line trail; the only difference was that avoidance now was generally more orderly.

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Based on the facts and arguments above, I think I can indicate the following major conclusions regarding the causes for the dramatic behaviour modifications exhibited by *P. fulva* on a trail on coming across some crushed nest-mates in their collective path:

A) Some phenomena, such as the transposition from a branch of the trail to another, showed that the ants in the experiment were responding to major elements in their environment, which, however, had only a mnemic or representational, but not sensory, presence. In a phenomenon such as moving from a branch to the other, the elements forming the other branch were too far to sensorily act on the ants. Therefore, their orienting themselves towards another, sensorily absent trail, was not a response to stimuli. They were rather addressing or going towards aspects of their environment they assumed to exist based on their memories, on a previous perception of their presence and position.

B) Some facts, such as a number of ants hesitating at the bifurcation point before taking the free or "unobstructed" branch, or doing so without hesitating or exhibiting the dramatic behaviour modifications usually observed on a single-line trail, show that their behaviour towards the crushed ants *was not an automatic response to alarm pheromones*, even if such substances, if at all existent, might be conceived to emanate from the crushed ants. Previous observations had already shown that these substances *were not needed to cause alarm behaviour* among the ants; the observation currently discussed demonstrates that, if it is true that ants release such substances on being crushed, they *are not enough to cause it or, at least, not enough without the concurrence of other conditions;* and

C) The results of this observation demonstrate that the presence of crushed ants on a trail does not cause markedly dramatic behaviour modifications in their nest-mates if there is another available route, enabling them to keep the kind of exchange with the environment they had been engaged in prior to coming across the dead ants. This finding supports the idea that these behaviour modifications have an emotional nature and are psychologically determined, since the availability, or otherwise, of alternatives for action, at least in the case of ants going up along the altered branch and towards the lure, was related to their memory of aspects of their environment in previous exchanges, rather than to the actual reception of stimuli in the present. This demonstration allows the express conclusion that the dramatic behaviour modifications shown by *P. fulva* (and, probably, many other ant species) on suddenly coming across one or more crushed nest-mates are not, as claimed by practically all biologically oriented students of the so-called alarm behaviour in ants, an automatic response to alarm pheromones. Should they be so, one might expect, given the long history of the species, that selective pressures during evolution would have caused this response to be prompter and more effective as a means of avoiding and escaping from the altered area than the crooked, tremulous, and often ineffectual march actually shown by the ants. However, the reader will certainly and reasonably ask how could the fact of being an

> emotional rather than an automatic response to pheromones enhance adaptive effectiveness. It certainly does not do so, but *emotion is the price to be paid by a creature for having and using a memory of what its surroundings had been and of the events and effects of acting upon them; this memory is indeed a major evolutionary acquisition and the ultimate reason for the appearance in the animal kingdom of its most recent adaptive resource: a psychology. In fact, the retention of individual past experience is an indispensable condition for certain organisms to pass from being merely responsive to stimuli from the environment to being able to act purposefully, greatly increasing their exchanges with the external world.* If we take into account the selective pressures to which these insects must have been exposed, it is not difficult to explain how emotional behaviour, on being faced with circumstances such as the presence of ants either injured or cornered by an actual threat, on the trail or elsewhere, might have acquired over time a nature of escape and flight, with the development of alarm substances as a possible contribution. This event, however, would always be secondary as compared to the advent of individual memory, the effects of which on behaviour could certainly not be equalled with these substances.

Given the conclusions above, I suppose the reader will understand why, during my stay at the University of Kansas, USA, in 1960 and 1961, immediately after the beginning and interruption of my research, I was indifferent to some articles kindly provided by the renowned Prof. Charles D. Michener, Head of the Entomology Department, after being informed about the subject of my research. Those articles already took for granted the hypothesis that alarm pheromones were the immediate cause of the so-called alarm behaviour in ants; they also recommended that, in order to increase knowledge in this area, the most proper, even inescapable procedure, would be for researchers to undertake a thorough chemical analysis of the substances coming from insect glands to the exterior of their bodies, so as to identify their active principles and concentration thresholds for effectiveness. My interest, as pointed out, was the meaning the crushed ants had for their nest-mates rather than the phenomenon of communication among them, and, after the findings of two months and a half of observations, I thought this analysis made as much sense to my problem as the chemical analysis of saliva to an understanding of human speech. It is up to the reader now. I have against me, I must recognise, the fact that I am probably the only researcher not to follow the path chosen by the advocates of pheromone research as a means for revealing the causes of the so-called alarm behaviour in ants. However, I can justify my position based on the precedent of Copernicus, the first researcher to go against the generally held opinion in his circle and times, and proclaim that the succession of night and day was caused by the movements of the Earth, not the Sun. It is true that I am no Copernicus. But do I have to be in order to diverge from a generally held opinion?

9 BEHAVIOUR MODIFICATIONS IN *P. FULVA* ON FACING DIRECT ALTERATIONS IN THEIR NEST OR FOOD INCENTIVE

Most of the observations reported so far are related to alterations in the ants' immediate environment, near the middle part of their trails. Therefore, for greater comprehensiveness in the inquiry, it would be natural to ask what their behaviour would be like if alterations were carried out at one of the ends most commonly found on a trail, to wit, the nest and the place or object to which, during a certain time span, their exchanges with their environment were directed.

9.1 BEHAVIOUR MODIFICATIONS IN *P. FULVA* FOLLOWING ALTERATIONS CARRIED OUT IN A NATURAL OR ARTIFICIAL NEST

As mentioned in the previous chapter, in São Paulo, the city where I lived, nests of *Paratrechina fulva* could generally be found in holes and crevices in floors and walls, under stones, bricks, tiles, sheets of tinplate, leather, rubber or plastic, reams of newspaper bound together by humidity, wooden planks, etc., in vacant lots, especially those in which organic waste was dumped. A direct alteration in a nest was generally so overwhelming that all activities conducted so far were interrupted. The destruction of a nest, even if only partial, – by removing a stone covering, for instance – would cause ants to leave trails they had joined and hurriedly engage in collecting and sheltering exposed immature individuals inside crevices, holes, underground passages, etc. Queens – often three or more – were generally the first to flee, not infrequently to the grass or vegetable waste near the nest, and were difficult to locate later on. When immature individuals had been collected, some workers remained in the open and set out to repair and reinforce the nest or to look for a new site for the nest. Having found a proper site, they would repeatedly return to the damaged nest to collect and transfer immature individuals, and even some adults still lingering there.

For the observation of behaviour modifications inside nests I also employed some devices as artificial nests. To establish these nests, generally short-lived and unsatisfactory for the survival of the colony, I experimented with a number of materials, and had some success with three kinds of device (Cf. Figure 31, below). Drawing on a suggestion by Lubbock (1898, p. 2 ff), I used a tile surrounded by water inside a ceramic plate and with a thin layer of earth, generally taken from the nest which had been dug up for the capture of part of the colony. This layer was then covered with a transparent glass sheet. Then, when the colony was established, this was topped with a removable cardboard sheet, to keep the nest – between the tile and the glass sheet – in the dark when this was not under observation, since, as reported by Lubbock in the work mentioned above, when inside their nests, ants react with panic when exposed to light. A second kind of artificial nest was a small wooden pencil case, commonly used by schoolchildren. The lid was replaced with a sheet of transparent glass, and then filled with a layer of plaster provided with holes and crevices to be used as chambers and tunnels, and covered with cardboard for darkness. The third sort of artificial nest was made with small ceramic pots interconnected with glass tubes and covered with Petri dishes and cardboard for protection against light. States of disorder like those observed in natural nests were reproduced in these artificial nests with such interventions as the sudden removal of a cardboard sheet and exposure to light, as well as physical impact, provisioning and cleaning operations, etc. Usually, when the commotion was over, their dissatisfaction with the nest was clear, since they would try, sometimes for hours or even days on end, to leave and establish the colony at a proper location – when the first kind of nest was used, they would even swim.

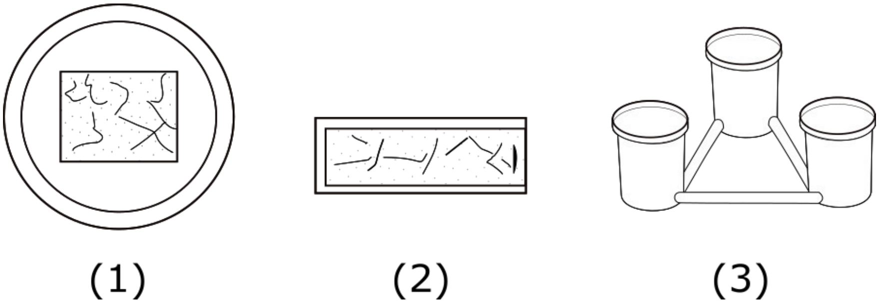

Figure 31: Illustration of some devices used as "artificial nests" to ants dug up in their natural environment.

(1): Nest formed by a tile holding earth, topped with a glass sheet, and placed in a plate with water.
(2): Nest built with a wooden pencil case.
(3): Nest built with ceramic pots connected by glass tubes.

9.2 Behaviour modifications in *P. fulva* on a provisioning trail after alterations in the humidity or dryness and composition of a food incentive

I report under this topic some observations carried out to watch the effects, on a trail of *Paratrechina fulva*, of interventions in the food incentive being used by them, such as modifying its humidity, or dryness, replenishing, or altering its contents or composition.

- *Observation 21: Behaviour of* P. fulva *on a trail towards the same lure, a piece of a sweet, when dry and when wet.*

This observation regards a 65 cm long trail, already established along a brick wall and connecting a nest o *P. fulva* and the dried piece of a sweet placed on a tap. The nest was located in a cavity in the wall, next to a cement floor. Figure 32, below, illustrates the situation.

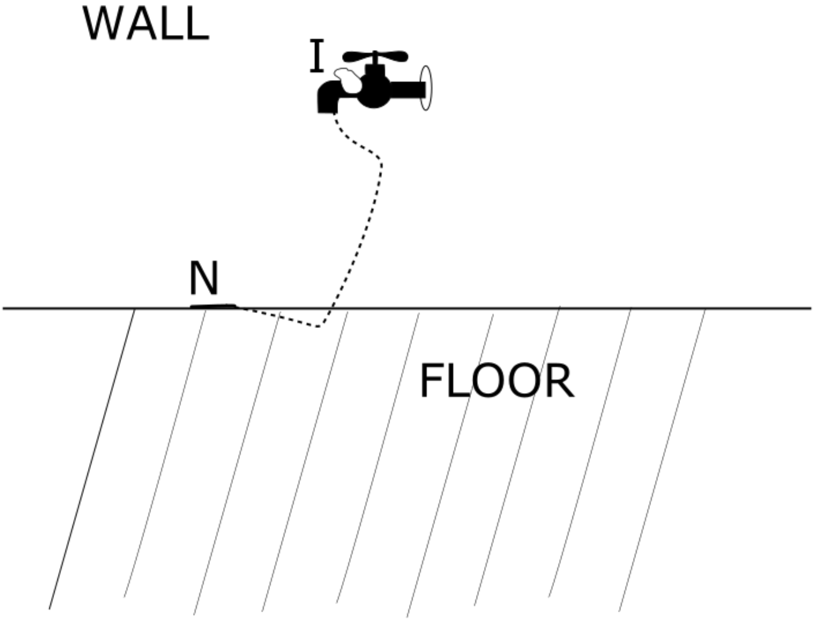

Figure 32: Approximate representation of the situation in Observation 26.

Legend:
Solid line: Junction of a brick wall and a cement floor
Dashed line: trail.
I : Incentive (piece of a dried-up sweet on a tap on the wall).
N: Nest (cavity in a wall, next to the floor) of *P. fulva* ants.

Since the trail was thin and slow-moving, I tried to enliven it by moistening the sweet used as a lure. Three or four minutes later, I noticed traffic was intense along the trail; this was broader than before, since the original path could no longer accommodate the increased number of ants.

Less obviously than the number of ants, speed also seemed to be affected by the now wet lure. In order to test this impression, I decided to use a stopwatch and measure the time that would be spent by individual ants from two different samples: ants going up towards the lure (fi), and ants going down towards the nest (fn), to cover a 23 cm-stretch on the wall, in five different circumstances, A, B, C, D, and E, described below. The reason for separate time-keepings for fi and fn was the possibility of different speeds for the two groups. As to taking the time in a number of different circumstances, the objective was to gather data on the effects of different humidity levels in the food; so, after the lure was moistened and throughout its ongoing use by the colony, different intervals were selected for examination. This was because exposure to air, together with consumption by the colony, would logically lead to an increased dryness of the lure.

Circumstances and measurements were as follows:

A) Time-keeping started 10 minutes after the lure was moistened, to measure the time ants would spend to cover a stretch of the trail, about 23 cm long, on the upper half of it, closer to the lure;

B) Time-keeping started 1 hour and 45 minutes after the lure was moistened, to measure the time they would spend to cover a 23 cm stretch of the trail, now on the lower half of the trail, closer to the nest – unfortunately, for comparison purposes, the stretch selected should have been the same as in A;

C) Time-keeping, as in the previous circumstance; it started 4 hours and 30 minutes after the lure was moistened;

D) Time-keeping, as in the previous circumstance; it started 4 hours and 55 minutes after the lure was moistened, but right after this it was moistened again. The lower stretch of the trail was selected, as in the two previous circumstances; and, finally,

E) Time-keeping, as in the previous circumstance; it started 5 hours and 15 minutes after the lure was first moistened and 10 minutes after this operation was repeated, as mentioned under D. The upper stretch used in A was selected.

Averages and respective standard-deviations for the samples of ants going toward the incentive, *fi*, and toward the nest, *fn*, are provided in Table 11, below, as well as the number of ants for each sample.

Circumstance	**Stretch of trail**	**Number of ants in samples: N of fi N of fn**	**Average time spent to cover the stretch and standard deviations: fi.s fn.s**
A: 10 minutes after moistening the lure	Upper	39 40	15.05 : (2,952) - 12,60 : (5.761)
B: 1 h 45 min after moistening the lure	Lower	11 14	22.91 : (5,213) - 21,07 : (3.807)
C: 4 h 30 min after moistening the lure	“	26 30	22.96 : (5,564) - 18,83 : (3.307)

Circumstance	**Stretch of trail**	**Number of ants in samples: N of fi N of fn**	**Average time spent to cover the stretch and standard deviations: fi.s fn.s**
D: New moistening, 4h 55 min after first moistening the lure	“	29 29	16.72: (3,247) - 15,03 : (1.829)
E: 10 min after second moistening	Upper	17 15	16.71: (2,607) - 12,53 : (3.095)

Table 11: Averages and respective standard deviations for the time spent, by different samples of *P. fulva* on a trail going up towards a lure (a sweet) and down towards their nest, to cover 23 cm stretches in five different circumstances.

A preliminary question in this topic is to determine whether it is reasonable to compare two different circumstances regarding the time spent by ants to cover stretches with the same length, but situated in different parts of it: one upper stretch, nearer the lure, and a lower stretch, nearer the nest. Evidence for an affirmative answer may be found in the result of another observation, not reported in this work. It showed that the speed of ants marching along a horizontal trail did not depend on how far they were from its extremities. This is not direct evidence, but, as long as it is not refuted by opposing evidence, the comparison will be considered valid.

It can be seen from Table 11 that both *fi.s* and *fn.s* spent considerably less time to cover the stretch in A, a few minutes after the lure was moistened, than in -B and C, which started, respectively, 1 hour and 45 minutes, and 4 hours and 30 minutes later. These differences were all statistically significant[21]. It can also be noticed, in Table 2, if we compare the time taken by both fi.s and *fn.s,* in phases C and D, a considerable increase after the lure was moistened again, 4 hours and 55 minutes after it had been done for the first time[22]. This result is even more significant if we consider that moistening the lure also attracted a larger number of ants to the trail, an event tending to reduce their pace. In fact, they tended to be delayed on encountering ants coming from the opposite direction, and the delay was in-

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[21] Following Guilford, 1950, the significance of average differences was measured by Fisher's *t* for small samples, and the significance of individual variability by Snedecor's *F* . For the differences in the time spent by upward moving ants (*fi.*s) to cover a distance of 24 cm in A and B, *t* was 6.313 . For the differences in time in A and C, for both *fi.s* and *fn.s*, *t* was 3.6 and 7.33, respectively. All these differences are, given *t* , statistically significant beyond the confidence level of 0.01.

[22] The *t* for the differences in the time spent by the ants walking towards the lure in C and D was 5.049, and for the ants going toward the nest was 3.8, both significant beyond a confidence level of 0.01.

creased by the greater number of ants. Unfortunately, this event reduces the reliability of the measurements taken for the time spent by the ants to cover a certain distance; therefore, caution is recommended when considering some conclusions that may be drawn from these results by comparing these circumstances. However, one conclusion, springing from the issue motivating this observation, seems beyond any doubt: that moistening the somewhat dried sweet used as a lure made the ants increase their speed both towards the lure and the nest. This certainly pointed to an increased motivation to provisioning, triggered by a suddenly enhanced incentive value of the now moistened sweet, notwithstanding the simultaneous decrease in its amount of sugar: probably because this operation increased the volume and fluidity of the lure and made ingestion faster and presumably more satisfying. I think that the ants already gone back to the nest, on receiving more satisfactory regurgitation, and on being increasingly solicited for food by other ants and larvae, due to their having received better food, might take this as an incentive for resuming foraging activities. The ants with increased motivation would only have to follow the trail outside the nest, if they had already been there before, or follow arriving ants on their return to the food source or, still, follow their tracks – and these events, as pointed out before, seem to be connected with the assumption, based on the memory of past events, of a now renewed food source outside.

An unexpected finding in this observation was that the apparent lack of enthusiasm caused by the drying up of the lure had already reached its highest level in B, for it did not increase in C, almost three hours later, notwithstanding the probable depletion of usable contents in the lure. In the case of ants marching towards the nest, this lack of enthusiasm decreased a little. Could it be because the food needs of larvae and workers remaining in the nest had increased to such a level that foraging ants felt stimulated to work harder in their task and overcome their lack of enthusiasm notwithstanding the increasing dryness of the bait?

A comparison of the time spent by both fi.s and fn.s to cover a given stretch of the trail in C and D, that is, about 4 hours and 30 minutes after the lure was first moistened and right after it was moistened again, confirms the effect ascribed above to the moistening of a used, dry-looking bait. This result, therefore, supports the interpretation, already stated, that moistening the sweet used as a lure significantly increased the incentive value it had before the long time of exposure and gradual drying--up. However, despite the increased speed after the lure was moistened for the second time, it did not reach the levels attained after it had been moistened for the first time. Although the differences in the time spent by fi.s and fn.s in phases A and D to cover a certain distance were not statistically significant, I believe it might express a loss, even if small, in the incentive value of the bait due to a lesser concentration of sugar after it was moistened for the second time. However, it is strange that the gradual increase in the time spent in extracting the sugary solution in the lure as it became increasingly drier did not cause a similar reduction in speed along the trail, as mentioned above.

Comparing the circumstances for variations in time spent by fi.s and fn.s along a certain stretch yields irregular and not easily interpreted results. Individual variation in fi.s was significantly lower in A, after the lure was moistened, than in B and C, 1 hour and 45 minutes, and 4 hours and 30 minutes, respectively, after the intervention. As for the differences after the first and the second moistening, that is, between A, and D or E, they are negligible and indicate that the speed of fi.s was reduced again after the second moistening to practically what it had been after the first moistening. As for the variation among fn.s, speed was significantly higher in A than in B and C, and was significantly reduced after the second moistening if compared to what it had been after the first moistening. The reason for this is not clear for me.

Although the main objective in this observation was a comparison of the results for each of the five circumstances, I think it may be interesting to focus on the differences in time measurement for the two samples of ants, fi and fn. Fn.s, in all phases in which the time for covering a given stretch of the trail was measured, were faster than fi.s. There is not as yet any clear explanation for this. Going up or down the wall, for instance, cannot be important for the explanation because the difference was confirmed with a horizontal trail. It could be said then that other variables apart from going up or down may be important. Is it possible that going towards the food or, as in this observation, towards the nest, could provide a stronger motivation? I think this possibility cannot be rejected in cases in which the ants had already gone a few times along the trail and had memories to anticipate their objectives in both directions and to affect their behaviour. But what is the reason for these different motivations? Could this difference be a matter of the nest having a greater incentive value than the bait? An examination of details in the march of fn.s and fi.s – how sinuous or redirected they are, for instance – could be useful in this case. However, coming from, rather than going toward, the nest or the lure, could be important due to a number of reasons associated with these orientations. Actually, whether an ant is an fn or an fi can be easily determined by an examination of its outward aspect: fi.s are generally leaner and darker than fn.s, which are considerably larger, lighter, with conspicuous yellowish bands in their gasters. Being heavier than fi.s, fn.s are probably less easily avoided during the march, and, conceivably, also slower in turning aside in the case of encounters and collisions. It seems, however, that turning aside is generally up to fi.s. I also notice that instances of hesitancy, or of an apparently full or partial return, are more frequent on leaving the nest than on leaving the lure; this is due perhaps to the transition of environments – from darkness to light during the day, from a place sheltered against odours and changing winds to another lacking these conditions. Therefore, I think many other observations will be necessary before we can interpret differences in speed as related to the direction of the march.

- *Observation 22 – Behaviour modifications in* P. fulva *ants on a trail caused by changing the contents of a food incentive.*

On a certain occasion, about three hours and thirty minutes after having placed some baits (cotton wads dipped in a solution of water and sugar) at a number of spots in an abandoned chicken coop, I found six ants feeding on one of them. The ants came from a nest about 1.30 m away from the lure, given the route they took on their way back, along the junction of a rough cement floor and one of the brick walls of the coop, where no trail could be discerned. I poured some orange juice over the lure. After some hesitancy (turning from side to side), the ants set out for the nest. Since they did not turn and scampered away disorderly, but at their usual pace, I think their behaviour evinced a rejection of a lure with a modified composition rather than a flight or escape response to the new stimulus.

- *Observation 23 – Comparison of behaviours exhibited by* P. fulva *towards two pieces of sugar-cane, one of them smeared with kerosene, placed on two separate stands.*

On another occasion, I placed a parallelepiped wooden block on a cement floor, 40 cm away from a nest of *P. fulva* and 15 cm away from a low wall edging a flower border. Then I placed a prismatic wooden domino 1 cm away from one of its edges, perpendicular to its length, previously smeared with a kerosene-based cleaning product. I placed a peeled piece of sugar-cane, found on other observations to be well accepted as food by the ants, on the domino piece. The floor, the low wall, and the neighbouring border were sometimes frequented by ants from that nest. Figure 33 illustrates the situation.

In the protocols for the observation I see that four minutes after this operation, a *P. fulva* approached the domino holding the piece of sugar-cane, "got excited" (I believe I meant "shook its antennae"), "seemed afraid" (retreated?), climbed the block, walked on it, apparently excited (with brisk movements and upward and sideway "sniffing" motions?), came down, started climbing the domino, "but then avoided it" (came down?), "went again to the block, and apparently tried to reach the bait, 1 cm away. I then reported, apparently after the ant had given up the bait and turned away, that I put the bait in contact with the wooden block, to see whether some ant would reach it after climbing the block, which was free from the cleaning product.

Eleven minutes later, another ant came down the wall to the floor, went towards the block, walked parallel to it, approached it, then "got quite excited, and, oscillating, fast, climbed the block, next to the piece of sugar-cane -- at the junction point – got excited and returned, hesitating a little, and quickly, as if "afraid" (I suppose, in an undulating march, as if in flight).

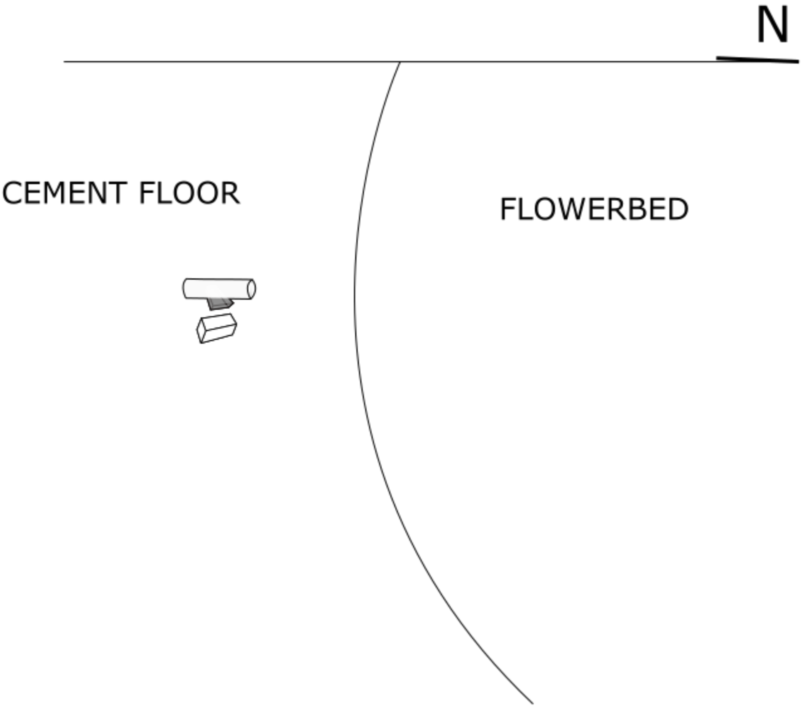

Figure 33: Approximate representation of the situation in the initial phase of Observation 24: a cement floor separated from a flower bed by a low wall, a nest of *P. fulva* ants in a hole in the wall, next to floor, a small parallelepiped wooden block and a piece of peeled sugar-cane on a wooden domino smeared with kerosene.

Two minutes later, another ant came from the wall towards the contraption (had it seen it from a distance?), ran along the floor at a distance of 2 cm from it, and then returned "excitedly" (in an undulating march and shaking antennae?) to the wall and the flower bed. Four minutes later, another ant came along the floor, "climbed the block, approached the bait, got excited, came down and, keeping close to the wall of the house, went towards the flower bed.

A small ant of another, unidentified species reached the domino, but returned without climbing it. Soon afterwards, another ant of the same species "sniffed" the domino and turned back.

I took the piece of sugar-cane and confirmed that it smelled of kerosene. I placed a kerosene-free piece on a tiny plastic disc in the same position as the domino in relation to the parallelepiped wooden block, but now at another spot of the cement floor, and noticed, as recorded in the pages following these remarks, that it was well accepted by the ants of the colony. Therefore, it seems clear that kerosene made food unacceptable and even repulsive for the two ant species under observation.

DISCUSSION AND FINAL CONCLUSIONS ON THE OBSERVATIONS IN THIS ITEM

The observations in this item show that alterations in a food incentive used by *P. fulva* on a trail, such as moistening it, or in its composition and contents, cause behaviour modifications that are very different from those caused by alterations found on their way from the nest to the lure, and vice-versa. Whereas in the latter case behaviour modifications generally take the form of a higher or lower level of disorganisation of the behaviour previously observed in the trail, in the former, behaviour modifications take the form of a greater acceptance, or outright rejection, of the altered food incentive. In other words, alterations along the way between the nest and the food source seem to act as an obstacle or hindrance to their progress, whereas alterations in the incentive, as in the present case, seem to affect the motivation in their provisioning behaviour.

10 BEHAVIOUR MODIFICATIONS IN *P. FULVA* ON A FORAGING TRAIL WHEN TWO OR MORE FOOD INCENTIVES ARE INTRODUCED AS AN EXPERIMENTAL ALTERATION

- *Observation 24 - Behaviour of* P. fulva *following the introduction of a second lure on the trail, similar to the first one, but with three times more sugar, 2 cm before the first lure.*

This observation considered a 2.80 m long trail, connecting the entrance of a nest in a doorpost and a cotton wad dipped in a solution of water and sugar. Most of the trail ran along the junction of a tiled floor and two walls. I placed a further lure, more humid and with three times more sugar, 2 cm before the first one. Figure 34, below, illustrates the situation.

After adding the second lure, I noticed that the most common reaction among ants coming from the nest was to pause, raise the front part of their bodies, and climb it. Apparently, they responded to the fact that the lure was new and nearer the nest, since these motions preceding their climb were not observed in the case of the first lure, which was climbed without any interruption in their march. One of the ants turned aside from the new wad, faced it, then the first one, sniffed both of them, walked back, and went to the new lure. Some would go straight to the new lure, while a few took a detour on the floor or crawled under the new lure and went towards the first one. As for the ants returning from the first lure, most of them would stretch their bodies, raise the front part of their bodies, make "sniffing" motions, and crawl under or avoid it. Many of the ants coming from the nest would stop 5 cm away from the new lure and then go towards the first one. After some time, the ants on the second lure outnumbered those on the first one. I think this observation showed that ants coming from the nest directed their behaviour to the first lure even before reaching it, and this was evinced by some wavering before the new lure before proceeding, as well as in their inspection of it before accepting or, as in many cases, rejecting it for the first lure. The final preference for the new lure seems to indicate, as it will be seen, that a further food source, similar to the first one, but closer to the nest, though giving rise to conflicting motivations, may be preferred if containing a higher concentration of sugar.

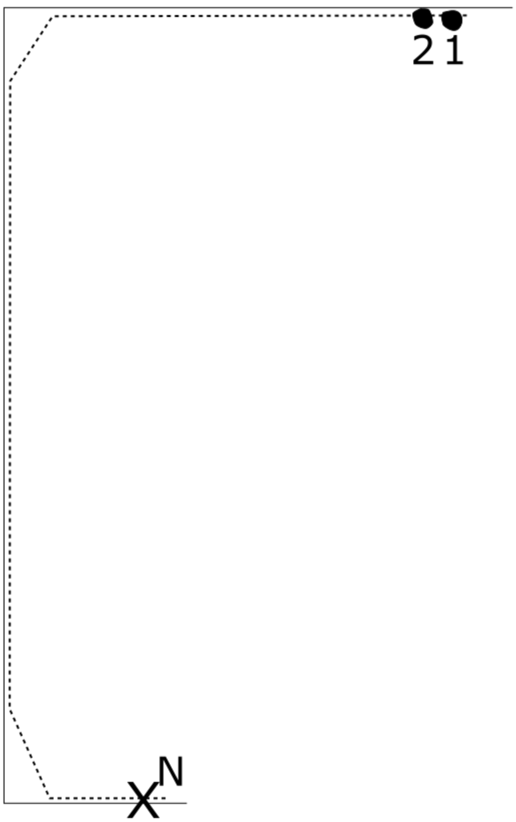

Figure 34: Representation of an ant trail in a kitchen, running along the junction of a tiled floor and two brick walls.

Legend:
Dashed line: trail.
1: Original lure, kept during all the observation.
2: New lure, 2 cm away from the first one.
X: Crevice in a doorpost, entrance to a nest N.

- *Observation 25 - Behaviour of* P. fulva *ants on a trail during 3 phases, when, in each of them, a second lure was placed on different parts of the trail.*

I used in the three phases of this observation a trail formed inside a small bathroom. To form the trail I placed a cotton wad dipped in water and sugar next to the wall and then waited for the ants to find it. Five minutes later, I noticed that a trail had already formed, extending from the lure in the bathroom, the adjacent hallway, to a hole in the ceramic floor in the yard. The trail reached the hallway by going under the bathroom door and round a doorpost, and then went the whole length of a wall keeping a distance of about 3 mm from it. The three phases of the observation started when the trail had gone back to its normal state, after the removal of a cotton wad dipped in petrol, used to observe their responses. These phases are reported below. Figure 35, below, illustrates the situation.

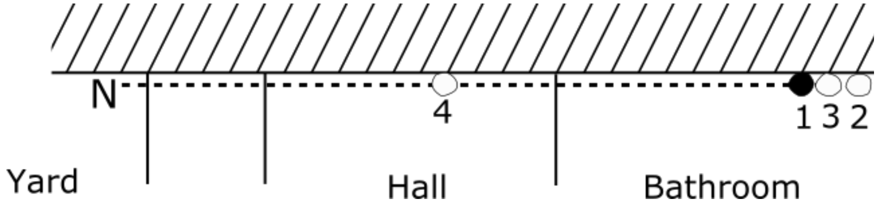

Figure 35: Representation of a trail next to a wall and two food incentives (cotton wads dipped in a solution of water and sugar), the second one being placed at different spots of the trail on three different occasions.

Legend:
Dotted line: trail on the floor, next to the wall.
N: entrance to the nest in the yard floor.
1: First food incentive, kept in the same place throughout the observation.
2, 3, and 4: positions of a second lure, similar to the first one, placed on the trail in phases A, B, and C of the observation.

- PHASE A – Behaviour of the ants after a second lure, similar to the first one, but more humid and with a higher concentration of sugar, was placed 1 cm away from the first one.

Only a few ants found the second lure, and this was when they were turning to leave the original lure; while moving round or away from it, they happened to face the other lure and would “sniff” it. Two ants climbed and accepted the new lure, even though they had fed on the first one.

- PHASE B – Behaviour of the ants soon after the lure introduced in Phase A was moved until it touched the first lure.

While this was done, I lightly touched two ants with the lure; they turned abruptly to the direction of the touch “as if”, as I wrote then, "to see what it was", and proceed to feed on it, with no signs of being upset. Gradually, the second lure attracted more ants, which would climb it naturally and without hesitation.

- PHASE C – Behaviour of the ants toward the same lure when it was moved to the middle portion of the trail.

The ants marching from the nest to incentive 1 would pause briefly when 2 or 3 cm away from the second lure, and then go towards it with no hesitation. On the other hand, the ants returning to the nest would pause longer before the second lure, and then go round or under it, or climb it for a brief taste, before resuming their march to the nest. Some, however, on reaching the second lure, raised their front legs and heads, "sniffed" it and went round it before going on. A few would undertake a partial return of 5 to 10 cm before proceeding to the nest. After a while, I noticed that no ant coming from the nest reached the first lure, and remained by the second lure instead. Even when this was removed, they would not go ahead until the moistness it left behind could be ingested. This observation seems to indicate, given the hesitancy exhibited by the ants coming from the nest upon reaching the second lure, especially when it was far from the first one, that they were bent on reaching the first lure before accepting the second one. It also seems to indicate that the ants were able to identify, from as far as 2 or 3 cm, the new object on the trail as being a food with the same nature of the one used before that they preferred the latter for having a higher concentration and being nearer the nest.

- *Observation 26 – Behaviour of* P. fulva *on a trail toward a second lure, similar to the first one, but placed, first (Phase A), 25 cm, and, then (Phase B), 1.78 cm before the first lure.*

A 2.20 m long trail, formed two hours before and used in a previous experiment, to be reported later on, was considered in this observation. It ran close to a brick wall, on a cement floor and a ceramic floor. The trail connected two holes in the cement floor, 32 cm apart, entrances to the same nest, and a lure described below. The observation comprised two phases, A and B, with the introduction of another lure on the trail in each of them. This second lure had been stored for about two hours before the observation; it was the other half of the piece of cotton used as a first lure, dipped in water and sugar.

- PHASE A – Observation .of the behaviour of ants on a trail towards a second lure, of the same nature and with the same concentration of the original one. This second lure, however, was intact and more humid, and had a stronger yellowish hue than the first. It was placed 2 h and 05 min after the establishment of the trail towards the original lure, 25 cm closer to the nest.

When this phase started, the trail, from which two cotton wads, out of three, dipped in kerosene and used in a previous experiment (to be described later as Observation 35) had been removed, had not yet recovered its normal aspect in some areas. To start the observation, I used a clean cotton wad to remove the lure I had preserved. Figure 36 represents the situation.

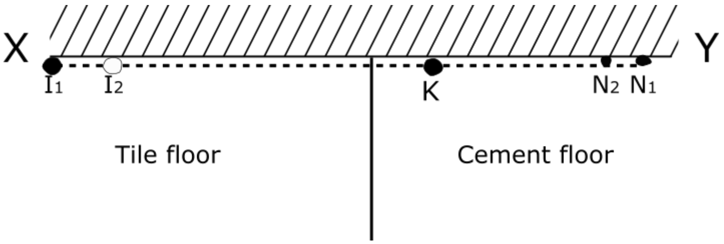

Figure 36: Schematic representation of the trail and other elements in Phase A, Observation 26.

Legend:
XY: junction of a brick wall and a cement floor adjacent to a ceramic floor.
N_1 and N_2: entrances to a nest.
(I_1): incentive (first food incentive, visited by the ants about 2 hours and five minutes before).
K: cotton wad dipped in kerosene.
(I_2): Second lure, introduced 2 hours and 5 minutes after the trail was formed with the first lure.
Dashed line: Trail

A number of ants marching towards the first lure, on reaching the second one, climbed it without hesitation. Other ants, in smaller numbers, after touching the new lure, went on towards the first one. After some time, many ants coming from the nest gathered on the new lure. The ants coming from the other end towards the nest, however, after bustling about for a while, climbed the new lure and some of them started to feed on it. Others climbed the new lure, stayed for a while on it, returned to the first lure, touched it with their antennae, and then returned to the new one. A few minutes later, there were only two or three ants on the original lure, and two or three marching from or towards it, whereas the second lure was crowded. Fifteen minutes after the start of the observation, some fi.s (ants coming from the nest towards the incentive) were going "empty-bellied" towards the old bait, while others, after gorging themselves on the new one, went to the old bait, inspected it, and went 10 or 15 cm beyond it, before going back to nest.

I believe the results in this phase support the conclusions suggested for the previous observation, both as regards the acceptance by fi.s of a new food source, similar in nature to the original lure, but with a higher incentive value, and the existence in these ants, which may be inferred through their behaviour, of a sort of regulation or postulation as to the nature of the bait to be found in each trip and to its distance. In fact, this regulation seemed to be manifested by fi.s as they marched on towards the original lure, by fn.s as they hesitated while going past the new lure suddenly found on their way to the nest, and by many ants that returned to the original lure and even went past it, as if suddenly unsure about the direction to take when returning to the nest.

- PHASE B – A new observation of the behaviour of ants on a trail towards a second lure, of the same nature of the first one and with the same concentration, except in that, being untouched, it was more humid and had a stronger yellowish hue. This lure was placed, after Phase A, 10 cm away from one of the two holes leading to the nest – the one closest to the first lure.

After Phase A, I took the second lure and placed it on the trail, 10 cm away from the entrance to the nest closest to the first lure. Figure 37, below, illustrates the situation.

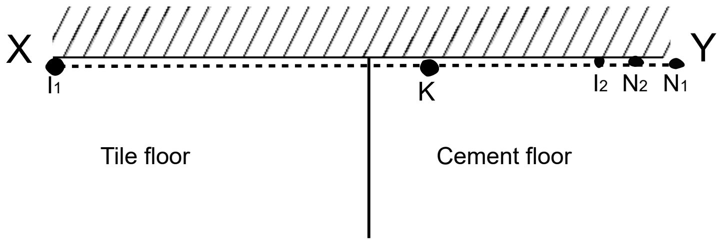

Figure 37: Schematic representation of the trail and elements of the situation in Phase B, Observation 29.

Legend:
XY: junction of floor (part cement, part ceramic) and brick wall.
N_1 and N_2: holes connecting the nest to the outside.
I_1: incentive (original lure, visited by the ants for about 2 h and 30 min).
K: cotton wad dipped in kerosene.
(I_2): Second lure, moved from its position in Phase A to a spot 10cm away from hole N_2 and 1.78 m from the first lure.
Dashed line: Trail

As expected, the relocation of the new lure caused the ants on it to run away. The ants coming from the nest, on getting near the relocated lure ran around it on the floor and the wall in an undulating march; many of them took a quick detour on the wall, while others returned to the nest. In 4 minutes, the first lure started to attract more ants than the new one. Most of the ants going to the nest went past the new wad in a quick undulating march; some climbed it as if to inspect it, but generally did not remain there.

After a while, many of the ants coming from the nest were squeezing their way through the 2 mm space between the wall and the new lure; some would return to a distance of 0.5 cm, "sniff" it, and then go, sometimes in an undulating march, to the end of the trail. On the other hand, fn.s, returning with dilated gasters from the first lure, at the end of the trail, would pause to "sniff" the second lure or hesitatingly take the narrow way between it and the wall; some would stop to "taste" it before proceeding. As to fi.s (ants coming from the nest), some would remain by the new lure and, after a while, their stationary position seemed to induce more and more ants to accept it. Ten minutes after the start of the phase, hardly any ant would pass between the space between the wall and the lure, and this was done with increasing hesitation, that is, with repeated pauses, slowly, and upward "sniffing" motions. Coming across a full ant seemed to encourage the others to go ahead.

The results of this and the preceding phase seem to indicate that the introduction of a new lure on a trail was apparently more disturbing to their behaviour the shorter the distance they had previously covered towards their destination on the trail. Given these results, one might say their adjustment to the previous situation prepares them both for finding the original bait and for the distance to be covered to the place where it should be. If so, the situation prevailing on preceding occasions was also present, in a certain way, in their current, altered situation.

- *Observation 27– Behaviour of* P. fulva *ants on a trail, established for a few days in the same location, towards a second lure, of the same nature as the first, placed on the trail.*

This observation dealt with a trail of *P. fulva* established for nine days and connecting a nest in a crevice in a brick wall, behind a rainwater pipe, to a lure (a cotton wad dipped in a solution of water and sugar and renewed a few times), attached with a pin to a crevice in the junction of an adjacent brick wall and one of the rounded ceramic pieces topping it. To this, a second lure was added, of the same nature as the first: half a cotton wad dipped in water and sugar; the other half was stored to be used two hours later, when the trail should be stable again. This second half was attached to the wall with a nail, right on the trail, between the two first lures and the nest, 68 cm above the floor. The objective of this observation was to see how the behaviour of the ants on the trail would be affected by the intervening lure, which was identical to the one used to reinforce the dried-up, original lure, except for the fact that it had not been used before. Figure 38, below, illustrates the situation.

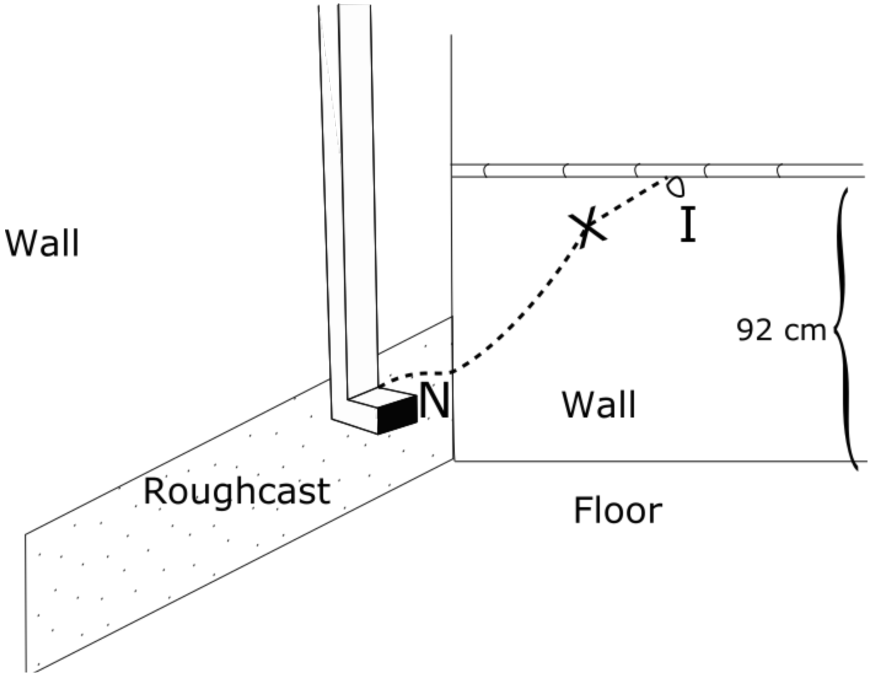

Figure 38: Representation of the situation in Observation 27.

Legend:
I: First incentives.
N: Nest in a hole in a brick wall, under a rainwater pipe.
-- - -: trail.
X: Alteration point (a new bait attached to the wall with a nail).

Fixing the nail in the wall at first caused a great turmoil among the ants in the vicinity. The first ants to have their behaviour recorded were *fn.s*, and all of them oscillated from side to side and went past the intervening bait by taking a detour at distances ranging from 2mm to 1cm. Among *fi.s*, most of them would stop and climb the bait and either stay there or move on after a while towards the original bait at the end of the trail. Some of them avoided it and proceeded to the terminal bait. *Fn.s* coming from the original baits avoided the new one and headed toward the nest; however, as mentioned above, I could see that, among the first ants reaching the area, three of them climbed the bait and walked on it for a while before proceeding to the nest. Fifteen minutes after the alteration, the traffic of ants seemed considerably reduced. One or other *fn* would stop by the bait and seemed to feed on it. I noticed that some of the *fi.s* returned from the interfering bait apparently without feeding to the nest, since they seemed as thin as before. As to the other *fi.s*, they accepted the new bait, but, even so, would often proceed to the original one. Its having been there for a few days may be involved in this behaviour, notwithstanding the number of individual differences. I think that these results reinforce the proposed interpretation of the results in the previous observation; the situation under way suffered the influence of an adjustment to or regulation of the aspects of the situation towards which the ants had behaved in previous trips.

FINAL REMARK ON THE OBSERVATIONS IN THIS ITEM:

The observations reported above seem particularly useful in suggesting or pointing to the following about these ants: 1) dramatic behaviour modifications practically do not occur when the object used to alter a foraging trail is a food item, especially if it is of the same sort as the one used to originate the trail and has a higher incentive value; 2) the ants have a mnemonic record, even if only approximate, of the distance and nature of a lure repeatedly visited; 3) they head, from each end of the trail towards the other, apparently anticipated as present at the furthest point of the trail, instead of engaging in a march elicited by stimuli on the way and interrupted at the end by a prepotent elicitor under the form of a food item or the entrance to the nest.

11 BEHAVIOUR MODIFICATIONS IN *P. FULVA* ON A TRAIL WHEN A LURE IS REPLACED WITH ANOTHER OF THE SAME NATURE OR OF A DIFFERENT NATURE

- *Observation 28 – Behaviour modifications in* P. fulva *ants on a foraging trail after a first lure (a cotton wad dipped in a solution of water and sugar) was replaced with a similar one, but with twice as much sugar.*

This observation is about a trail between a nest in the basis of a doorpost and a cotton wad dipped in a solution of approximately 70 g of water and 5 g of sugar. The lure was attached with a pin inserted in a narrow crevice between the doorpost and a tiled wall, 1.20 m above the floor. The observation started when the trail was entirely formed and stable. In aspect, it was a column rather than a single line, with ants marching on the crevice between the wall and the doorpost, and beside it, on the wall. Most of the ants found on the upper third of the trail were going toward the nest *(fn.s)*; on the lower third, the branch on the wall was almost entirely taken by ants going toward the food incentive (fi.s). Inside the crevice, both *fi.s* and *fn.s* were to be seen. Figure 39, below, illustrates the situation.

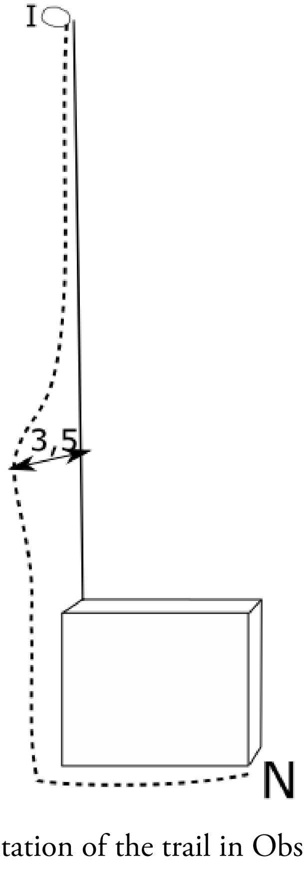

Figure 39: Representation of the trail in Observation 28.

Legend:
I: incentive.
N: nest.
Solid line: crevice between a tiled wall and a wooden doorpost.
Parallelogram: protruding base of a doorpost.
Dashed lines: routes followed by the ants.

About 1h 30 minutes after the establishment of the trail, and only 2 minutes after its aspect had become stable, I counted for 25 minutes, one by one, the number of ants going up towards the incentive. Then, using a stopwatch, and alternating *fi.s* and *fn.s*, I measured the time they spent to cover a distance of 15 cm, the length of the last but one tile before the lure. Some 20 minutes later, I transferred the lure to a notebook on the floor in order to see how the ants would orient themselves on leaving it, a kind of observation that will be considered in a later section of this inquiry.

On the site previously occupied by the lure, I noticed some ants "sniffing" at the air, or entering the crevice between the wall and the doorpost, where they apparently tried to hide for a while. I also observed ants going upwards along the crevice, with pauses for reorientation at every 1, 2, or 3 cm. I think that both the "sniffing" motions and the oscillating march past the site where the lure had been, but towards the crevice, might be an expression of their being in search of a missing lure. As for their hiding inside the crevice, most of the ants involved were probably those who had been able to leave the lure as it was removed, as well as ants in the vicinity; and this was probably an instance of defensive behaviour, of searching for shelter.

Eight minutes after the original lure was removed, I replaced it with a similar one, but now dipped in a solution with twice the amount of sugar, and attached it in the same way and using the same pin employed with the first bait. I noticed that *fi.s*, both the newly arrived and those returning from their apparent search for the lure further up, would climb the wad unwaveringly. On the ants initially deserting the site where the second lure had been placed, the density of the trail decreased for a while. So, I waited for 10 minutes, and then, during 24 1-minute periods, counted the number of *fi.s* going towards the lure. The trail had by then recovered its usual, crowed aspect. After this, the following remarks were included in my records: "It seems that the effect of a more concentrated bait is to be seen at first among a high, tremendous, number of ants, but this frenzy lasts only for a few excursions – if repeated – or a few minutes". I added that the massive return of ants when the first bait was removed, together with a number of ants on it, and then replaced with a second bait, caused a number of ants to give up returning to the trail.

Five minutes after this counting, I used a stopwatch to measure, alternating fi.s and fn.s, how long ants would take to cover a distance of 15 cm (the length of a tile). As I had done in a previous observation, and being relevant in the present case, I wrote in my protocols: "I see that, in large groups, speed tends to decrease, due to shocks and hesitancy (turning first to one side, then to another). And that along free stretches of about 10 cm, ants generally proceed at an evener and faster pace. Therefore, measurements for speed include many variables and are not good". Anyway, results from the counting and speed measurement are provided in Table 12, below.

Data categories	**Control phase**	**Experimental phase**	**Statistical significance indexes (for differences between phases)**
Fi. average flow in 25 minutes	16.56	19.54	T = 2.048*
Standard deviation for fi. Flow	3.868	5.937	F = 2.36*
Seconds spent by fi.s to cover a 15 cm stretch of the trail	8.93	8.04	T = 1.96
Standard deviation for time spent by fi.s to cover the stretch	1.12	2.027	F = 3.275**
Seconds spent by fn.s to cover a 15 cm stretch of the trail	9.33	8.48	T = 1.400
Standard deviation for time spent by fn.s to cover the stretch	2.388	1.97	F = 1.469

Table 12: Data for average flow density, average speed and respective standard-deviations presented by ants, first (during control phase), on a trail established between a nest in the ground and a lure attached to a gap between a doorpost and a tiled wall, and then (experimental phase), on the same trail, as another lure was introduced, of the same nature, but with twice as much sugar.

* Significant at a confidence level of 0.05. ** Significant at a confidence level of 0.01.

The results in the table above show that replacing a first lure with a similar one, but with twice as much sugar, after causing a number of returns to the nest and a momentary thinning of the trail, led, a few minutes later, to an increased, though more variable from minute to minute, number of ants. They also show that the time spent covering a given stretch of the trail became shorter after the replacement, both among the ants going towards the lure and those going towards the nest. The difference, however, was not significant. Relatively increased difficulties to their marching, due to the greater number of ants on the trail, contributed to this situation. Variation in the time spent by fi.s to cover this stretch was also significantly increased after the replacement. Could it be because, among the ants marching towards the lure, there was an increased number of newly-arrived ants? As a whole, the results from this observation support the assumption that an increase in the incentive value of a lure provides increased motivation for ants to go foraging for the colony.

Differently from Observation 26, *fn.s* were slightly slower than *fi.s*, both in the control and experimental phases of this observation. This difference, however, turned out to be not statistically significant.

12 BEHAVIOUR MODIFICATIONS IN *P. FULVA* ON A TRAIL ON BEING REMOVED FROM A GIVEN LURE TO ANOTHER, OF THE SAME NATURE OR OTHERWISE, BUT OUTSIDE THE TRAIL

- *Observation 29 – Behaviour of* P. fulva *on (A) being removed from a food source to another, of a different nature, or (B) of the same nature as the original one.*

In the first phase, A, of this observation, I tried to induce the formation of a trail towards a cotton wad dipped in a solution of water and sugar placed on the tiled wall. To increase the chances of success, I removed a cockroach that had attracted a number of ants. The wad was 2 cm long, 1 cm wide, and 0.5 cm thick. It was attached to the wall 80 cm above the floor and 29 cm away from the doorpost. Figure 40, illustrates the new situation.

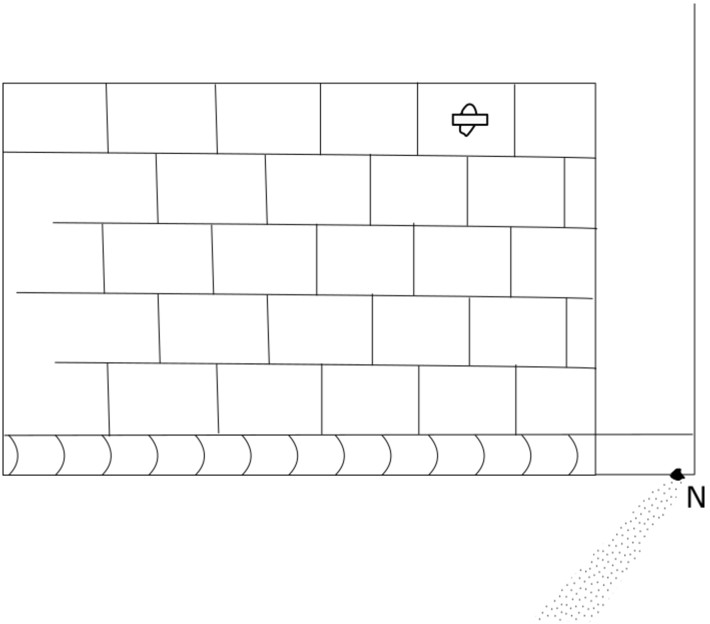

Figure 40: Approximate representation of the situation in Phase A, Observation 30.

Legend:
Rectangles: tiles on a wall.
))))))): rounded ceramic pieces.
Dotted lines: trail remaining from the previous situation.
N: nest.
Trapezoidal figure: strip of adhesive tape holding a bait against the tiled wall.

I caught three ants – one by one – on a strip of paper to take them to the lure attached to the tiled wall. My strategy was to hold two strips of paper and slide them along the floor, gradually confining the ant between them, until it stepped onto one of them while fleeing the other; then immediately raise the strip and put it next to the bait on the wall. In this way, I caught three *P. fulva* ants, 1 cm away from where the cockroach had been. Moving the strip of paper in such a way as to keep the ants on its upper surface, I took the ants, one by one, near the lure, so that they could easily access it. One of them even stepped on the lure, but left it in a hurry down the wall, exhibiting jolts, and then fell off the wall. Another one, as soon as I had corrected the position of the sheet, hurried away from the lure and along the wall and then fell off. The third one fell from the paper to the ground when already near the bait.

I caught a fourth ant that had slowly approached a strip of paper left on the ground and, after some “sniffing”, had climbed it. As soon as I raised the paper to take it to the lure, however, the ant started running down the wall and, on going over the wad, fell to the ground. A fifth ant also climbed one strip, but, then I raised the paper and, while rotating it to keep the ant on its upper surface, it started running in a sinuous course and fell from a height of 70 cm.

In the second phase, B, my intention was to take the cockroach by one of its antennae and place it against the door. However, the antenna broke, and the ants on it started running around the floor and returned to their nest. I took the cockroach with a piece of paper and attached it to the wall with a length of adhesive tape, positioned perpendicularly and next to the piece of adhesive tape holding the cotton wad. Figure 41 illustrates the new situation.

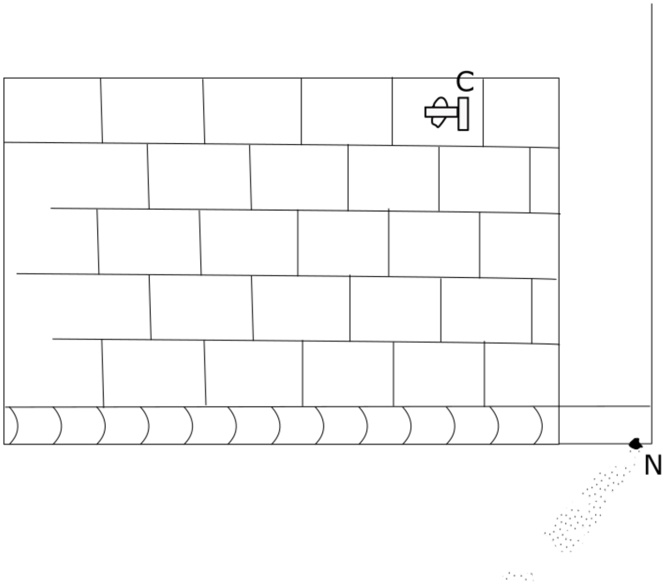

Figure 41: Approximate representation of the situation in phase C, Observation 30.

Legend:
N: nest opening.
Trapezoid figure: : cotton wad dipped in water and sugar, attached with adhesive tape.
Dotted line: a lingering trail, heading towards the secretions of a cockroach, now removed.
C: a cockroach, removed from its original position and attached to the wall with adhesive tape.
Rectangles: tiles on the wall.
)))))): rounded, concave ceramic pieces.

Seven ants came "sniffing" from the nest to the place where the cockroach had been, and started sucking a sort of mucus that had been left behind. Some of them would suddenly go meandering, with brief hesitating motions and frequent reorientation, within a range of 15 to 30 cm round the spot, as if searching for the removed cockroach. I captured one of these ants with a strip of paper. It ran from the paper to the wall and, on approaching the cockroach, suddenly halted near the first outstanding feature it came across, the remaining antenna, took hold of it with its mandibles, and pulled it once; then it went down, following a course with 20 cm-radius meanders, and then went up the wall in a similar meandering course; again, it pulled the remaining antenna, for a longer time now. Then it crawled under the cockroach and started pulling the hairs off one of its legs.

The results from the two phases of this observation seem to indicate that ants removed from a trail on the floor of a small bathroom to a bait attached to a tiled wall bordering the floor rejected the bait when its nature was different from the one they had been using, or accepted it when it was of the same nature. Based on these results, one might say that these ants, when on their trail, were not addressing a mere food item with their behaviour, but a specific, habitual food item, and that this fact conditioned both the acceptance and rejection, even the avoidance of a new bait to which they were transported, depending on its being different from or the same as the original one.

FINAL NOTES ON THE OBSERVATIONS IN THE PRESENT TOPIC

The observations related above seem particularly useful in that they suggest or point to the following conclusions about the ants being studied: 1) Dramatic behaviour modifications practically do not occur when the object employed to alter a foraging trail is a food incentive, especially when it is of the same nature as the one originally used to form the trail, or when it is nearer the nest; 2) Ants on a foraging trail rely on a mnemic record, even if only approximate, as to the location and nature of a food item repeatedly visited; and 3) On a foraging trail already visited, ants head, from the start, and from whatever end of the trail where they happen to be, towards the opposite end of the trail, assumed as a goal. In other words, while on their way from the nest towards the incentive, or vice-versa, their behaviour consists in heading towards a required goal rather than in automatically responding to stimuli on the way.

13 BEHAVIOUR MODIFICATIONS CAUSED BY THE ALTERATION OF AN ENVIRONMENT IN WHICH A PREVIOUS BEHAVIOUR HAD BEEN TAKING PLACE, BUT WITHOUT THE INTRODUCTION OF ANY EXTRANEOUS ELEMENT

A point shared by all the observations reported so far, undertaken in order to investigate the causes of behaviour modifications exhibited by the ants when faced with a sudden alteration of their behaviour situation, is that all of them involved the sudden introduction of elements extraneous to the situation. Therefore, the question was raised of how they would behave with the alteration of only one element in the situation, without the addition of any source of stimulation it had not already contained. Once, during my expeditions to vacant lots in search of ants, I happened to come across such a situation, which was the object of the observation reported below.[23]

- *Observation 30 – Modifications in the excavation behaviour for an initial nest of a Camponotus sp. queen following a sudden alteration in the pattern of stimulation of light and shade projected by a bush on the queen and the soil.*

Once I found in a vacant lot a *Camponotus* queen – probably a *Camponotus melanoticus* – engaged in the initial efforts of colony foundation. As it is usually the case among founding queens of many species, it had probably just alighted from its nuptial flight.

The fertile female had already shed her wings and was frantically excavating the soil with legs and mandibles, building the chamber in which she would lay the eggs that would originate a new colony. As with other founding queens (Cf., for instance, Cunha, 1988), she probably had not randomly chosen the site, but visually inspected it from above, and, after landing, probed the ground with her antennae until a proper site was

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[23] It seems that this observation has not been recorded in my protocols; however, it has been remembered and frequently considered.

found, that is, one meeting all the requirements of humidity, consistence, etc., set by a pre-programmed action mechanism.

The spot chosen for the nest was among some bushes, whose sunlit branches and leaves, stirred by irregular gusts of wind, cast changing patterns of light and shade, apparently unpredictable in duration and sequence, on the soil. Having observed her excavating toil for a while, I stood up and held up my hand between the evening sun and the ant, thus casting an area of stationary shade on her and the surrounding terrain. The queen stood still at once and so remained for a while – about 1 or 2 minutes. Feeling tired, I finally withdrew my hand, and, a few moments later, the ant resumed her work.

It was – it might be correctly said – an automatic action based on a pre-programmed response mechanism. With such a response, the queen, whose colour resembled that of the soil, could manage, like many other queens in her own and other species, to go unnoticed by predators with a sharp perception of vibration and movement, like birds, lizards, anteaters, armadillos, spiders, and other ants. I admit it, but I cannot help being impressed by the feat. What impressed me the most were the skills and accomplishments revealed by the action. Indeed, it showed, first, that the ant, while digging, did not stop paying attention to certain events in the environment, and would even record and perhaps arrange them into a representation or model; second, that she seemed to use this record-model as a sort of probe or standard, in order, as I now assume as a hypothesis, to gauge the agreement between her present environment and the one previously recorded, and thus use the outcome, in the case of a significant discrepancy, to trigger a state of alertness to events in the surroundings and any emergency actions required by them. I state this based on the fact that it was clear that the sudden alteration of a state of regularity of the environment would interrupt the excavation and prompt the ant to stand still, which certainly made her less noticeable to predators.

This observation was different from the others previously reported in that it concerned the behaviour of a fertile *Camponotus* female instead of *P. fulva* workers. However, I think it is useful in clarifying the issue under investigation. In fact, I have observed similar instances of temporary immobility among fertile females of other ant species (for instance, *Camponotus rufipes* Fabricius, 1775, *Camponotus fuchsae*, *Solenopsis saevissima* Fr. Smith, 1855, *Paratrechina (Nylanderia) fulva* Mayr, *Atta sexdens rubropilosa* Forel 1906, etc.), as well as in workers of these species, generally as a result of some impact vibrating through the substrate, in the case of excavating workers, or, also, of sudden variations in luminosity, in the case of fertile females. In some cases I have observed that, after an interruption in the excavation caused by a sudden variation in luminosity or by a different vibration spreading through the terrain, an ant, whether a founding queen or a worker, instead of immediately standing still, if at a certain distance from the tunnel being excavated (for instance, if on its way to dispose of a clod at a certain distance from the perforation point), it could first rush into the tunnel and then freeze.

An important consideration in this connection is that, on alighting and starting the process of founding an initial nest, fertile females seem indifferent to normal variations of light and shade, and wind, in their surroundings. It is only after some time of exposure to stimulation conditions in their surroundings that a variation in these conditions, however slight, leads these ants to interrupt the activity they are engaged in and stand still as a form of protection. This same indifference to a number of variable stimulation conditions in their surroundings seems to be the rule in the case of *P. fulva* workers, which, inside or at the entrance of the nest, on being warned by a nest-mate that a new food source has been found outside, tracks down the route it had used to the nest and hurry towards the food. As soon as the trail towards the incentive is established, however, they seem to become more sensitive to changes in their environment and tend, on coming across them, to hesitate in their march or even to interrupt their activities and return to the nest.

14 BEHAVIOUR MODIFICATIONS WHEN ALTERATIONS OF THE SITUATION ARE EFFECTED ON THE ANTS' BODIES

The observations reported so far generally concern behaviour modifications exhibited by ants in response to alterations in some area of their path, nest, the food source being used, or even their surroundings. The observations to be reported now were selected in order to indicate the effect of alterations in which the ants themselves were directly affected in some way.

- *Observation 31 - Behaviour modifications in* P. fulva *ants on a trail caused by the vibrations of a mechanical impact transmitted to a food item they had been using.*

The objective of this observation was to see the effect, on *P. fulva* ants on a trail, of a direct impact against a saucer containing a lure being used by them. The trail, about 1 m long, was on the floor of a garage. The trail was crowded and connected the nest to a china saucer holding three peeled pieces of ripe papaya. One half of the trail – the one nearer the nest – was on a sunny area; the other was in the shade and part of it under an old wicker basket. Near the saucer, the trail was more like a column than a single line. Figure 43, below, illustrates the arrangement of the trail and the surroundings. The trail had been established the night before and the lure renewed in the morning. Notwithstanding the heat (around 30° C) at that time (about 2 p.m.) – something which usually inhibits trail formation – the number of ants and their speed were higher than usual, probably because the colony had been undergoing severe deprivation of liquids and food.

The observation comprised two phases with 20 1-minute periods each, as kept by a stopwatch: a control phase, with no alterations, and an experimental phase, in which the saucer holding the lure was made to repeatedly vibrate by a mechanical impact. The vibrations were produced by raising one side of the saucer by the edge and then releasing it from a height of 4 cm.

Qualitative results of this observation can be described as follows. After the impact and the vibrations in the saucer, the ants, as shown in Figure 43, below, went underneath the wicker box, and then along the single trail towards the nest, but visibly going over its limits. As I then wrote, they left, "very fast, but in an orderly fashion; I was unable to count them, so many were they, all of them at the same time, or almost, a moving chain of particles: a most beautiful exhibition, undoubtedly a mass evasion, as evinced by the speed and concomitance of individual motions, if compared with what had been seen during the control phase. And it was clearly a purposeful, not a blind process, even though the ants did not strictly follow – nor would they have fitted within – the limits of the trail they had previously used. Clearly, on going over these limits and rushing along in the right direction, they proved they had the general direction to be taken on their way to the nest”

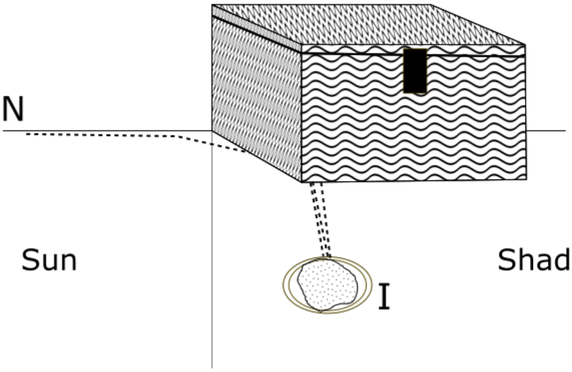

Figure 42: Approximate representation of a trail on a garage floor.

N: nest.
I: Incentive (ripe papaya pieces on a saucer).
Dashed line: trail.

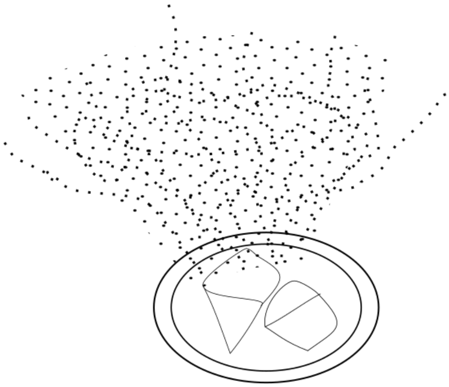

Figure 43: Illustration of the routes (dashed lines) taken by the ants feeding on ripe papaya pieces on a saucer, right after the vibrations caused by a mechanical impact against the saucer.

Half a minute after the impact, when the swarm of returning ants had thinned, I started to count the number of ants reaching a previously selected spot on their way back to the nest, during twenty 1-minute periods. Although I did not measure their speed, they seemed to move faster than during the control phase, and, but for one or two occurrences, without undulation in their march. The average number of ants returning to the nest was of 24.3 per minute, with standard deviation of 0.1432, against the average of 21.85 with a standard deviation of 0. 2048 in the control phase. The difference in the average number of ants in the two phases, though of only 2.45 ants per single period, produced a Student's t of 42.73, showing that the impact against the saucer holding the food incentive caused a statistically significant reduction[24] in the reflux of ants in the experimental phase.

Right after the impact, however, it was clear that the trail persisted, renewed by the arrival of new ants coming from the nest towards the food incentive, even though the calculations above indicated it had not totally recovered its original volume. This fact suggested that, although the behaviour of the ants returning to the nest after the impact was much altered, it was not enough to discourage the ants on their way to the lure. It is possible that the reduction in traffic during the minutes after the impact was therefore due to the fact that the ants directly affected by the impact had given up going back to the lure.

It seems clear then that a strong impact against a food incentive caused the ants feeding on it to flee and hurry back to the nest; curiously enough, however, it was not possible to show that the sudden encounter with a swarm of ants returning to the nest induced other ants heading towards the lure to also return to the nest.

- *Observation 32 – Behaviour modifications in* P. fulva *ants on a trail when disturbed by my breath, exhalation, and even death rattles at a short distance while feeding.*

The trail in this observation marched on a tiled wall, coming from a crevice in it, then on a marble sink and through the cabinet under

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[24] Beyond the confidence level of 0.00l.

it, towards a dead cockroach nymph lying on a kitchen floor. It was a crowded trail, with hundreds of ants which, having removed the cockroach's head, were extracting a soft, porous matter out of its body, and, as result, their gasters were gradually bloating, exhibiting some yellowish bands. It is important to report now some facts evincing an exceptional plasticity in this ant species in their dealings with a food item they like.

In fact, using a torchlight and a linen tester, a magnifier used by clockmakers, with ten times power, I could, as I wrote then, "almost touch the cockroach when examining how the ants on and in it behaved. Initially, I made them flee, but new ants came and I could breathe over them causing practically no disturbance nor scaring them away... Finally, there was a surprising event: as I smoked over the cockroach, they almost totally deserted it for a few seconds. After that, however, as I breathed on the cockroach, neither the arrival of ants nor their feeding was interrupted".... "Later, I poured some water and sugar in one of the grooves running along the edge of the sink and, using the linen tester, examined ants in various positions while they fed on the sugary solution. Now, in order to watch ants through a linen tester, a short range lens, under a torchlight, my face had to be very close to the sink; in fact, my nose was very close to the sink, and I breathed freely; 0.5 cm away, the ants were feeding on the sugary water, indifferent all the time, coming and going, and I believe, would even have entered or climbed my nose, had it contained any sugar. It was only when I dragged a glass on the sink, hit the sink with the tester, or breathed more forcefully that they would start running around, but would soon resume feeding ... Very well. I opened my mouth and carefully exhaled: they ran around for a while and started feeding again. There were about two hundred of them. I rested my chin on the sink and did the following: facing them, with my mouth open, I inhaled and exhaled, slowly and gradually increasing the force of the exhalation, until I was panting heavily, like a comatose patient, or even harder. Nothing! It was as if everything were normal". Even on the trail, with my breathing in and out through the mouth, their march was not affected. Only a sudden change in my breathing, a sudden increase in its force, would send them running around, only to gather together and start feeding again on the sugary solution a few moments later."

These facts are in sharp contrast with those observed when I inhaled or blew towards spots on the trail lying far from both the nest and a food source, when the disorganising effect was much stronger than those found in this observation. It might be said that the presence of food acted to counterbalance or reduce the discouraging or upsetting effects produced by the alterations effected in the environment. Or, better, perhaps, the disorganising effect of an experimental alteration might be said to be more intense in a phase in which behaviour is directed towards an objective than in a phase in which the objective has already been located.

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Blowing or breathing towards the ants, or stopping doing so, caused, as already seen, behaviour modifications in ants on a trail. The fact made me wonder what would be the effects of a more permanent alteration, such as marking the ants with paint. Observation 33, reported below, offers some contributions to an answer.

- *Observation 33 – Effects of applying paint to some body parts of* P. fulva *ants under two different conditions: a) before, and b) after a trail was established between a nest and a food incentive.*

On a certain occasion, in the garden of a house where I once lived, I took two cotton wads dipped in a solution of water and sugar, rolled them together, and placed them on a tap on a wall as a bait for the ants. I took some ants roaming around the cement floor under the tap, one by one, and carried them to the bait; after a while, a somewhat irregular trail was established towards the bait. The ants came from two different spots, probably temporary nests of the same colony. The entrance to the nest on my right was a hole in the wall, near the junction with the floor; the nest on my left was in a crack on the floor of a cabinet protecting the water meter and was not visible from the outside.

Most of the ants, from both sides, started climbing the wall when right under the tap, but one or another ant attempted, though haltingly, a shorter route, well before reaching this spot. Some ants coming back from the bait and towards the soil would also try other routes to the nest, straighter than the collective path. I noticed that these apparent attempts at a shortcut were more frequent towards the nest on my right, and the trail tended to go that way: probably, I suppose, because the nest was older and more populous than the other. Figure 44 illustrates the situation.

At a certain point, in preparation for an experiment I had in view and did not carry out, I tried to apply white shoe paint, using the tip of a rice straw, on all the ants going up and down the intermediary length of the trail. The ants tried to flee from the moving straw as soon as they noticed it: they ran and hesitated in their march. Also, on coming across a spot of paint on the wall, they ran waveringly, sometimes reversing the direction of their march, in a response that seemed an attempt to escape or flee the paint. Some of the ants going down, on being painted, seemed disoriented and started going up, while some of those going up started going down. Could this be simply an instance of disorientation or an actual return? My impression sometimes, especially as regards the ants going downwards, was that they had simply lost their bearings.

This behaviour was in sharp contrast with the one observed in two ants which, at the start of the observation, I had carried to the bait and painted with the same paint, and using the same method – as I had done many times before when trying to induce trail formation. These ants, on being marked, had not fled and did not seem more upset than the ants marked with paint in this observation. They were certainly being faced with a situation to which they had not been exposed before, of being captured and laid on a wad soaked in water and sugar, and being painted was only a part of a new situation. Besides, having found the lure after being carried to the tap, they seemed to focus their attention on it, certainly because they had been outside the nest in a motivational state Cornetz (1914) called "foraging state".

A further and more interesting difference between the behaviour of the ants I painted on the bait, to mark them as having found the lure, and those in this observation, painted when on the trail, should be mentioned now. Whereas the former, after having ingested the sugary solution, went to the nest and back to the lure, the former went to the nest and did not come back.

The events above must be considered together with another finding from previous observations: ants sometimes climb a piece of paper placed in an area of the environment (the soil, for instance) where a lure has been laid, but do not do it when the same piece of paper is found covering an intermediate stretch of an already established trail. One would say that, being in search of food and having smelt some in the vicinity, they seem to concentrate their attention on it and become temporarily oblivious of or indifferent to any change in stimulation which is not an indication of food nearby.

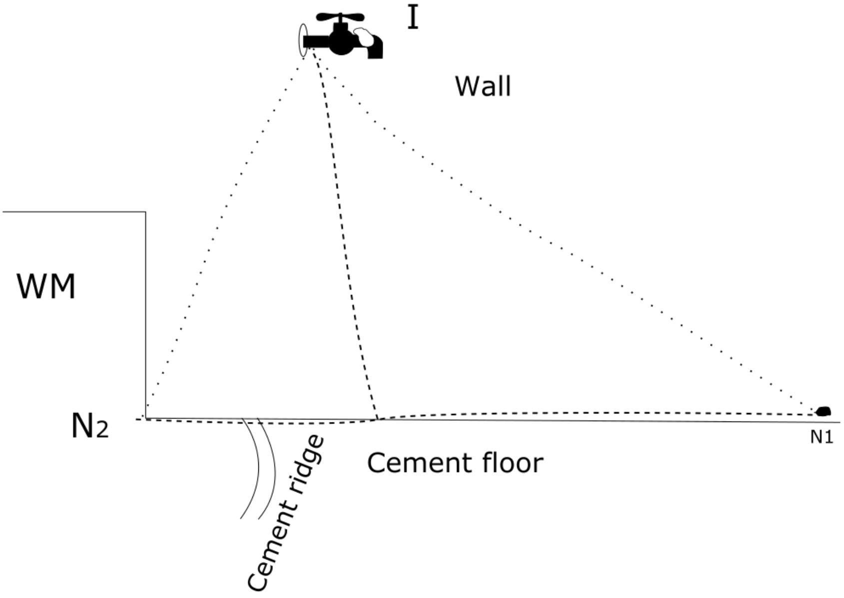

Figure 44: Situation in Observation 24.

Legend:
N_1 and N_2: entrance to two temporary nests of the same colony of *P. fulva*.
I: incentive (cotton wads dipped in water and sugar).
Dashed lines: trails.
Dotted lines: scattered ants attempting shortcuts.
WM: cabinet holding water meter.

For at least fifteen minutes after the paint was applied, the number of ants was greatly reduced. Since I knew the paint, once dried, would persist on their teguments for a long time, it seemed reasonable to conclude that only unpainted ants had remained on the trail, even if some of them had avoided leaving the nest on encountering painted nest-mates. As a matter of fact, however, thirty minutes after the painting operation, I noticed that, although the trail had been gradually growing thicker, none of the painted ants had come back. Not even those two ants which had been among the first to be marked and had repeatedly come and gone were to be seen: perhaps because they were tired or had moved on to another activity?

Puzzled by these differences in behaviour, I decided to paint *P. fulva* on the lure. I thought two things could happen. First, they would not leave the trail and would keep on coming and going between the nest and the lure. This would be an indication that the ants near the lure were so absorbed in it they would not either notice or care too much about unusual events. Or, second, the ants, once back in the nest, would not return to the lure, and this because the usual features of the environment, imprinted in them, would not have included the experience of having their teguments painted. Apparently, a variation in the conditions already registered by the ants as part of their environment would, as with the founding queen mentioned above, be in some way a deterrent to the continuance of a previous behaviour.

Then, using the rice straw and white shoe paint, I marked some ants on the lure. One or other returned at once to the nest, with little agitation; most of them, however, hid in gaps between the cotton wads soaked in sugary water and the wall. After some time, I could only find new ants to mark among the newly-arrived, but even these were increasingly excitable, perhaps because of some paint on the exposed sides of the wads, which had not been originally there. Newly arrived ants tended to expose themselves on the lure more than the others, probably because they had not yet been touched.

During five minutes I occasionally painted the ants on the visible side of the lure: about twenty, and, after their return to the nest, I did not see them again at the food source. I tried to paint only the back of their thoraxes and abdomens, since I noticed that, when their heads were painted, the ants were more upset and spent more time cleaning their heads and antennae with their forelegs. During the twelve minutes after the painting was finished, no painted ant came again to the lure. No painted ant could be seen, not even on the floor and away from the lure, except those returning to the nest. The ants at the lure would sometimes appear on its visible surface, but not as often as when I had started marking them. Sixteen minutes after the marking of ants on the lure had started, I carefully inspected the trail: no painted ant could be seen, not even those that had been marked forty five minutes before in the middle of the trail.

Forty five minutes after having painted the ants on the lure, I inspected the trail again. I saw a painted ant going down the wall and towards the nest. Could it be one of the ants first marked, or one of the ants marked during the two final phases of the observation, or even one of those painted on the lure, which had been hidden behind it all the time?

Unless another explanation could be found and demonstrated for the ants painted in this observation not having gone out again, I assumed the results lent support to one of the conjectures above: that the ants painted on the lure at the start of the observations did not leave the environment outside the nest because there had not been time enough for them to be impressed by the conditions of stimulation prevailing in the open air, and also because they were highly motivated for exchanges with a food incentive. Later on, however, the paint on the ants would turn the situation of a given instance of behaviour different from those previously experienced, and apparently it was this difference that caused ants to be in a state of alertness, return to the nest, and discontinue their foraging behaviour. A more general cause for the behaviour modifications we had been studying, therefore, would be some alteration in their immediate environment making it inconsistent with an environment by which they had been impressed, or which had been registered by them and which, in some way, had been involved in their current behaviour.

15 FINAL CONSIDERATIONS AND CONCLUSIONS ABOUT THE INVESTIGATION REPORTED IN THIS CHAPTER

In this chapter we have seen how behaviour modifications in ants can be caused by a great variety of experimental alterations, in the sense of modifications in their immediate environment. A question arising from this variety was whether the alterations shared one factor, or set of factors, that might be considered as the cause of the phenomenon. During the report we have seen how, by analysing the data, some hypotheses as to the identification of this factor or set of factors could be rejected as inadequate. More specifically, these factors did not seem to be alterations in the immediate environment under the form of stimuli automatically triggering action programs inbuilt in the genome of the species, as considered in the course of its evolution. In the specific case of particularly dramatic behaviour modifications in *P. fulva* on a trail on encountering one or more crushed nest-mates, it was noticed that, in opposition to what is still usually affirmed by practically all biologically-oriented researchers, they were not brought about by specific, intrinsically "modifying" substances, triggering automatic, pre-programmed responses, the so-called "alarm pheromones". Also, they apparently could not be ascribed to sheer interference with the olfactory track underlying a trail or the suppression of a part of it, since behaviour modifications were exhibited in response to changes which, as a focus of light or shade on the soil, did not involve any material modification of the track. Eventually, this search for a stimulation factor shared by all the alterations that had caused this phenomenon, proved impossible, since these behaviour modifications could arise even from the halting or suppression of a given stimulus, as found out, for instance, by Turner, in the previous century, after suppressing the smell of xylol on a stretch of a trail on the soil, or of stimuli which had been modifiers and to which they were now used. These behaviour modifications evinced a disturbance of the behaviour that had been previously carried out, and, not infrequently, seemed to indicate that these alterations had the general nature of a disturbing obstacle, something to get away from or be avoided, or, at least, something intriguing, to be cautiously inspected and from a certain distance, before the continuation or interruption of the activity then under way.

One would say that, given the feature mentioned above, the various experimental alterations employed, being, as they were, qualitatively different, could only cause qualitatively similar behaviour modifications, since they acted on a given common, central factor brought into the situation by an individual animal. This factor could not obviously be involved in those occasions in which, though alterations in the environment had been effected, no behaviour modifications were exhibited. What could this factor be?

During the investigation, it was seen that an alteration in the immediate environment, by itself, was generally not enough to cause the behaviour modifications under consideration, since the ants, provided they were being exposed for the first time to that given situation, failed to exhibit these modifications in response to undoubtedly severe alterations in their behaviour environment. This was the case, for instance, when I marked with white shoe paint ants crossing the terrain in an attitude that Cornetz (1914) considered to be an indication of a "foraging state", and carried them on a sheet of paper to a food incentive. The marks were made with a rice straw dipped in paint as soon as the ants showed signs of having accepted the food and before a trail was formed. An absence of behaviour modifications was also the case with the founding queens that, after their nuptial flight, started digging an initial chamber in an environment with highly changeable stimuli, such as wind, noise, rustling leaves, changing patterns of light and shade, etc.; this was also the case with *P. fulva* workers, which, on being faced, at the entrance of, or inside the nest, with a nest-mate that had just found a food source outside, would leave the nest and track the route they had used or simply go ahead, moving their antennae until coming across the food source, indifferent to variations in stimuli (such as pebbles, stems, tussocks, winds, patches of sun and shade, etc.) found on the way or simply dealing with them with brief, apparently exploratory motions ("sniffing"). Or, still, this was also the case with the ants that Cornetz (1914) called "pioneers": those walking on a terrain on their own, relying on no olfactory track. As the reader will probably remember, Cornetz mentioned that these ants could face a stretch of swept, or even superficially scraped, soil and not exhibit disorganisation in their behaviour, in contrast with ants coming across similar alterations when on a trail. The reader will also remember that, in my observations on ants found roaming on their own, that when a finger was placed in their way, for instance, they would generally pause for a while and "sniff" it (that is, move their antennae as if inspecting it), or even touch it with their antennae, but not interrupt or show signs of disorganisation of the behaviour in which they had been engaged. An important exception to this rule, the absence of dramatic behaviour modifications in ants first exposed to a specific environment, seemed to be the instance in which the ants were faced with the same finger, but after it had been used to crush one of their nest-mates. As we could see, this alteration generally caused severe behaviour modifications in the ants thus stimulated, even though their route, as it seemed, had not been habitual and was being used for the first time. Only apparently was this an exception, however, since their usual nest-mates, with their usual aspects, odours, and activities, were certainly, among all the objects experienced by the ants of a colony in their individual histories, the most frequent. I believe this could even be the reason why the modified body of a nest-mate, or one typical odour, or set of odours, originating in it, even if mixed with others not previously experienced, when found all of a sudden, were the cause of particularly dramatic behaviour alterations.

What was the condition shared by all situations in which an alteration of the environment was followed by the phenomenon under study, but absent in those cases in which the alteration was not followed by it? According to the data collected, it seems clear: a previous exposure, either prolonged or habitual, to an environment that would later be altered. *The immediate cause for the behaviour modifications considered in this work may be thus stated: it was a discrepancy between the behaviour environment habitually, extendedly, or repeatedly experienced and the environment with which the ants were suddenly faced.*

Pointing out this immediate cause, however, is not enough to explain why a usual or established behaviour should be suddenly disorganised or modified when prevailing aspects of their behaviour environment are altered. It is necessary to find out why this cause should have this effect, and this will be one of our goals in the next chapter of this work, in which I try to develop a general interpretation both of the factors or processes involved in the performance of the usual, normal behaviours of ants and those involved in the phenomenon of behaviour modifications caused by a sudden alteration of aspects of the environment in which their behaviour had been taking place.

16 CONSIDERATIONS ON THE FACTORS PROBABLY INTRODUCED IN A BEHAVIOUR SITUATION THROUGH THE REPEATED OR SUSTAINED EXPOSURE OF THE ANTS TO A GIVEN ENVIRONMENT

What factors could make the ants exposed in the way described in the previous paragraph different from those which were not, as regards their possibilities and disposition to act? Based on the data presented so far, I think I can venture some hypotheses that seem to be supported by the data in this investigation; these are presented below.

An important difference could be related, I suppose, to the very elements forming the behaviour situations in both cases. The situation would include, for the ants in the former case, but not for those in the latter, not only the stimulating elements in their immediate environment, but also other elements which, though not presented to their senses, had previously been experienced by the ants as regularly following these stimulating elements. Previous exposure to a given situation, especially if it is repeated, could be important, I think, in that it would enable the ants, on other occasions, to address not only sensory aspects actually perceived, but also those assumed as present through memory. It might be said, to clarify this point, that such event is similar to what happens when a human who, on his way to grab a glass and a bottle on a sink already expects, through the action of memory, to experience coldness to the touch and a given weight before actually touching them.

As already mentioned, this instance of memorisation was seen in Observation 20, in which ants were crushed on a doubly-bifurcating trail. It allowed the ants, as already mentioned, certain independence as regards the realm of stimulation and a wider range for their action in the environment. More specifically, a mnemonisation of aspects of the environment would allow ants, I think, to start using stimuli received from the environment through the senses as no longer, or not only, at least, immediate response elicitors, but also as signs of the presence of other aspects in the environment that, in the past, had invariably followed the same stimuli, and, in the case of ants properly motivated towards an object that might be properly attained through these means, as releasers leading them to behave towards these aspects as if they were already present. Therefore, it is also possible that the most important part in the effects of behaviour-modifying experimental interventions could stem, in a general way, not so much from new stimuli introduced by them, but from their reshaping of a pre-existing mnemic situation; this would be the more conspicuous the more habitual or usual this situation had become, and, of course, the greater the number and importance of recorded aspects influencing the behaviour under way. This reshaping seems to have become, in the course of evolution, a condition prompting insects, depending on their situation and previous experience, to actions ranging from inspection to flight and search for protection and shelter, and even attack against the elements altering their habitual situation, and these actions certainly have and adaptive value.

It is even possible that not only recent, but quite remote experiences might be recorded and mnemically brought into a situation to form, together with the stimuli actually acting on an organism, an environment that, being mnemic and perceptual, is no longer strictly physical, but psychological. It is such a world we humans find in our experiences – a world which cannot be reduced to the here and now of Physics, but one with a past, a present, and even a future, in the form of a retrieved past taken as something to succeed the moment actually being experienced. That ants seem to behave as if in a psychological, rather than in a strictly physical world, is suggested, not only by the findings in Observation 20, but also by the fact that when ants are seen walking away from the nest on their own, that is, apparently not following any trail, it is practically impossible to disturb them without sending them back to the nest straightaway. In this case, it seems clear that their behaviour is not made up only of responses to stimuli acting on their senses on the occasion, but also includes their rushing back to the nest based on a spatial representation of their environment, a *cognitive map* – a concept originally formulated by E. C. Tolman (1948), based on studies on the orientation behaviour of white rats in mazes.

Starting from the hypotheses above, I will try to show in the next chapter the factors that a previous exposure of ants to a given environment, especially when repeated or sustained, could act in determining the behaviour usually exhibited by them, and also to formulate a general explanation for the phenomenon of behaviour modifications arising from a sudden alteration in this environment. This alteration, I think, is the factor deterring or even disarranging the role of a memory previously acquired by ants when engaged in a habitual exchange with their environment, as well as causing, secondarily, modifications in this behaviour because of its intrinsic and situational features. Individual memory, and its action on the processes of an organism, is the evolutionary creation that enabled certain organisms to exhibit other behaviours besides reflexes and fixed-action patterns, and constitutes *the sole reason* justifying our discussion, in connection with these organisms, of a *psychology*: a set of phenomena which, by virtue of being historically determined, take up discrete forms in each organism, and, for this reason, are, as well as historical, also "historial", as meant by Heiddegger (1967): they make individual organisms institute and define their own situations, since their properties are dependent on the history of each specific organism (Cf., on this issue, Cunha, 1985 and 1986). As for the other chapters, they are meant as an exposition of other findings in this inquiry that seem to provide further support to the interpretation developed in the next chapter, both as regards normal behaviour and its modifications in the face of sudden alterations in a familiar environment.

17 SOME WORDS TOWARDS A CLEARER DEFINITION OF "EMOTION" AND "EMOTIONAL"

It must be mentioned that this task has not been accomplished, either by philosophers or psychologists and other scientists, not even by such especially gifted authors as Marcel Proust. This term has been defined by psychologists in many different and often contradictory ways. This is shown by Arno Engelmannn in a book on subjective states, a survey of the meanings of "emotion" and related terms from the earliest philosophers to the psychologists dealing with the subject up to the time the book was written. Reacting (pp. 57ff.) to a definition of "emotion" advanced by J. R. Reid, based on the ordinary usage of the term, Engelmann wrote, with evident irony, that the author had been too modest, and that "a better characterisation of 'emotions and/or...'", in a parody of Littman's 1958 definition of "motivation", would be the following: "These are consciousness phenomena and/or neural and/or visceral internal physiological phenomena, and/or theoretical constructs and/or mere chapter headings, taking up the form of independent discrete entities and/or points in a continuum; distinguished by their unusual intensity and/or low and average intensity, and for following generally unrestrained drives and/or conflicts between drives; they involve the perception of an external situation and/or of occurrences internal to the organism, and/or the perception of occurrences external and internal to the organism, simultaneously or successively, and are basically mechanisms acting towards adapting an organism to its environment, and/or occurrences totally devoid of an adaptive function, and/or, according to circumstances, adaptive or non-adaptive".

Engelmann remarks that this definition, "even though promoting, who knows, an armistice between advocates of different positions, is useless in the development of a proper theoretical conceptualisation of the phenomena being discussed", and that Max Meyer, as early as 1933, had predicted that by 1950 the term "emotion" would have disappeared from psychology. However, we may follow Engelmann, who said that, notwithstanding the prophecy, the term is still very much alive. But the author suggests that even though the definition of "emotion" is unsatisfactory, we can at least have a relatively clear idea of what psychologists observe in their investigation when they say they are dealing with "emotion", and classifies the phenomena observed by them in three classes: 1) directly observable movements, postures, and modifications of an organism; 2) movements and modifications in an organism that are observable only through instruments; and 3) directly observable products of movements by an organism. At this point, I must say that ever since the start of my research on ant behaviour in 1960, I have been using the phrase "behaviour modifications with respect to a previous behaviour" or simply "behaviour modifications" to designate disturbed behaviours as evidence of emotions.

The title of this book, *Emotion in the Circumspect Procession*, was consciously devised to include these connotations. As to the term "emotion", my definition is clear: it refers to behaviour modifications in organisms that, being adjusted to a habitual or familiar behaviour situation, when experiencing a sudden and unexpected alteration of this situation, find themselves suddenly unable to go on with a purposeful action in which they had been engaged until a new adjustment to the situation is accomplished, incorporating the alteration. It is a conflict of experiences disturbing the use of a memory of the habitual situation in the performance of a habitual psychologically mediated action.[25]

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[25] In my interpretation of the phenomenon, presented in my Ph.D paper (Cf., Cunha, 1980), adjusting to a situation, as we could say based on E. Chace Tolman´s psychological system (1932 and 1958), included an expected behaviour interrupted by a suddenly altered situation, until a new adjustment is achieved. A problem with this interpretation, which forced me to replace it, was that expectation will increase and decrease sometimes, as in the case of a goal in a football match; this variation must be explained, but it will not enable us to claim that what produces a behaviour is actually an expectation, even though it may be present in human actions. An expectation would be a preparation for certain events and its disruption would occur when real events turned out to be different.

CHAPTER III

THE USUAL BEHAVIOUR OF *PARATRECHINA (NYLANDERIA) FULVA* MAYR ON A TRAIL AND THE PHENOMENON OF ITS MODIFICATIONS IN THE FACE OF AN ALTERATION IN THEIR BEHAVIOUR ENVIRONMENT: AN ATTEMPT AT A GENERAL INTERPRETATION

1 OBJECTIVES OF THIS CHAPTER

It may be claimed, on the basis of the inquiry reported in the previous chapter, that the behaviour modifications exhibited by *Paratrechina (Nylanderia) fulva* Mayr, *1862,* which were reported in this work, are not a phenomenon of independent, autonomous behaviour, customarily exhibited by an individual insect, whether spontaneously or as a direct response to specific stimuli. Therefore, it is evident that a thorough explanation of these behaviour modifications involves, in the first place, identifying the nature of, and characterising, the behaviours usually exhibited by ants of this species in the environments where they are found; then, investigating and trying to find out the factors involved in the performance of such behaviours, and how these are affected by a sudden alteration in their behaviour environment leading to the behaviour modifications being studied. This chapter aims at a description of all stages gone through in the accomplishment of these tasks.

2 A CHARACTERISATION OF THE BEHAVIOURS MOST FREQUENTLY OBSERVED DURING THIS INQUIRY: BEHAVIOUR IN A FORAGING TRAIL AS AN INSTINCTIVE ACTIVITY WITH TWO PSYCHOLOGICALLY-MEDIATED APPETITIVE PHASES AND TWO COORDINATED CONSUMMATIVE PHASES

The behaviour most frequently observed in this work was that of a colony's workers on a foraging trail, not only because it is the one most easily found in the environments they inhabit, but also because it is easily induced with the use of food as a lure.

On an already stabilised foraging trail of *P. fulva* two series of discrete actions may be found: one comprising behaviours that could be said to be conducive to attaining a given object or situation – a food source or, on their way back, the inside of their nest – and one comprising actions through which the insects, their object or situation having been attained, would finalise the preceding actions. The latter are the actions of food ingestion, in the case of ants coming from the nest, and of regurgitation of ingested food to nest-mates, in the case of ants coming from the food source. Regurgitation is generally carried out inside the nest, but may also exceptionally occur on the way back from the food source, especially during the early stages of trail formation.

These two series of actions, of *heading towards* and *attaining* a goal, for each leg of their course, precisely correspond to those Wallace Craig (1918) identified as the discrete, but interconnected phases supposed to make up all instinctive activity, named by him as, respectively, *appetitive behaviour* (or its opposite, *aversive behaviour*) and *consummative action*. This proposition, according to Hinde (1959), would be the first step of a researcher in moving from the descriptive to the theoretical stage of Ethology. Once this correspondence is accepted, it may be claimed that the behaviour of ants on an already stabilised foraging trail is an *instinctive activity*, according to the modern conceptualization of the term by Comparative Ethology (Cf., in this connection, Klopfer and Hailman, 1950; Tinbergen, 1951; Thorpe, 1956; Schiller,1957; Fabricius, 1961; Hess, 1962; Eibl-Eibesfedt, 1970; Hinde,1970; Lorenz, 1981). This conceptualization concerns relatively recent developments in the science of animal behaviour which compelled researchers to recognise again the legitimacy of naturalistic studies on instinct, which had been abandoned as unscientific for about two decades in the 20th century, replaced with studies inspired by a conception – later shown to be incorrect – of instinct as a sequence of chained reflexes (Cf., on this, Miller, 1962; Cunha, 1965 e 1983).

Wallace Craig, according to Lorenz (1981, p. 22), defined appetite as a state of constant alertness while a specific stimulation situation, called by him "appetitive stimulus", is not attained. Aversion was defined by him as a state of agitation which continues as long as a certain stimulus, referred to as the disturbing stimulus, is present. When this disturbing stimulus stops acting on sense-organs, this state ceases, being replaced with one of relative rest. According to Lorenz (1981, p. 400), aversive behaviour, under this definition, may also be considered an appetitive behaviour in search of a state free from a disturbing stimulus.

Appetitive behaviour, according to Tinbergen (1951), is generally a kind of movement called random movement, exploratory behaviour, search behaviour, and other terms along these lines, and is characterised by (1) its variability and plasticity, and (2) its being purposeful, a term Tinbergen seems to employ with the sense of "having a definite function or result", which is to promote a new phase in appetitive behaviour, or a final, consummative phase in the instinctive activity as a whole. Appetitive behaviour could be, according to Tinbergen, a simple taxis, as when a frog, on seeing a fly, immediately orients itself towards it, sometimes repeatedly, until its body axis is lined up with the fly and directly facing it; or it could be a very complex and prolonged behaviour, as in the case of migratory behaviour among many species of birds and other animals. A consummative action, on the other hand, would be formed by stereotyped movements in an animal species bringing to an end the variable phase of an instinctive activity ("consummating it", in Wallace Craig's words). One instance of such movements would be suction-drinking, exclusive to pigeons among birds, pioneeringly recognised by the American zoologist Charles Otis Whitman as being as much characteristic and defining of what is taxonomically understood as a species, genus, family, order, etc., as the morphological characters used in evolutionary taxonomy. Whitman wrote in 1898 what is considered by some as the inspiring beginning of Ethology as we know it: "Instincts and organs are to be studied from the common viewpoint of phyletic descent." The usefulness of the stereotyped acts bringing to an end an instinctive action for taxonomic determination was later independently discovered by Oskar Heinroth, while conducting studies on the behaviour of geese and ducks. Lorenz, who took part in these studies under Heinroth's orientation, noticed that the stereotyped movements with a defining value for taxonomy discovered by Whitman and Heinroth were the same stereotyped patterns in Wallace Craig's consummative behaviour; he called them "endogenous movements" or, also, "instinctive movements". Later, they would be called "fixed action patterns", "fixed patterns", or, simply, "fixed actions".

A major part of Lorenz's theoretical system consisted in demonstrating 1) the endogenous generation and build-up of motivation for the performance of fixed action patterns – something which would clearly distinguish them from reflex activity; and 2) the internal blocking of these patterns. Based on his observations, Lorenz showed that the occurrence of a fixed-pattern action was related to two conditions: the time elapsed since the last occurrence of the pattern, and the presence of certain specific stimuli. In fact, it was possible to counter the adequacy of the stimuli by depriving the animal of an opportunity to exhibit its instinctive movements. The greater the deprivation, the greater the possibility that the animal would exhibit these movements when faced with mere fragments or coarse models of the object or situation effective in releasing them. In the prolonged absence of adequate stimulation the pattern could sometimes occur "in a vacuum", that is, without the presence of the relevant external releaser. A classical example would be the nest-building movements of a well-nourished weaver bird in captivity during the mating season, with no access to straw. Its movements are exactly the same as those the bird would perform when building a nest in its natural environment and using the proper material. On the other hand, a weak motivation for activity could be countered by increasing the adequacy of external releasers. For instance, it has been seen that the probability and vigour of a stickleback's attack against the plastic model of a rival, even a coarse one, is greater the closer it is placed to the fish's territory. It has also been seen that the probability and vigour of the attack is increased when, to a typical sign of a rival, such as the reddish colouring of the belly, another one is added: a vertical position, with the head pointing downwards. However, a real fish of the same species, as still as the model, but lacking these signs, did not elicit any response (Tinbergen, 1951).

By considering facts like these, Lorenz concluded that a tendency to instinctive action, under conditions of stimulation deprivation, was continuously generated and accumulated in an animal's nervous system until a precise stimulus, acting on the damming-up mechanism, released the action that would dispel it. And he also concluded that this energy would not be spent if only the taxis components of the action were presented. This energy was called by him *specific action energy*. It is even possible to demonstrate these assumptions using physiological preparations. Thus, for instance, Lorenz (1955), on referring to the neurophysiological observations carried out by Sherrington – supposedly the first to discover the endogenous generation of movements – reports some intriguing phenomena exhibited by beheaded seahorses in a physiological solution. Whole seahorses swim thanks to undulating movements of a vertical fin running along a groove on their backs. A complete undulation of this fin is achieved when the fin is expanded to its maximum height and then contracted towards the bottom of the groove. In a preparation with a beheaded seahorse, however, the fin remains firmly protracted at an intermediate position, that is, not extended to its maximum height, but halfway. According to Lorenz – who used the interpretation Eric von Holst developed for these phenomena – it is possible to provide a replacement for the brain by pressing the neck of the seahorse with thumb and forefinger just below the area where the head has been severed. The result is a complete contraction of the fin. If the pressure is maintained for a while and then released, the fin will undulate a few times and then stop at its original halfway position. When it is maintained longer and then released, a longer sequence of undulations will be observed. According to Lorenz, these facts include the essentials of ethological theory on the control of fixed-pattern actions by nervous centres located above the centres responsible for the muscle contractions which produce these patterns in an organised way: the higher centres – usually the brain or the cephalic ganglion – have the function of keeping under permanent inhibition the lower centres responsible for these movements until the occurrence of some specific stimulation, previously fixed by the nervous organisation, which lifts the inhibition.

Lorenz's conception of nervous action would reverse the traditional notion of neural control: animals, including us, would not be continuously dependent on stimulation to act, but would, like spirited horses held in check by their bridles, wait for an external cue in order to act. Strictly speaking, we would not be responsible for performing an action, only for actively keeping it inhibited. The supposed mechanism for blocking motor action was called by Tinbergen "*Innate Releasing Mechanism*", IRM for short. Jointly developed by Lorenz and Tinbergen, it was up to the latter to experimentally elaborate and refine the concept, and to investigate its physiological characteristics and functional limitations (Cf. Lorenz, 1981). As expressed by Lorenz (Cf. 1955 and 1981), this mechanism was made up of a perceptual element (a stimulation filter) and a motor element (a triggering action, usually a command prompting a shift from one behaviour to another within a sequence of behaviours: this is what happens, for instance, with sticklebacks during their mating season; on reaching shallow waters, a stickleback interrupts his migration and starts collecting mud for a nest; a rival seen in the vicinity will be attacked, whereas a receptive female, identified by her protuberant belly, made more conspicuous by her slanted posture, head upwards, is courted). Given this composition, Lorenz – apparently relying on an analogy stated by the American ornithologist F. Herrick more than half a century before on the subject of instinctive action – the IRM would be similar to a lock in its action. The perceptual element would be like a key way, fitting only certain stimuli, called *key stimuli* or *sign stimuli*, such as those mentioned above in the case of sticklebacks. A particularity about these stimuli was that, in a natural environment, they would occur only in biologically appropriate circumstances or moments in a life cycle. The motor element would be similar in action to a bolt: given the right stimulus, it would release the lock or block, and trigger activity. As regards certain behaviour patterns, some species would be born with an extremely rigid IRM which, outside the relevant natural situation, would respond only to some highly unlikely stimuli. Other species, however, would be endowed with a mechanism in which the perceptual element would remain vague and undefined until shaped and completed by experience. This is what happens, for instance, in the process of "imprinting", as when the hatchlings of certain goose species follow objects in their environment. Lorenz showed that goslings, as soon as hatched, tend to immediately follow the first moving object they see, provided its size is between that of a box of matches and that of a canoe. Normally, it is their mother, but, when hatched in an incubator, it could be Lorenz himself, walking on all fours and honking like a goose, or even moving in his ordinary way. According to Lorenz (1937), the object the gosling followed within a few hours after hatching, the "critical imprinting period", would be the object to which it would address its filial responses, and determine the class of objects towards which the bird would exhibit sexual behaviour on reaching its reproductive age. According to Lorenz, over time, no other object will determine the following response. Thus, it is as if evolution had endowed the species with a malleable IRM, like a bit of wax, accepting a variety of releasers when soft, but, once solidified, receptive only to an already experienced releaser or class of releasers.

Now, after these notes on the advent of Comparative Ethology, I resume the characterisation of the behaviour of *P. fulva* on a provisioning trail. As already mentioned, the appetitive phase of this activity ceases at one end of the trail with the ingestion of food, and at the other end, usually, with the regurgitation of part or all of it, to mates inside the nest, which, on their turn, transfer it to larvae or fertile individuals, if present. Considering these two phases, which may be considered consummative in a provisioning trail, the former, food ingestion, seems to me subordinate to the latter, that of regurgitation, which may then be considered the main one. This is supported by the fact that these trails are generally long-lasting – as mentioned, they sometimes persist for hours on end – and seem to be the outcome of repeated single visits to a food source, for it does not seem feasible that a trail could last so long if each worker ingested the food at the end of the trail only once. As a matter of fact, on a few occasions in which I marked some ants first climbing a food incentive, they returned from the nest to the lure 5 or 6 times in a row before disappearing; later on, about half an hour later, one or other of these ants could be seen on the trail again. Apparently, ants on a provisioning trail stop visiting the food incentive only when they are no longer receptive to the food carried in their crops or "social stomachs". In this case, the food remaining in this crop and the tiny individual stomach seems to be sufficient to meet the nutritional needs of an ant for a considerable time. However, the factor leading to repeated visits to a food source by ants on a foraging trail seems more elusive. Could it be the opportunity of new regurgitations, as gratifying acts in themselves, or the food-begging behaviour on the part of their nest-mates as too powerful a signal? Or perhaps the undernourished condition of the ants or, better perhaps, the emptiness of the crops of individual ants, as evinced by their thinness and dark colour when on their way towards the food source, a condition caused by undernourishment or by regurgitations in the nest at the end of each trip? It has been experimentally ascertained that this "empty stomach" conditions lead, in rats, to food searching (Cf. Tinbergen, 1971). That this condition may effectively prompt an appetitive behaviour, that of foraging, in ants is suggested by the fact that when there is a prolonged absence of foraging trails, one sees a thin, darkish ant walking away from the nest, usually in a straight course, occasionally interrupted by erratic sideway detours. It will almost certainly interrupt its march to ingest food if it comes across any on the way. It was to workers exhibiting this behaviour that Cornetz (1914) referred to, correctly, I think, as being in a "foraging state". However it is, repeatedly going from the nest to a food source and back does not seem to be the result of endogenous generation and accumulation of specific motivations for these actions in individual ants. If there exist generation and accumulation in this case, they apply to the colony as a whole, and their existence would certainly be a good argument for scientists advocating the concept of a superorganism (Cf. Allee et al., 1949, section 24 *et passim*) as applied to insect societies.

Before moving on to another topic, I think it is appropriate to mention that considering regurgitation as a consummative action prevailing over food ingestion on a normal foraging trail seems to fit the data on the phylogenetic development of ants. These insects, together with bees, wasps, and termites, are among the few animal species that meet the requirements to be biologically classified as eusocial: members of different generations living together in the same colony, and the existence of one or more castes, the members of which look after immature individuals and perform the tasks needed for the maintenance of their common dwelling, without, however, taking part in procreation. For this task, in the case of ants, it was extremely important that workers could evolve, as well as their tiny individual stomach, a social stomach, or crop, to store food for the colony, and specialised organs to distribute the food, such as the proventricular valve, which acts like a pump in the suction of digested food from the individual stomach into the crop, to be given to the larvae through trophallaxis. It should not be forgotten that, as shown by Morley (1954), the development of a regurgitation mechanism was at the very centre of the various modifications in morphology and habits undergone by ants in their evolution, such as the development of a crop, of a more elastic and flexible tegument allowing for the dilation of the gaster during food ingestion, the loss of the habit, exhibited by founding queens in primitive species, of going outside the nest after prey, the change from solid to liquid food, etc. According to Morley (*Opus cit.*), the crop is the fundamental organ in the social life of ants, and the act of regurgitation, the essence of their lives – the *crux dominium* of their existence. According to Lorenz, it is a characteristic of instinct the fact that it can be fooled. In food donating through regurgitation it obviously is, for it is known (Cf., for instance, Wheeler, 1910; Forel, 1921-1923; Dumpert, 1978; Hölldobler and Wilson, 1990), that many of the various species of animals called myrmecophiles, which live inside ant nests, including rove beetles, arachnids, springtails, bristletails, cockroaches, lacewings, butterfly and fly larvae, have "found out" how to receive regurgitated food from their hosts by using soliciting gestures and postures similar to those that ants use among themselves.

I start now to consider the appetitive phases in the behaviour of ants on a foraging trail. When considering instinctive behaviour, Tinbergen (1951, p. 119) wrote that, in the most complex case, consummative behaviour is a set of chained responses, where each of them may be the combination of a taxis and a fixed pattern. But appetitive behaviour, differently, is a truly purposeful activity, exhibiting all the problems of plasticity, adaptability, and complex integration that beset the scientist dealing with behaviour in its entirety. And, later, that the appetitive behaviour is a cluster of elements of widely different orders, reflexes, conditioned responses, "discerning" behaviour, etc. It is therefore a veritable challenge for positive science, and our distinction between appetitive behaviour and consummative behaviour is but a first step in the analysis.

The phrase "discerning behaviour" certainly does not apply to a sequence of appetitive activities in which every individual action randomly leads to a result or situation that contributes for the beginning of the next – for instance, a sequence of actions such as those of a male stickleback during the mating season, when he migrates to shallow waters and, upon arriving, goes about locating and gathering slime and moss to build an upright ring-shaped nest, in the vicinity of which he will remain, threatening and attacking male intruders, etc. (Cf. Tinbergen, 1951). This would certainly apply to those activities in which, on certain occasions, an animal would head, from the start, towards an object or situation that could be recognised on the basis of a memory of past events. This is the nature, I think, revealed in the observations in the preceding topic, discussing the behaviours of going towards a food source and returning to the nest as exhibited by ants on an already stabilised foraging trail. One could say these behaviours are, on the basis of these and other observations in this work and the criteria developed by Edward Chace Tolman (1932, 1958), purposeful and cognitively determined. This was probably the reason for the perplexity of Tinbergen and other ethologists, mentioned above, perhaps for their considering that instinctive activity was the expression of innate programming, and for still not having clearly realised, as Lorenz (1965) later would, that in certain cases this programming could also involve an evolutionary mechanism for the adaptive use of individual past experience. Or, in my words, the reason for this perplexity could be the failure of many ethologists then, if not now, to clearly understand that psychological processes arose over the course of evolution as an adaptive resource in addition to reflexes, fixed patterns, and blind or random appetitive behaviour, in certain animal species, working towards the fulfilment of their demands, either innate or acquired.

The fact that a behaviour changes when alterations in the environment occur and persists until a given result is attained would be, as originally claimed by Edward Chace Tolman (1925) – supported by many other students after him – an objective definition of the purposeful character of this behaviour[26]. More specifically, according to Tolman (1932, 1958), this character could be experimentally demonstrated by showing

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[26] Tolman recognised in this work that his proposition had been influenced by two articles published by Perry in 1918 and by William McDougall's *Outline of Behaviour*, published in 1923.

that a given object or situation in the environment constitutes, in relation to this behaviour, a target or goal-object and goal-situation, that is, by showing that: a) this behaviour persists and varies until this object or situation is attained by the animal; b) this object or situation being suppressed leads to the cessation of this behaviour, and its being brought back, to the reestablishment of the behaviour; and, c) variations in the position or features of the object or situation are followed by corresponding variations in behaviour. All these conditions would express, according to Tolman, the essential characteristic of a purposeful act: its *docility*, that is, the fact that it is modifiable by past individual experience and persists until the objective is attained. However, this characteristic is not applicable to all purposeful actions, only to *psychologically mediated purposeful action.* In fact, the appetitive phase of many instinctive actions is a random wandering or migration automatically determined by hormonal and seasonal factors such as the luminosity and temperature of the environment, and these actions are suspended when a condition is met that may trigger a new phase in the appetitive activity (for instance, shallow water in the case of sticklebacks in the mating season – Cf. Tinbergen, 1951), or the consummative phase of the instinctive activity (for instance, oestrus in female wild cats – Cf. Thorpe, 1952).

The demonstration of the purposeful, psychologically determined behaviour of *P. fulva* on a provisioning trail is so apparent in the results of the observations reported so far that I think it would be idle to go over the details again. It is enough, in this connection, to briefly point out how they generally conformed to the requirements in Tolman's proposition mentioned above. Thus, the fact, frequently observed in this investigation, that ants on a habitual route, engaged in a given behaviour, make a detour on coming across any alteration in their path, as well as the fact that they go on provisioning the nest under the new circumstances, certainly meet condition (a) in the proposition, revealing the character of goal-object of both the food source and the nest, or, better perhaps, of the action of regurgitating the food to nest-mates. There is a new point in this event, as compared to the data presented by Tolman, which is the existence of two targets in this behaviour, one for each direction of their progress along the trail. The greater the eagerness in the provisioning behaviour of workers after a dehydrated bait was moistened, and the cessation of this behaviour after a habitual bait was replaced with another one, of a different nature, as seen in Observations no. 26 and no. 29, reported above, meet requirement (c) in Tolman's proposition. As further evidence of the conformity of the behaviour of ants on a provisioning trail to the requirement being discussed, I can still mention that, on two other occasions, I noticed that a change in the contents or nature of a food incentive caused both the ants already on it and later arrivals to leave and extinguish the trail. On one of these occasions, the change was the addition of some orange peel juice to a cotton wad dipped in a sugary solution. On the other occasion, I saw that the *P. fulva* workers that had accepted freshly peeled pieces of sugar-cane, started to reject them as soon as these were placed on a small wooden block (a domino) smeared with kerosene. As for requirement (b) in Tolman's proposition, it should be mentioned that, in order to lengthen or shorten an established provisioning trail, it was enough to move the food incentive further ahead or before its original position. Only the fulfilment of the first condition in requirement (b) – the cessation of foraging behaviour by suppressing the lure employed to establish the trail – has not been mentioned, and only because it has been unnecessary. I should only add, as an event not expressly considered by Tolman's condition (c), that the extinction of the trail was not always immediate, since some ants, sometimes many of them, would go on visiting the spot where the food was usually to be found, and sometimes roam around the area for a while, before retreating to the nest "for good" or engaging in other activities. Their persistence certainly evinced the effect of an individual past experience. My impression is that these frustrated visits were more insistent the greater the number of ants that had been previously engaged by the incentive, and this I think might be due to how attractive the food was or how deprived the colony had been.

As well as those exhibited on a provisioning trail, I believe many other behaviours may be purposeful and psychologically mediated, including the following: trying to locate a food source outside as a nest-mate enters the nest with a favoured food item; searching for a suitable location for a new nest after a flood or partial destruction of the original one; the frequent transportation of the brood by workers inside the nest to sites temporarily having the temperature and humidity needed for their protection or development, as well as their removal to sheltered places when the nest is damaged or threatened; the disposal of corpses and waste outside the nest; leading disoriented workers back to the nest, etc.

3 CONSIDERATIONS ON THE FACTORS PROBABLY INTRODUCED INTO A BEHAVIOUR SITUATION BY A REPEATED OR PROLONGED EXPOSURE OF ANTS TO A GIVEN ENVIRONMENT

As already mentioned at the end of the previous chapter, the immediate cause for the behaviour modifications exhibited by *P. fulva* consisted in an alteration of a given behaviour environment, but only if the ants had been repeatedly of habitually exposed to this environment. What factors would distinguish a behaviour situation of ants that had been exposed to a behaviour environment and ants that had not? Based on the data presented so far, I present below some considerations and hypotheses on the matter that will help me find an answer to this question.

One important difference could be, I suppose, the very elements comprising the *behaviour situation*[27] of the ants in both cases. This situation would probably include, for the former, not only the stimulating elements in their immediate environment, but also aspects or elements of their preceding behaviour situation, brought into play by individuals as evocations or assumptions based on mnemic records. Previous exposure to a given situation, especially if repeated, could be important in that, I think, it would enable the ant, on a future occasion, to behave towards aspects of the environment not yet present as stimuli, but assumed to be present through the action of memory. This is so, of course, because ants have developed over the course of evolution capacities or inclinations allowing this use. And the reader will certainly remember that it has been shown in Observation 20, for instance, in which ants were crushed on one of the branches of a doubly-bifurcating trail, how the behaviour exhibited by the ants could not be understood without reference to elements and aspects

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[27] By "behaviour environment" I mean those aspects of the environment providing actual or potential stimuli to animals in it. It is, therefore, a factual concept. On the other hand, "behaviour situation" is used for the set of such factors as sense reception, and the perceptions, evocations, assumptions, tendencies, motivations, states, biases, etc., that probably determine the behaviour of an animal in a given behaviour environment. It is a theoretical concept. The situation may be said to be "psychological" if a memory established through one or more instances of exposure to a given behaviour environment is implied in it and has some part in determining behaviour.

of the environment that could only affect them by having been brought into the situation through a memory of what had been found in previous instances rather than directly through sense reception of actually present stimuli. This memory, as already pointed out, seems to have allowed ants some independence in relation to the domain of elicitation and a broader range for their action than that provided by the environment, seen as the stimuli actually at work in a given moment. More specifically, as far as my observations allow me to suppose, the mnemic record of their experiences as they expose themselves to and address a given environment would enable ants, as well as many other animals endowed by evolution with proper mechanisms, to use environment stimuli perceived by the senses as *no longer*, or *not only*, as immediate response elicitors, but also to evoke and consider as actually present those aspects of the environment found to have invariably followed the same stimuli in the past, and – as long as the animal is properly motivated towards an objective that can be properly attained through these aspects – cause them to pursue them in advance. Therefore, it is also possible that what is most important in the effect of any behaviour-modifying alteration in the usual behaviour environment comes not so much from new stimuli being introduced, but from behaviour being adulterated, and this would be the more evident the more the situation had become habitual or usual, and, of course, the greater the number of aspects at work and their importance for the behaviour under way. During the course of evolution, this adulteration seems to have become a condition bringing about in ants, depending on their situational conditions and previous experience, actions ranging from investigation to search for protection and shelter, and even attack in responding to the elements altering the habitual situation, actions that probably have a great adaptive value.

It is even possible that not only recent, but very early experiences could be recorded and mnemically brought into a situation to form, at a given moment, together with the effects of the stimuli actually acting on an organism endowed with the proper means to make adaptive use of its individual experience, a behaviour environment which is no longer strictly physical, but psychological, since it is mnemic and perceptual. Such an environment is what we humans have in our phenomenology – a world which cannot be strictly reduced to the here and now of physical events, but having a past and a present, and even a future, under the form of a past which is retrieved or projected as bound to follow the moment actually being experienced. That ants seem to live in a psychological rather than in a strictly physical environment is suggested, for instance, by the fact that it is practically impossible to disturb ants leaving the nest on their own, that is, apparently not following any trail, without sending them immediately back to the nest. Although it has been already pointed out, I think it should be emphasised that, in this case, it seems clear that their behaviour is not only a response to stimuli actually acting on their senses at a given moment, but also a heading towards the nest based on a spatial representation of their environment, something like a *cognitive map* of the environment, as the concept is defined by E. C. Tolman (1948).

Starting from the hypotheses above, I intend to show under the next topic what factors could be created by a previous exposure of ants to a given environment, especially if repeated or prolonged, and in what way they could act in determining the behaviour usually exhibited by them. And, also, I will try to formulate a general explanation for the phenomenon of behaviour modifications following a sudden alteration in the environment. This alteration, as I see it, is a factor that hinders or disturbs the use the animal has been making of the mnemic record of a situation usually found during a habitual exchange with the environment. Individual memory and its action on the processes of an organism is, I think, an evolutionary creation that enabled certain animal organisms to exhibit a *psychology*, that is, a set of phenomena influenced by a properly individual memory as the latest resource in adapting to the environment. Among these phenomena, there would be the possibility of many animals exhibiting, besides reflexes and fixed action patterns made possible by older mechanisms inscribed in their species genomes, also psychologically determined purposeful behaviours, that is, oriented toward targets or results that can be anticipated thanks to individual past experience.

Not only for ants: even for humans, it seems that being marked by the environment, having a broader range for action, encompassing more than the mere elements and aspects of an immediate situation, but also those that habitually follow them, seem to be necessary for the performance of an act directed towards an anticipated result. This is what is suggested by our arrested action when, for instance, we wake up in the middle of our first night in a hotel room and, feeling the need of going to the bathroom or reception, we need, before acting, to recall where we are, where the required room or the light switch is before we get up and walk. Before that, it seems that we can only act by trial and error, as when we find the floor further down on trying to get out of a hotel bed, forgetting we are in a strange place, or when we trip on a stool we forgot that was there. However, even in these cases, in the absence of a previous record of the habitual consequences of stepping on the floor, groping along the wall, turning on the lights, going to the bathroom, etc., even a trial and error approach to the unfamiliar hotel room seems impracticable.

Since the behaviours considered here are to a large extent the outcome of the exposure of an organism to past things and events, we must admit that they are *historically determined and, as such, cannot be accounted for only in terms of present stimuli acting on the response mechanisms and physiological states of the individual at the moment these behaviours take place*. For this reason, they often seem gratuitous and *arbitrary.* For instance, objectively, there is nothing in a telephone, a stapler, a ball, or the sense impressions these objects produce, that compels us to deal with them the way we do. In order to understand the way they are dealt with we must consider how each of these objects has been introduced in the actual life of each individual. The different attitudes of human individuals, for instance, faced with a lock of hair are clearly determined not only by the stimuli originating from the object, but also by the chance occurrence of their being hairdressers, wigmakers, or people keeping the lock as a relic or memento of someone dear. On the other hand, since the history of each psychological organism is different, we have to recognise that it is also *historial*, in the sense given to the term by Heiddegger (1967), that individuals, largely because of their specific histories, are the institutors and definers of their own situations (Cf. Cunha, 1985, 1986 and 1989). A lecture delivered by a botanist exhibiting samples of native plants, for instance, is totally different, in psychological terms, for his or her colleagues, lay people, aboriginals or countrymen, who are surrounded by the plants from which the samples were taken, or a baby in its mother's arms in the audience.

Following this, I will present new observations, the results of which may reveal or even clarify the role played by individual memory in different aspects of habitual activities of ants, as well as those of still other factors.

4 INTERMISSION: A REMARK ON THE TENDENCY TO REJECT THE EXISTENCE OF INDIVIDUAL MEMORY AND PSYCHOLOGICAL PROCESSES IN ANTS AND OTHER INVERTEBRATES AND REDUCE BEHAVIOUR PHENOMENA EXHIBITED BY THEM TO AUTOMATIC ACTIONS INSCRIBED IN THEIR GENOMES, EMBRACED BY THE OBJECTIVISTIC MOVEMENT IN ANIMAL BEHAVIOUR STUDIES, AN ALLIANCE OF STIMULUS-AND-RESPONSE NEO-BEHAVIOURISMS AND THE ANTI-PSYCHOLOGISM OF CLASSICAL ETHOLOGY

If William Morton Wheeler were still alive, he would probably extend his criticism of Bethe, found in his book *Ants: Their Structure, Development and Behaviour* (1910, ch. 30, p.533), to many recent and current students of ant behaviour. According to his criticism, Bethe's opinion, that ants follow trails by reflex and, therefore, do not have even a rudimentary memory, stems from a superficial knowledge about these insects and the literature on the subject then available. Opinions like Bethe's, probably influenced by the law of parsimony, advocated by C. Lloyd Morgan[28] as early as 1894, might be said to spring from an extreme objectivistic attitude, of which Bethe seems to have been a forerunner and that would be embraced by most behaviour students since about 1910. This attitude amounted, and still does, to interpreting behaviour, as much as possible, without recourse to internal factors of a mental kind, and considering behaviour, if innate, as being formed by reflexes and – later, in the 1930's, with the advent of Comparative Ethology – by fixed action

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[28] This law refers to the application of a famous canon advanced by E. C. Lloyd Morgan in his *An Introduction to Comparative Psychology*, 1894, as a way to rid animal behaviour studies of a then popular trend among researchers, especially when relying on the so-called "anecdotal method", in which folk or literary accounts about our "half-siblings", tending to glorify and idealise the mental capacities of animals, were accepted as scientific evidence. According to this canon, researchers should never interpret an activity performed by an animal in terms of higher psychic faculties when this could be done in terms of faculties lower down in the evolutionary and developmental ladder (Cf. Cunha, 1964). In animal behaviour studies, this application originated a trend of considering as more scientific, even without enough evidence, interpretations based on processes of a mechanomorphic nature, to the point that by 1940, according to comparative psychologist R. H. Waters (1939, 1960), a paradoxical situation prevailed, in which human processes could no longer be used to explain human behaviour and – I would add – experience.

patterns, and, if acquired, as automatically formed according to the rules of conditioning, as formulated first by Bechterev and Pavlov, and later by Konorski, Skinner, and other authors. In the case of ants, this has gone to the point of it being claimed, as mentioned in Chapter I, that the action of a few pheromones could explain in their entirety all complex phenomena in the life and social organization of ants.

I oppose this objectivism, which has become the prevailing atmosphere in animal behaviour studies thanks to a close interpretive alliance of S-R behaviourism and the anti-cognitive neo-behaviourist movements following it, with the Ethology of early ethologists and many of their successors, in their conspicuous anti-psychologism, certainly because they failed to perceive that Psychology is also a part of Ethology, and one of the most important ones, as I hope to demonstrate. I will advocate that science does not need an economy of concepts of a mental kind – mental meaning, as I see it, mnemic or ultimately due to memory -- but that it needs concepts, whatever may be their origin in human experience, to explain and foster discoveries. Explaining facts is not the most important thing for the cultural progress of humanity: common sense, myths, and religion have done that before science. What is really important for this progress is developing explanations that, as well as accounting for facts, have verifiable implications.

I believe that students who think that the usual behaviour of ants when following a trail is merely reflex and totally devoid of memory probably consider only the way in which the trail most commonly found in a natural environment – a trail for provisioning the colony – usually starts, that is, when a worker finds a food source outside the nest, lowers its abdomen towards the substrate, and returns to the nest leaving a trail of warning pheromone, and, once inside the nest, gives some regurgitated food to other ants, which then walk in and outside the nest following the trail left by the scout until they finally reach the food source. However, during my observations, it frequently happened that, when tired of waiting for an ant to find a food incentive I had placed outside the nest to induce the formation of a trail, I would carry one or more workers that I could coax onto a paper sheet to the food source. In these cases, the forced discoverers did not deliberately leave a warning track because they had not gone along the path towards it themselves and did not have a direction to follow back to the nest, a journey which was generally erratic and painful. Since I marked the discoverers with paint as soon as they had accepted the bait – when I could even prod them with a straw without disturbing their ingestion, so intent they were on it – it was easy to identify them when, some forty or fifty seconds later, after finding and entering the nest, they came out, thin again, after regurgitating food to other ants. Some nest--mates usually came with them, following their tracks, which, although not marked in the way mentioned above, was, so it seemed, left behind in some way, even if scantily, along the path they had used when returning. Sometimes, even when the discoverer did not leave the nest immediately after entering it, some ants would soon appear at the entrance, vigorously flicking their antennae, apparently excited, and start to follow the path taken by the discoverer. Would it not be a sign that these workers were able to discriminate a trail among others and that thanks to the memory of something previously experienced? For instance, on leaving the nest through a tiny orifice in a cement floor, it was evident that the trail of the discoverer had been mixed with those of other ants coming in and going out in many different directions, assuming that these trails had lasted for a while. In these cases, could correct tracking dispense with a memory of the trail to be followed? Let us admit, for the sake of argument, that it could. However, what is seen when an ant follows a trail left by a nest-mate shows that this trail is often lost or simply abandoned from time to time in favour of apparently exploratory lateral deviations. When a small group of ants closely follow a discoverer, as it is commonly seen, the ant right behind often overcomes the group and gyrates for a while, especially when the discoverer progresses slowly, as if uncertain about the way to follow. Even though only older and therefore more experienced workers tend to leave the nest in search of provisions, these behaviours give the clear impression of being a search for a supposed food source outside the nest. It is not wholly unlikely that these behaviour patterns may be innate in *P. fulva*. However, I think that following the tracks of a discoverer once one of these patterns is seen, where tracks from other ants are often present, does not seem entirely feasible without recourse to memory.

In the observations carried out during this inquiry, once a food item was found by ants that had been deprived of food, a trail was generally established on a given area of the terrain, followed sometimes for hours on end by individual ants, going outside the nest towards the food source and back again. In every trip the ants would ingest and carry food in liquid or viscous form inside their crops, or social stomachs, to the nest. Using some devices for temporarily accommodating ant colonies, allowing for the observation of the interior of the nest, I was sometimes lucky enough to see what happened on the rare occasions in which these devices were accepted for a while as nests and the ants visited some food source outside them. Workers inside the nest would receive the regurgitated food by the external collectors and then go through different parts of the nest feeding regurgitated food to other nest-mates, larvae, the fertile queen, and, when present, newly eclosed winged, fertile individuals. Usually, the finding of a food source in the natural environment outside the nest fails to induce the formation of a trail only when workers are busy with the nuptial flight of fertile forms, or when the nest is besieged by enemy ants, damaged, being reconstructed or abandoned, or, still, when it is well provisioned.

Under the next topic I will go on with the task of identifying the factors brought into play in the determination of psychologically-mediated purposeful behaviour in ants through their exposure, especially if recurrent or habitual, to a given behaviour environment. These factors, as I hope to demonstrate, are those introduced by a mechanism acquired in the course of evolution, in addition to reflexes and fixed action patterns, allowing individuals of certain species, while dealing with their usual environments, to make use of a properly individual memory for adaptive purposes. Natural evolution has, so to speak, found out that there is no better way of predicting future events than taking into account the way past events were and ensuring that they be used when this behaviour situation is repeated. Of course, should the usual situation change, however slightly, on a given occasion, this device would be faulty and in need of correction to recover its effectiveness, in which case the use of individual memory would be not only useful, but essential.

5 OBSERVATIONS IN WHICH ONE OR MORE ALTERATIONS WERE REMOVED AFTER REMAINING IN THE ENVIRONMENT FOR SOME TIME

Under the present topic I will report two other observations that, although resulting from an initially random procedure, seem to provide, perhaps more clearly than the preceding observations, a demonstration that ants, in their habitual activities, make a continuous mnemic record of their behaviour environment. Also, these observations seem useful in that they show that this record is ultimately the source of the two other phenomena that give rise to psychologically mediated purposeful behaviour – treating aspects of the habitual environment, at each point of it, as present even before they are actually present as stimuli, and addressing these remembered aspects to achieve a required result.

- *Observation 34 – Observation of the behaviour of* P. fulva *on a trail during 4 discrete phases: I) 1 hour and 30 minutes, in which they were faced with four beans placed on the trail at 10cm intervals ; II) in the same area, after the beans were removed; III) 50 further minutes in which the same beans were again placed on the trail, in the same way as in phase I, but on another stretch of the trail; and, finally, IV) in the same area, after the beans were again removed.*

In this observation I employed a trail of about 2.80 m between the entrance of a nest and a food incentive. The trail ran along the junction of a rough cement floor and the low step of a cement staircase and a brick wall. The entrance to the nest was a gap in the junction of the floor and the staircase. The lure was a cotton wad with a low water absorption ability dipped in a sugar and water solution, placed next to the wall.

The observation covered two twin experiments, here called *experiment 1* and *experiment 2,* each of them comprising two phases: phase A, in which I observed the behaviour of the ants before each of the four raw beans placed at intervals on the trail, and phase, B, when I observed their behaviour, in the same area, after the beans were removed. Figure 45 illustrates the situations in phase A, experiments (1) and (2).

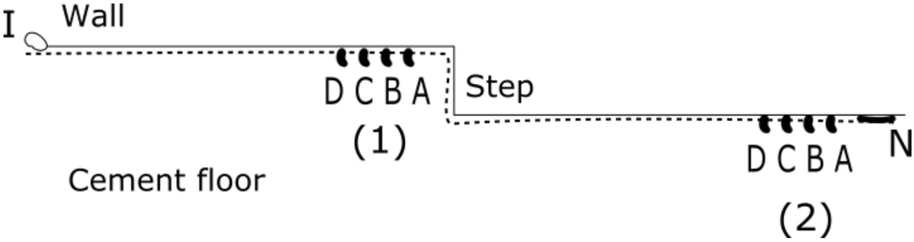

Figure 45: Approximate representation of the situation in Observation 35.

Legend:
I: incentive
N: nest.
Dashed line: trail.
(1) and (2): Position of the beans in experiments 1 and 2, phase A.
A, B, C, D: raw beans laid on the trail at two different moments.

Some thirty minutes after the incentive was positioned, a somewhat thin trail had formed, marching at a distance of about 0.5-1 cm from the junction of the floor and the wall. I sat down at a distance of 0.5 m from the trail and 90 cm from the bait. The day was cold, rainy, and very humid. It had rained all night and the sun was hidden by clouds. There was a light drizzle and the wind generally blew over the bait and then the nest.

EXPERIMENT 1

For this observation, I laid four raw beans across the trail, at a distance of 10 cm from each other, starting 160 cm away from the nest. I called these, from right to left, A, B, C, and D. My intention was to study the effect on the behaviour of ants coming and going in both directions of their coming across each of the beans, as well as the possible influence of each encounter on the next ones – a study of the phenomena called behaviour sensitisation and habituation, mentioned by psychological theories then current. As it will be seen, however, an unplanned procedure in the first experiment led to some unexpected results, which, on their turn, compelled me to replicate the experiment in search of confirmation. As I expect to demonstrate in the discussion below, the results seem to be conducive to a major finding.

RESULTS OF THIS OBSERVATION:

PHASE A

The first *fi* (an ant marching towards the bait) returned on coming across the first bean. Subsequent *fi.s* made "sniffing" motions (antennae outstretched, dorsoventral oscillation, and vice-versa) at A, and then went along either through the space between the wall and the bean, or over it, in which case they made a pause before going on. Before bean B, they paused and "sniffed" it. They did the same, though more briefly, with bean C. From then on, they went ahead between the bean and the wall, without apparently taking any notice of bean D.

I then observed the *fn.s* (ants going towards the nest). The first one went alongside D without stopping; it "sniffed" C and B, turned aside and accelerated its march somewhat, whereas, before A, it turned aside again, almost without acceleration. I observed others: the first bean to be found, D, was clearly outside the trail, and the ants progressed normally, using the space between the bean and the wall. Before the other beans, they turned aside after a pause. In either case, their march tended to undulate before the three last beans found. They might touch the beans with their antennae, but would always turn aside afterwards. They never climbed them.

Observing again the *fi.s*, I noticed that they generally paused and touched the first bean with their antennae, and then climbed and walked on it before going ahead; the action was repeated upon the finding of the second bean, although by fewer ants; by the third bean, one or other ant would sometimes pause before the bean, wag the antennae at it, and then climb it; by the fourth bean, this was hardly ever repeated, and most ants simply marched on.

I then set out to take notes on the individual behaviour of, alternately, *fi.s* and *fn.s*:

- *Fi*: It paused before the first bean and turned aside; it paused a little longer before the second bean, touched it with its antennae, and went ahead; it climbed the third bean and walked on it; it climbed the fourth bean and remained longer; then it climbed down and went sideways for about 3 cm, exploring the vicinity, before returning to the trail;

- *Fn*: it avoided the first bean, going through the gap between it and the wall, proceeded along the open floor area past the second and third beans, and went through the gap between the fourth bean and the wall;
- *Fi*: paused, climbed the first bean and remained for a while (about twenty seconds), avoided the second and the third, then touched the fourth bean, retreated slightly, and then avoided it;
- *Fn*: It went along the open floor, avoiding the first bean, hesitating before touching the second, longer before the third, then touched it, and finally hesitated longer before the fourth bean, looked as if about to return, and went through the gap between the bean and the wall;
- *Fi*: It touched the first bean, turned away and went along the open floor, hesitating by the second and the third, when it made a wider detour; then it took a detour through the space between the fourth bean and the wall;
- *Fn*: It avoided all beans without pause or hesitancy;
- *Fi*: It climbed the first bean, remained there for some time, went down and round the bean, climbed it up and down again, walked for 2 or 3 cm along the open floor; it climbed the second bean, walked on it, came down, went round it and then ahead, avoiding the third and the fourth beans with no pause at all.

A light rain started. Although the floor next to the wall was wet after ten minutes, the trail persisted, which seemed to indicate that this interference with the olfactory track presumably underlying the trail did not affect the ants any more, probably because they had repeatedly walked next to the wall and this was enough for their orientation.

I pushed bean D closer to the junction of floor and wall, since it had clearly been dislocated further away from the trail. The ants had moved the course of the trail closer to the junction at that point. I noticed that only *fi.s* climbed the beans, and would generally do it only upon coming across the first and the second bean, and tended to hesitate and pause before the third and, though more briefly, before the fourth bean, now laid right across the trail, and then finally avoided it. They also seemed to make longer detours than *fn.s,* going outside the trail for a short stretch, in an apparently exploratory way, especially when near the first beans they found. *Fn.s*, on the other hand, paused less often, made shorter detours, going through the gap between the bean and the junction of wall and floor, or along the open cement floor. It seemed clear that *fi.s* were, so to speak, more willing to investigate what they found on their way, whereas *fn.s* were clearly more intent on reaching their destination as soon as possible.

One hour and twenty minutes later, I recorded in the protocols for this observation that it was evident that, over time, the beans practically ceased to bring about modifications in the behaviour of the ants on this trail. Among *fi.s*, for instance, none was seen climbing the beans. Any hesitancy and exploration around the beans occurred only among *fi.s* and near the first two beans found.

PHASE B

This phase started when the four beans were removed from the trail, one hour and thirty minutes after being placed there. This intervention was not meant as an experimental procedure, but rather as an adequate measure to allow the trail to recover the appearance it had at the start of the observation and then repeat the observation using other objects. However, I could not help observing their behaviour in the area from which the beans had just been removed, for I wrote the following, clearly contradicting myself: "Except for one or other *fn* that went one or two centimetres outside the trail, apparently in exploration, and one that stopped to clean its antennae, a few that apparently paused briefly, stirring their antennae more vigorously, and except for one or other [among the][29] fi.s that gyrated near the first bean[30], it was as if they had not noticed the removal of the beans."

The contradiction in this comment is clearly the incompatibility of the initial reports and the claim closing the statement. It was evident that many ants now exhibited modifications in behaviour – not the same modifications observed when the beans had been positioned, but modifications suggesting they were acting as if searching for the beans or missing

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[29] [ ] My addition.

[30] Or, preferably, "near the place where the first bean had been".

them. If not all of them did it, this might be perhaps because many of them had not been more than once on the trail, something I could have ascertained had I marked individual ants. That I noticed the contradiction seems evident on what follows: “It is a pity I cannot see whether flow, speed, etc. have been affected.” The fact that I repeated the experiment using another stretch of the trail seems to support this opinion.

EXPERIMENT 2:

PHASE A

Right after the notes above, I laid the four beans across the trail again, at a distance of 10 cm from each other, but now on another stretch, starting 10 cm after the crack in the junction of the floor and step that served as the entrance to the nest. Number “(2)”, Figure 45, above, shows how the beans were placed. Once again I noticed that *fi.s* were the only ants that would initially walk on or round the first two beans they found, but in a lesser proportion than that observed in the first experiment: perhaps – I wrote – because they had already been exposed to them in the first experiment. The frequency of pausing and going round the beans of *fi.s* tended to progressively decrease from the first to the fourth bean they found. The hesitancy of *fn.s*, on the other hand, gradually increased, with apparently exploratory detours, as long as two centimetres from trail, towards the open floor, as each bean was found.

I then pushed beans D and C closer to the junction of the floor and the step, but still leaving some space between them and the junction. I noticed then that *fn.s* tended to pause by D, the first bean to be found, a little longer than before, and even longer by beans C and B, which they would pass by with a detour of about 1 cm along the floor, after oscillating briefly from side to side; before the fourth bean, A, they tended to pause very briefly. *Fi.s*, would exceptionally return upon coming across the first bean.

A little later (I did not record when), I wrote that *fn.s* seemed apparently more upset before the second than before the first bean they found: they would turn right and left, hesitate, touch the bean and proceed along one of its sides. *Fi.s*, on the other hand, seemed to hesitate more before the first bean: they would explore ("sniff") it, climb the first and second beans and walk on them more often than upon finding the other two beans. Soon the frequency of climbing decreased, and I wrote that it would certainly cease over time. I decided to leave this trail alone for a while in order to observe others in the same yard; before this, however, I noticed that a brief backward movement, which seemed caused by a sudden fright before the first bean, was more common among *fi.s* than among fn.s.

When I returned, forty-eight minutes after the beginning of this second experiment, I noticed the trail was much thinner. *Fi.s* still hesitated more than *fn.s*, especially before the first two beans. *Fn.s* avoided the beans, as did *fi.s*, but showed a definitely greater tendency to turn aside briefly, as if about to return, or to pause, turning slightly from side to side before the first bean, D, more often than before the others.

PHASE B

Fifty-six minutes after the start of phase A in this second experiment, I pulled the beans away from the trail, keeping them, however, aligned with their previous positions so as to keep them in mind.

At the two ends of the stretch on which the four beans had been previously placed, right beside the place occupied by the first bean on the trail, both *fi.s* and *fn.s* would gyrate or go as far as 1 cm away from the trail. From time to time, it was commonly observed that the ants would sometimes briefly turn away from the trail and into the open floor. Halting and "sniffing" also occurred. I wrote in the protocols that it seemed clear that the ants were somewhat "bewildered" by this stretch of the trail. Unfortunately, I did not go on with this observation, and started instead two other observations, also dealing with the behaviour of ants faced with successive experimental alterations on a trail, dispensing, however, with an observation phase in which the alterations would have been removed.

DISCUSSION OF THE RESULTS OF THIS OBSERVATION

The results of this observation may be summed up in the following way: first, the occurrence of behaviour modifications in ants on a trail when faced with certain alterations in their immediate environment, to wit, four raw beans laid at regular intervals by the trail; second, a gradual decrease and a tendency to partial or even total cessation of these behaviour modifications as they went by the beans; third, the occurrence of new behaviour modifications as the ants went through the stretch of the trail from which, in a certain moment, the four beans had been removed.

Really new results in this observation were those in the third moment mentioned above, and this was probably so only because the experiments described in the literature specialised in the effect of independent variables on behaviour – generally the introduction of a change in the environment – usually do not go beyond the second moment.

In current scientific practice, events like the first result, the occurrence of modifications in the behaviour of ants faced with the four beans placed at regular intervals on the trail, are usually interpreted as due to the *responsiveness* of an organism to stimulation. Changes in the environment, as long as they involve alterations in the energy conditions prevailing in the sense receptors of an organism, would be the causes – called *stimuli* – for the responses by this organism. An investigation into the nature of stimuli, sense reception mechanisms, neural transmission and the effector activity of organisms, is the logical consequence of this interpretation, known in scientific literature as the *S-R interpretation of behaviour* (Cf. Scott, 1972, p. 4-14).

An embarrassing question for this interpretation, a question that led me to reject it, has already been treated in the previous chapter: it did not explain how very different alterations in the environment, such as placing objects on the trail, blowing on it, projecting light and shade on it, rubbing one's fingers or menthol or camphor pieces on it, etc., *caused behaviour modifications of a generally similar aspect in the ants.* The explanation I proposed, which I think is correct, was that these stimuli did not cause the behaviour modifications directly, but through their action on a central factor or set of factors, brought into the situation by the ants, thanks to their previous exposure to a given behaviour environment. This central factor, as I think, would be a memory ants would form in their own terms, that is, in terms of the effects on them of a previous exposure to a behaviour environment, a memory that would allow them to address aspects of the environment taken as present even before they are presented as stimuli, enabling them to cease having their behaviour exclusively elicited by stimuli received and have it also conducted towards required results or objectives.

The second result mentioned – the decreasing frequency and cessation or, at least, a tendency to cessation over time, of the behaviour modifications exhibited before the beans placed on the trail – would certainly lead many researchers to mention an "extinction" or "habituation" of "responses". Since Clark L. Hull (1943), extinction has been interpreted as a reactive inhibition created by the very act of repeated responses when these are not followed by some reward. As to habituation, it was defined by Thorpe (1963, p. 54) as the relatively permanent vanishing (probably because of an innate mechanism) of a response to a repeated stimulus when this is not followed by some form of reinforcement. Other scientists, however, refuted the need for repetition, the duration mentioned, and the reference to reinforcement theory (Cf. Sato, 1995, for a discussion of habituation and the problems in its characterisation). Humphrey (quoted in Sato, 1995) supposed that the biological function of habituation would be that of preserving a behaviour pattern preceding a disturbance by eliminating useless movements. And Thorpe (1963) claimed that habituation means not responding to stimuli that are not significant for an animal's life. However, I think it would be dangerous to say that the behaviour modifications mentioned above are useless or that the environment alterations considered as "stimuli", in this case, are devoid of biological relevance.

However, I think that what is important to establish is that, contrary to what researchers generally think, the decrease in frequency and cessation of behaviour modifications in the ants does not mean that they had ceased responding to the alteration on the trail or in its vicinity. In fact, if they had, the alteration could then be suppressed and this would have had no effect in their subsequent behaviour. However, the opposite was the case: after the decrease in the frequency of modifications, it was no longer possible to remove the alteration from the environment without causing new behaviour modifications. The presence of the alteration, therefore, had become essential to normality in behaviour. Repeatedly facing alterations in the environment did not, therefore, cause them to stop behaving towards these alterations, but to gradually behave towards them in another way. This led the ants to progressively incorporate them into their mnemic record about the environment, changing them from altering elements of this environment into integral parts of it, that could not be suppressed any more without rendering the new mnemic record of effects obtained in the environment inappropriate for their addressing aspects of it that, although expected by them, were not yet present. This incorporation, therefore, was essential to their adjustment to the altered objective situation. The phenomenon of behaviour modifications exhibited upon the removal of the beans, which had lain on the trail with some intervening space between them for a prolonged period, could not have been simply caused by the action elicited by the alteration of the energetic conditions acting on the sense receptors of the ants; it could be due, in fact, as in the case of behaviour modifications caused by a sudden alteration of a behaviour environment already considered as habitual, to the fact that the presence of the alteration, once incorporated into the behaviour of the ants, could not then be suppressed without causing new modifications in the behaviour under way. That the modifications observed when this suppression was carried out differed from what they had been when an alteration was introduced can be thoroughly explained by the fact that the factor or set of factors brought into the situation was not the same. In one case, the situation did not include the alteration in the behaviour environment, whereas in the other, it did.

This phenomenon is an evidence of behaviour determined by the memory of past events and, therefore, as I see it, of psychological processes in ants – however unprecedented this may sound to many students of insect behaviour.

Notwithstanding the above, the absence of a gradual decrease in frequency and, finally, cessation of behaviour modifications before experimental alterations repeatedly faced by ants in their behaviour environment is not a necessary and ubiquitous indicator of a gradual incorporation of these alterations into the psychological behaviour situation. This is what is revealed in the observation reported below, as well as the fact that not only well conceived and executed procedures are conducive to learning, but also chance events and faulty procedures.

- *Observation 35 – Behaviour modifications consequent, first, on the successive placing of 3 cotton wads dipped in kerosene near a trail and, later, the removal of two of these wads.*

For this observation, I took a cotton wad dipped in stain remover – a kerosene-based cleaning product – and divided it into three pieces of about the same size and rolled them into rough balls with about 1.5 cm in diameter.

The trail in this observation was 2.20 m long and established on a floor with two contiguous stretches, one of cement, the other ceramic mosaic. It marched close to a brick wall and connected the entrances of a nest (two separate orifices in the cement floor) and a food incentive (a cotton wad dipped in a water and sugar solution). The observation was carried out at night, under the light of an electric bulb, placed on the wall, 2 m above the nests.

Twenty seven minutes after the start of the trail, I placed a cotton wad dipped in stain remover, A, one of the three I had prepared, 60cm to the left of N_1, 1.5cm from the junction and 1.3cm from the trail. Then, after 28 minutes and 63 minutes, respectively, I placed the two remaining previously prepared, identical (about 1.5cm across) wads, B and C, at identical distances from the junction, in such a way that the wads were 32 cm apart. Ten minutes after the last alteration (placing of C), I removed wads B and C, leaving the first one, A. Figure 46 shows the layout of the trail and relevant aspects of the situation.

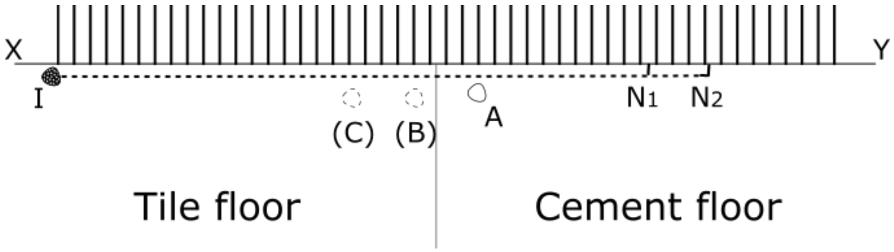

Figure 46: Approximate representation of the trail and other aspects in Observation 35, Part 2.

Legend:
I: incentive.
N_1 and N_2: orifices providing access to the nest.
Dashed line: trail.
XY: junction of cement and mosaic floor, and wall.
(C) and (B): dotted circles: removed wads.
A: wad preserved next to the trail

I must say that before the two wads were removed the ants still exhibited behaviour modifications while going past the wads, despite the time elapsed: basically hesitancy (halting for a while, briefly turning to left and right, as well as undulation in the course of some ants while going past one or more wads).

The effects of the removal were surprising. Some ants, while passing by the tiny humid spots left by the removed wads would hesitate, exhibit more pronounced undulation in the march, and sometimes stop and return for a moment, "sniffing" as if – I wrote in my records – "they noticed the absence of the wads". Five minutes later the stains had disappeared, and even then some ants would go outside the trail for a while. Some of them paused. I saw one of them walk some 5 cm outside the trail, that is, about 10 cm before the spot where wad C had been; others, both *fn.s* and *fi.s*, at regular intervals, went 1 cm outside the trail, stopped, and turned round; in some places along the trail, some ants exhibited unexplained undulation in their march, pauses, and a sort of upward investigation ("sniffing"), during which they stood only on their medial and hind legs; sometimes they would also go 2 or 5 cm outside the trail towards the open floor and the wall – and this when they were 10, 15, 30 cm from the lure and the places previously occupied by the wads. On the other hand, between the only remaining wad, A, and the entrances to the nest, except for some behaviour modifications near the wad, regularity prevailed: there were no pauses, returns or departures from the trail. I noticed that now many ants would hesitatingly approach the lure, go up the wall and proceed for 10 cm or more beyond the wad or walk round it for a while before climbing it. On the stretch between wad A and the lure, the occurrence of intermittent progress (alternating brief forward motions and pauses) as well as one or other jolt, was more frequent with ants at different parts of the trail other than the stretch between the wad and the nest.

I interrupted the observation of this part of the experiment after 20 minutes, in order to carry out another observation, not to be considered here, but not before witnessing an *fn* that, having marched 25 cm from the lure, was literally thrown back and upwards by two vigorous jolts. I then wrote in my records that the presence of wad A seemed, by and large, to "tranquilise" the ants, for, in fact, no behaviour modifications were observed to its right

DISCUSSION ON THE RESULTS OF THIS OBSERVATION

This observation shows that, over time, the ants started to include in their behaviour environment the alteration posed by a succession of wads dipped in kerosene placed next to the trail, even though still showing they were disturbed by them: after a while, the wads could no longer be removed without causing behaviour modifications, and these would be different from those that had been caused by their introduction and continued presence. Therefore, a conclusion seems to be clear in this discussion: that a gradual mitigation of behaviour modifications coming from successive encounters with certain alterations in their habitual environment, as seen in the preceding observation, is not an essential and necessary simultaneous counterpart to its being mnemically recorded by the ants in their own terms – that is, according to its effects on them – and then used in some way in their exchanges with the environment.

This realisation gave rise to two questions. First: why, in one case – the experiment with raw beans – did the ants' incorporating the presence and features of the beans into the mnemic record of their behaviour environment lead to an adjustment to their presence over time, to their ceasing to exhibit behaviour modifications when near them, whereas it did not in the second experiment, when cotton wads dipped in kerosene were employed? The second is: what is the role of these new elements in the behaviour of these ants as they are introduced into their psychological environment?

Let us consider the first question. A comparison of the two experiments shows that they differed especially in two aspects: in how the objects used to alter the environment were temporally introduced, and the intrinsic nature of these objects.

Now consider the first aspect: how the objects employed to alter the previous behaviour environment of the ants were temporally introduced in the experiments. I think it is possible that the introduction of experimental alterations at intervals, in the experiment with cotton wads dipped in kerosene, in contrast with the experiment employing raw beans, did not leave enough time for the phenomenon of gradual mitigation of behaviour modifications caused by a previously introduced alteration.

Let us now go on with the second aspect in which this observation differs from the preceding one: the different nature of the objects introduced. It is true that, in both experiments, the sudden introduction of objects new to the ants' behaviour environment immediately caused behaviour modifications. This occurred, as already said, partly because, whatever the nature of these objects, they were not part of the memory the ants had brought into their present behaviour environment, and this, when they were immediately before the area in which the objects had suddenly been placed, prevented them from finding the aspect or element toward which they would head, based on their recollection of what they had habitually found when in their habitual behaviour on the trail. They would only resume their march along the trail upon coming across it at a spot in which the environment was the same as the behaviour environment they had habitually experienced before. In addition to this, however, it seems also to be the case that these objects also had a part in altering the behaviour environment because of their intrinsic stimulating properties. Regarding these, differently from the cotton wads dipped in kerosene, the raw beans used in the first experiment do not seem to be in themselves, I think, aversive to ants, since, on coming across one of them, a scouting or foraging ant would probably not avoid or get away from it, as they did upon facing cotton wads dipped in kerosene. It does not seem unlikely that, for the ants heading towards the bait and with an ingestive motivation, the beans might even have some potential value as food, notwithstanding their being a behaviour-modifying element, for not having been included into the mnemic record of their previous behaviour environment. In fact, as seen in Observation 35, some of the ants would even climb some beans on their way, apparently in exploration. I believe that if this did not happen with ants moving the other way it was probably because, besides the fact that the beans disturbed their use of memory in their handling of the situation, they had also fed and no longer had an ingestive motivation: differently from *fi.s*, they seemed to be in a hurry to transfer the food they had collected to their nest-mates inside the nest, and, for this reason, handled the beans suddenly found on their way as obstacles to be avoided. However, in the experiment in which cotton wads dipped in kerosene were used to alter a habitual situation, the ants would avoid the kerosene-soaked wads more clearly than they did on suddenly coming across the beans, and, on going past them, would take a detour closer to the wall. These facts suggest that the raw beans, although disturbing the use of a recollection of a previous situation in the ants' orientation, were probably affectively neutral or even attractive to, at least, part of the ants, and that the kerosene-soaked wads, on the other hand, were definitely aversive. These conclusions seem to be reinforced by the preceding observations: the first, in which it was seen that kerosene made the ants avoid a favoured food item on their coming across it; and the last, by observations such as those in the preceding topic, in which the ants on a trail would eventually, and after repeated encounters, cease to exhibit behaviour disturbances before a food incentive, at another spot of the trail and with a higher concentration of sugar: therefore, with a higher incentive value than that of the lure they had been visiting further away from the nest.

In short, I would say: it seems that the fact that a given object, suddenly introduced in an already habitual behaviour situation, has intrinsic properties that make it neutral, aversive, or attractive to the ants, does not prevent it, after some time and repeated exposure, from being incorporated into their behaviour situation and then help to define it. Apparently, however, it will also affect the way they will respond to it, that is, with relative indifference, aversion, or attraction.

And now, the other question raised by the realisation that the ants in the two observations just reported, on being repeatedly exposed to alterations in their behaviour environment, would gradually incorporate them into the memory they had formed of the environment. The question was: What role would these new elements incorporated into the ants' psychological environment have in their behaviour?

The answer seems to be pointed out by what happened to their behaviour upon the suppression of the alterations, that is, two out of three cotton wads dipped in kerosene and placed at different moments on the trail, in the latter observation, and the raw beans in the former. In both cases, the removal led the ants, on the one hand, to apparently search for the suppressed objects, and, on the other hand, created an embarrassment to their dealing with the new situation, as if it had become different from the previous one. One would say, on seeing their behaviour, that the objects, by the time they were removed, had ceased to be elements altering their behaviour situation and already become part of it.

6 THE PHENOMENON OF INCORPORATION OF ONE OR MORE ALTERATIONS IN A BEHAVIOUR ENVIRONMENT INTO THE ANTS' MNEMIC RECORD OF THIS ENVIRONMENT AFTER THEIR PROLONGED AND REPEATED EXPOSURE TO THEM. THE PSYCHOLOGICAL ORGANISM AND THE BEHAVIOUR ENVIRONMENT AS A SYSTEM OF MUTUAL TRANSFORMATIONS

The various facts discussed in connection with the two observations reported above – the occurrence of behaviour modifications when ants are faced with sudden alterations to their trail and adjoining areas, followed or not by their gradual mitigation and a tendency to cease over time and after repeated exposure, and the occurrence of new modifications upon the suppression of the alterations – as a whole and in this precise order, reveal and demonstrate the phenomenon which in previous works (Cunha, 1985, 1986, 1989, and 1995) I called the insects' "functional, regulatory, or psychological adjustment to the immediate environment", a designation that perhaps should be replaced with "updating" of the mnemic record to a given behaviour environment.

In fact, if not in this way, how could an organism exhibiting behaviour modifications before a sudden alteration in its behaviour environment start to exhibit totally different behaviour modifications upon the sudden suppression of the alteration, unless by being gradually modified through exposure to the alteration, in such a way as to include it into the mnemic record of its behaviour environment? As already explained, purposeful behaviour, as observed on a foraging trail, is only possible thanks to the mnemic record of a given behaviour environment allowing the ants, at every point of the trail, to head towards the next point in the sequence until they reach their required destination – the lure or the nest. With the sudden introduction of an alteration into the behaviour environment, the expected point from which to proceed to the next one is missed, interrupting and disorganising the ants' habitual behaviour until a new mnemic record of the behaviour situation is formed, enabling the anticipation of what is to be found in the modified area.

What is the process through which the organism updates its mnemic record of a given behaviour environment, or, in other words, what is the process through which a sudden alteration in the environment is incorporated into its behaviour situation?

As pointed out in the previous topic, a sudden alteration in the ants' habitual behaviour environment causes behaviour modifications the outcome of which will vary over time and after repeated encounters, according to its affective nature. So, when the alteration seems to be affectively aversive, as in the case of a cotton wad dipped in kerosene, behaviour modifications tending to avoidance persist even when the alteration is incorporated into the new mnemic record of the ants' behaviour environment. On the other hand, when the alteration seems affectively appealing, as when a new lure, of the same nature as the first, is placed on the trail, either nearer the trail or, especially, when it is more nutritious, the ants will prefer this to the original lure. Finally, when the alteration seems affectively neutral, as in the case of the raw beans sparsely laid along the trail, the behaviour modifications it causes gradually abate over time and then disappear. Among these three cases, the third seems to allow for a better understanding of what happens during the process of mnemic updating of a behaviour environment driven by a sudden alteration on the trail or in its vicinity, and that is why I will take it for consideration in the arguments presented below.

If behaviour modifications caused by a sudden alteration in the ants' behaviour environment are mitigated with their repeated exposure to this alteration this must be so because each exposure modifies the organism and the next one acts on the traits of the previous one(s) in a cumulative way. Each new exposure would have a lower modifying value, until, at some point along the sequence of exposures, or after some time of exposure, the alteration would not reach the critical threshold value needed for modifications to occur. At this moment, we could say that the organism has converted an alteration in its environment into a non-alteration of its situation, or has incorporated the alteration into its situation, or still, that it has adjusted, gauged, readjusted to it. A proof is the fact that it was no longer possible to suppress the alteration without triggering new behaviour modifications. .

The adjustment mechanism being discussed – which I call "psychological" because it is attained through an individual animal being exposed to, and being modified by, an altered situation – would turn an alteration that is repeated in a given behaviour environment into a non-alteration, and a non-alteration, within a series of alterations, into an alteration.

However, in order that each exposure may have a lower effect, it seems necessary that the organism react, not directly to the energy stimulating the alteration, but rather to the relationship, either of difference or similarity, that the new situation bears with the situation prevailing so far. Or rather, since the previous situation does not strictly exist at a given moment, it is necessary that the organism react to the difference that the new, altered situation bears with the behaviour situation corresponding to the situation before it was altered and brought into the present through the marks left by exposure and previous adjustments. The organism and its behaviour environment, in opposition to what is assumed by S-R psychologies, cease to be independent entities acting on each other from outside, and then constitute a system of mutual transformations. Given this system, the organism enters History, not only as a historical entity (that is, an entity determined by previous conditions), but also, according to Heidegger (1967), as a "historial" entity, that is, as an entity that, given its history, contributes to the determination of its conditions. In fact, each exposure of the organism to a given environment, on changing the organism, makes the following exposure, even though physically identical, not strictly the same as the first as regards its effects on the organism. This being so, and since, strictly speaking, each organism modified by its previous experience – and which, therefore, may be called psychological – has a different stimulation history, it might be said that each of them will turn a situation which, although having a number of aspects in common with other individuals of its species, into a situation that, given certain aspects, is strictly individual and unique.

It should be mentioned that the responsiveness of an organism capable of functional, regulatory, or psychological adjustment to a given environment alteration (or, in other words, the modifying effectiveness of a given behaviour alteration) cannot be known independently from the adjustment environment of this organism. Since the psychological organism and its behaviour environment constitute a system of mutual transformations, it must be said that, for this system, the environment, in physical terms, to which this organism is exposed generates a behaviour situation which cannot be defined without the participation of the organism, which, on its turn, cannot be known, as regards its behaviour possibilities, without considering what its previous environments had been. A behaviour situation is dynamic, that is, it changes over time, for it will always reflect the adjustments and new exposures the organism – a historical and historial entity, as pointed out – may come to experience. It will also reflect the tendencies, states, and regulatory operations of an organism at a given time.

7 ANOTHER BIOLOGICAL FUNCTION OF THE PSYCHOLOGICAL ADJUSTMENT, OR MNEMIC UPDATING, MECHANISM IN THE FACE OF ALTERATIONS IN THE ANTS' BEHAVIOUR ENVIRONMENT: FREEING A GIVEN USEFUL EXCHANGE BETWEEN THE COLONY AND ITS ENVIRONMENT FROM EXTERNAL INTERFERENCES

Considering again the two experiments reported above, it may be said that the ants had already evinced a relatively stabilised relationship with their behaviour environment and its various elements, to wit, their nest, the floor and wall, their collective path and nest-mates, food, light, wind, etc., before being affected by a sudden change in the environment. Through one of these relationships they would, for instance, forage for the colony and for themselves. The introduction of one or more alterations into their behaviour environment would trigger behaviours differing from those that had been established towards this environment. Over time, however, through a process of gradual readjustment, a new relationship of the ants with their behaviour environment would be established, through which provisioning of the colony would be resumed. The new element in this relationship seems to be the fact that, over time, the ants started to include in their memory of the new environment aspects of their new path expected to follow from other given aspects. This allowed them to resume the behaviour directed to reaching a required goal by heading from one spot to another in the series of spots remembered as comprising the route towards the goal. The adjustment process considered here, therefore, has the function of freeing an organism's relationship with its behaviour environment from external interference. And it does so by turning these initially disturbing elements into essential elements, assumed as present even before being found, necessary for the later unaltered occurrence of this relationship.

Based on the features I have just pointed out, I find that the phenomenon of psychological adjustment mentioned above can and must be considered as a specific case of biological adjustment: an organism's ability of adaptive modification when faced with variations in its environment, a modification in consequence of which this organism may persist as a system of norms, tendencies, and response mechanisms. This ability neutralises variations in the environment which might otherwise threaten the organism with dissolution, and, by doing so, they turn these variations into something essential for the organism's survival. In fact, as already mentioned in another work (Cunha, 1985), we can take, for example, a well-known case of adaptation to changes in the external environment: the annual development before winter of fur with a greater power of thermal insulation, which allows many mammals living in temperate areas to survive extreme cold. However, this same fur will make the animal not adapted to its environment and threaten its survival during an anomalous winter: developing this fur in the absence of cold will pose a threat of suffocation, unless other adaptive mechanisms are activated, such as an ability to perspire, look for cooler locations, etc. In the case of psychological adjustment, which allows the ants to rid an adaptive relationship to a given behaviour environment of external interference, it also seems clear that there are mechanisms intended to interrupt the exposure of the ants to potentially dangerous alterations in the environment, such as overheated substrates, enemy ants in the vicinity, etc.

8 AN ILLUSTRATION OF THE COMPLEXITY OF STUDIES ON PSYCHOLOGICALLY PRODUCED BEHAVIOUR IN ANTS: THE EXISTENCE OF UNSUSPECTED EFFECTS OF A MNEMIC RECORD ON THE BEHAVIOUR MODIFICATIONS EXHIBITED BY THEM WHEN FACED WITH SOME INSTANCES OF STIMULATION

At this point in the investigation, I think it is important to report two other observations that perhaps demonstrate, better than the previous ones, how ants – at least the ants of the species considered here – keep a record of their individual experiences which will affect, in a significant and even unpredictable way, their later behaviour when they are faced with the same situation. The phenomena revealed by these observations are sufficiently surprising and important to justify my choice of these reports as an end to my treatment of the factors pointed out as underlying the behaviours exhibited by ants on their usual trails, the alteration of which give rise to the phenomenon of behaviour modifications. These are two observations carried out on the same day, the first using *Solenopsis saevissima* Fremont-Smith, 1885, and the second, inspired by the facts seen in the first observation, with *Paratrechina fulva* Mayr, 1862. These observations are reported below.

- *Observation 36 – Behaviour modifications in Solenopsis saevissima* Fremont-Smith, 1885 workers on a usual trail, in two discrete phases*: A) after marking them with paint, and, B) after blowing on them from above.*

The trail in this observation connected the entrance of a nest – a crack in the junction of a cement floor and the wall of an outhouse – to an orifice in the same junction, some 3 m away, at the end of the outhouse, proceeding underground for about 50 cm under a wall, and then emerging again onto the floor. From this point the trail headed towards a rubbish bin (with kitchen scraps) which was daily placed on a square cement platform. Figure 47 illustrates the situation.

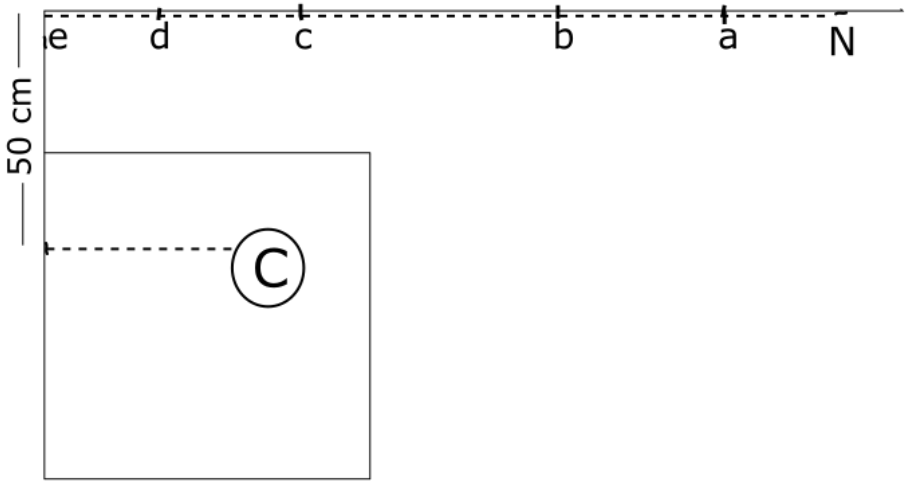

Figure 47: Approximate representation of the trail and other aspects of the situation in Observation 36.

Legend:
N: entrance to the nest
Dashed line: trail
Square: cement platform C: container with kitchen scraps
a, b, c, d, e: points of the trail referred to in the text

I suppose the path was chosen for safety reasons, so as to prevent ants from going astray and as a defence against the dangers of a march through an unsheltered area. In fact, the preference for forming trails along stimulation heterogeneities formed by the junction of two different surfaces, or by gaps and cracks in the floor, as well as for sheltered paths, seems to be very common, perhaps because, in the former case, it is easier not to miss the target, and, in the latter case, because it is less vulnerable to external alterations. As for the latter case, observation shows that ants will give up following the trail more frequently right after coming out of the nest, when there is a sharp transition from a relatively stable environment to a variable one, than after their having gone over a good stretch of it. That the two visible parts of the trail belonged to the same trail was shown by the fact that only ants coming out of the orifice next to the wall and towards the nest would carry fragments of food. The observation was carried out from 3:00 p.m. to 4:00 p.m. under sunlight.

In the first phase, (A), of the observation, in order to be sure that the ants marching along the two visible stretches of the trail were really the same, I decided to use a straw dipped in white shoe paint, to mark the dorsal area of workers walking next to the outhouse wall near the nest and towards the incentive, the container with kitchen scraps. With very few exceptions, the ants, as soon as painted, turned away and returned to the nest. Since this suspension and reversal of their march seemed to be motivated by safety concerns, I also marked the ants near the wall and walking along the junction of floor and outhouse towards the nest. These ants also turned away and returned to the underground stretch of the trail, but exceptions were more frequent. I thought that again safety was the reason. In fact, when going out of the orifice on the corner of the wall and the outhouse, a number of ants would spontaneously turn back, while others would hesitate before going ahead, suggesting that, in any case, facing daylight or going outside were somewhat unnerving tasks for them.

I then decided to mark ants on the rubbish bin and the stretch between it and the point where they emerged from the wall. A number of them would roam around the area, as if disturbed by the marking, but many of them returned to the hole in the wall or entered the container, when they were on it. It so happened, however, that I did not see any ant marked in this stretch of the trail coming out on the corner of the wall and the outhouse (point “e”, Figure 47) and heading to their distant nest. These marked ants, therefore, tended to remain in the sheltered area of the trail.

I noticed that the ants marked on the head were the most disturbed: they would always turn back and even lose their bearings. Those marked on the abdomen, especially those going to the nest along the junction of the floor and the outhouse wall did not turn back. I also noticed that the ants marked on the abdomen near the incentive were the least likely to interrupt their previous activities, although, like the others, they generally raised their gasters and seemed about to bite the straw used to paint them.

Generally speaking, since none of the ants marked far from the incentive remained outside, and those marked in its vicinity did not reappear on the stretch of trail close to the outhouse, I concluded that, having undergone an unexpected interference with the trail, they tended to leave it for the shelter and avoided coming out for some time, and this was certainly motivated by safety.

Forty minutes after these records, I resumed my observation of the trail; there were no marked ants on the stretch next to the outhouse, and two were found in the area between the container and the wall.

In the second phase, (B), of the observation, I carried out an experiment with very interesting results. I started to lightly blow on some ants on the stretch next to the outhouse. I noticed that in all its extension, except for the 25 cm or less from the orifice leading to the underground part of the trail, on the corner of the wall and the outhouse, the ants walking from the nest to the wall, on being blown on, returned more often and definitely, whereas those going towards the nest, undergoing the same alteration, would return to the orifice more often only when at a distance of 25 cm or less from it. Outside this range, they either turned back briefly and then resumed their march or, after pausing for a while or accelerating, went ahead towards the nest in the junction of floor and outhouse. At any point more than 25 cm away from the orifice on the corner of the wall, the ants coming from the nest towards the orifice would return more often the more they had distanced themselves from the nest. At a distance of 50 cm from the nest, something interesting occurred: all the workers come out of this nest returned on being blown on, and this “for good” (in other words, they entered the nest and were not seen coming out for more than half an hour). On the other hand, none of the ants coming out of the orifice on the corner of the wall and towards the nest returned when blown, except for a few, and then only when I blew harder, and only for a short stretch.

In short, and considering Figure 47, above, I may describe the effect of blowing on *Solenopsis saevissima* ants in this way:

- on the 25 cm-long stretch of the trail between “e” and “d”, instances of return among *fn* ants (ants going towards the nest) were more frequent than among *fi* ants (ants going towards the incentive), which were either non-existent or short-lived;
- on the stretch between “d” and “c”, differences between *fn.s* and *fi*.s were barely noticeable;
- on the stretch between “c” and “b”, about 1 m long, instances of return were more frequent among *fi*.s;
- on the stretch between “b” and “a”, instances of return among *fn*.s were rare or short-lived; and, finally, between “a” and N, there was no return among *fn.s,* whereas all *fi*.s *returned.*

Given the results in the two phases of this observation, I thought I might conclude that the workers on the trail under observation had a cognition of both the direction they were following and their distance from both ends of the trail (the nest and the incentive), and that the nest served as a shelter and safe place. And more: that the underground sections of the trail were sought as a refuge when the ants underwent sudden alterations in the external environment. Along the middle section of the trail the ants, upon being blown on, would hurry into a small cavity or crack in the substrate, where they would stay for only a few seconds, since they were not totally isolated from the external environment. I noticed that the two orifices next to the wall seemed to have the apparent function of shelter or safety. This observation gave me the idea for the next observation, which I report below.

- *Observation 37 – Behaviour modifications exhibited by* Paratrechina fulva *Mayr, 1862 on a trail when under a soft and as uniform as possible breath reaching them from ahead and above from a constant distance of about 35 cm.*

The observation, as the previous one, was carried out in the evening of the same day, with a 3.20 cm-long trail of *Paratrechina fulva* in a kitchen. The trail connected a cotton wad dipped in sugar to two nests of the same colony – a main nest, with the entrance in a crevice of a door frame, and a secondary nest, with the entrance some 15 cm up the wall, in a hole in the junction of two tiled walls. The bait was placed on the floor, next to the junction of floor and wall. Seven points of the trail were chosen, at which the ants were to be blown on. Figure 48 illustrates the situation.

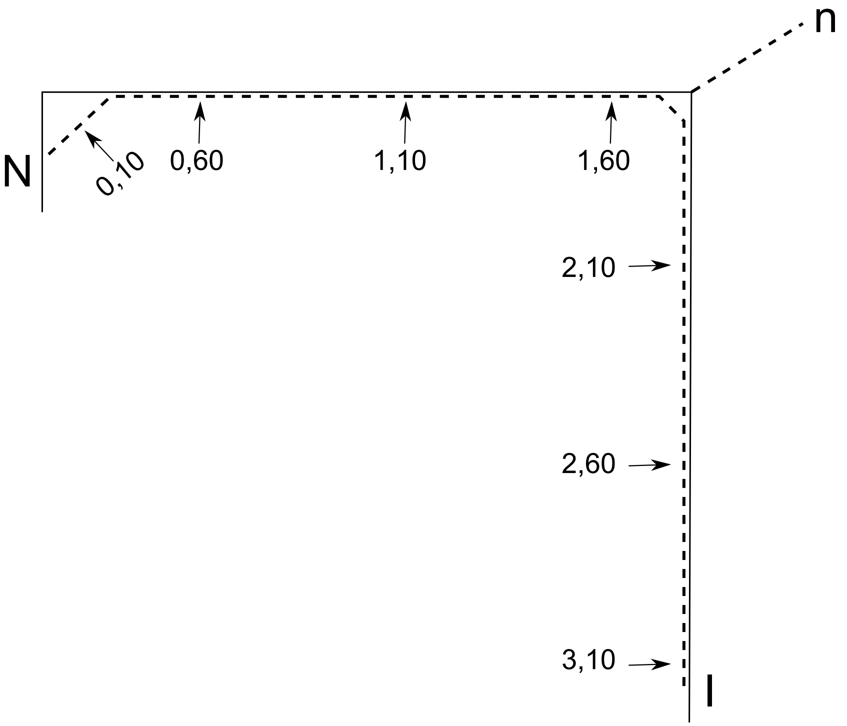

Figure 48: Situation in Observation 37.

Legend:
N: main nest
n: secondary nest
Arrows: spots from which the ants were blown on and distances from the main nest
I: incentive.
Dashed line: Trail

For this experiment, the spots where I was to blow on the ants were randomly chosen, at the following distances from the main nest: 1) 1.10 m; 2) 2.60 m; 3) 10 cm; 4) 3.10 cm; 5) 60 cm; 6) 2.60 cm; 7)

2.10 cm. I chose to record data only for those ants which, whether going towards the incentive or the nest, on being blown on – an occasion when all ants would halt for a while – either returned, totally or partially, or proceeded along their original course. Partial returns are those cases in which the ants went as far as 15 cm back before resuming their original course. The results of this observation are shown in Table 13, below. It must be pointed out that I blew more on ants going towards the food than on ants going towards the nest, and this was because I was mainly concerned with the behaviour of the former.

Data categories	**Point at 10 cm** **Nfi= 88** **Nfn= 68**		**Point at 60 cm** **Nfi= 74** **Nfn= 43**		**Point at 110 cm** **Nfi= 90** **Nfn= 76**		**Point at 160 cm** **Nfi= 74** **Nfn= 46**		**Point at 210 cm** **Nfi=117** **Nfn= 80**		**Point at 260 cm** **fi= 72** **fn= 46**	
	Fi	*fn*	*fi*	*fn*	*fi*	*fn*	*fi*	*fn*	*fi*	*fn*	*Fi*	*fn*
Return	75	0	59. 5	0	62.2	5.3	24.3	0	53	25	32.6	2.1
Partial return	9.1	2.9	9.5	2.3	14.4	1.3	10.8	4.3	3.4	25	10.5	0
Continued march	15.9	97	31	97.7	23.3	93.4	64.9	95.7	43.6	97.5	56.7	97.7

Table 13: Percentages of ants, marching in both directions of the trail, that returned, either temporarily or definitely, or went ahead, upon my lightly blowing on them from each of the seven points selected on the trail.

Fi= ants going towards the incentive.
Fn= ants going towards the nest(s).
Nfi= number of fi.s blown on when reaching the spot.
Nfn= number of fn.s blown on when reaching the spot.

By examining this trail, we see that most of the ants at a distance of as far as 110 cm from the main nest and heading towards the incentive reversed their course on being blown on, whereas most of the ants going towards the nest went on along their original course. At 160 cm away from the main nest, precisely halfway along the trail for ants going either way, most of the ants tended to keep their course. At the two points farthest away, however, *fi.s* tended to return more often upon being blown on than when halfway along the trail. Undoubtedly, this was because the three points farthest away from the main nest were precisely those where not only ants from the main nest were to be seen, but also ants from the secondary nest, which tended to return to this nest on being blown on.

By the way, even ants coming from the main nest, further away, were seen to retreat into this secondary nest, a sign that they had memorised its location. I see this results as an indication that the ants on this trail had a record of their previous experiences on the trail that allowed them to: 1) estimate the distance to each end of the trail at every point at which they were blown on, and, 2) keep a memory as to the specific nature of their goal – nest or food – prompting them, generally, towards the food only when this was nearer than the nest, which, apparently, had a far greater appeal as a source of safety and shelter than the incentive.

A major point to be stressed in this observation is that blowing on the ants, although it was a physically uniform action at all spots where it was carried out, was, if we consider its effects on their behaviour, not always the same stimulus for all of them, but a very different one, depending on their direction and their distance from the nests and the incentive. From this point of view, one might say that the behaviours exhibited by the ants on being blown on, although the distribution and features of the stimuli acting on the response mechanisms involved were the same, seemed gratuitous and arbitrary, as psychologically mediated behaviours in humans, in which the response triggered by the stimuli – a ball or a telephone, for instance, as already mentioned – is not direct and immediate, but generally dependent on a specific set of motivations and experiences that can and do vary from individual to individual.

The fact that blowing on the ants was a sudden alteration of their usual behaviour environment certainly had to do, as already claimed, with the behaviour modifications exhibited. Therefore, on dealing with the results, I tried to find out whether the frequency of returns among ants I blew on decreased over time. To do so, I compared the number of returns and instances of continued march among ants walking towards the incentive and blown on at the first two and last two positions out of a total of seven positions used on the trail. I thought that the decrease of returns and increase of instances of continued march were to be expected because the smell of my breath would gradually linger on the floor, in such a way that blowing on ants that had already gone through this experience would not alter their behaviour environment as strongly as it would alter the behaviour environment of ants that had not. One might also think that some ants, even many of them, after being blown on and returning to the nest would later enter the trail again and undergo the same experience. Apparently, however, this was not the case, for as I observed, after the return of a number of ants to the nest, the trail was gradually thinning out. Data for the comparison of results at the first two spots and the last two spots of the series, in which the average distance covered in each stretch was 1.85m, are shown on Table 14, below.

	At the two first positions	**At the last two positions**	**Total**
Return	84	38	122
Continued march	70	95	165
Both	154	133	287

Table 14: Number of ants that returned or continued their march towards the incentive upon being blown on from at the first two and last two spots in Observation 38.

The chi-squared distribution of these results was of 19.70 – indicating that over time there was a decrease in instances of return and an increase in those of continued march, statistically significant beyond the level of 0.01 per cent.

In short, I think the results from this experiment allow for a number of important conclusions. They show that the act of blowing, in physical terms, was not the same for all the ants in the experiment; they also show that it was not even the same stimulus for a single ant along its way; and more, that it was not even a *stimulus* in the sense adopted by current behaviourist trends, that of a *correlate* – of whatever species considered: elicitor, reinforcer, discriminating, or conditioned reinforcer – of *response*, because it was not exactly to it that the ants were responding so diversely; and, finally, because each ant was not itself a stable response-system throughout the experiment. In fact, the ants proved, regarding the way they tended to respond, one thing when going towards the nest, and a very different one when going towards the food, and the variation was connected not only to the distance from the ends of their course, but also the time since blowing had started. Therefore, talking of an ant as a response system, as if it were an entity existing separately from the effects of its relationship with the pre-existing environment seems totally inappropriate.

The effect of the alterations carried out in the ants' behaviour environment, and made as objectively the same as possible, seemed to depend on their positions in relation to a whole set of elements in the environment which – surprisingly – seemed not to be even present any more as stimuli when the alterations occurred. These manipulations of the experiment, that is, blowing on them, served as probes to assess the state and properties of the relationship the animals had with a current environment regulated by their relationships with past environments rather than as exciters or response elicitors. However, the apparently simple character of the behaviour modification observed – pausing for a while, waving the antennae, and then either going ahead or returning – might induce a heedless observer to see this behaviour as a direct response to the stimulus ("independent variable") employed. I am sorry to say that most experimental students of behaviour – ethologists and psychologists – have often acted like this. And this because they have adopted a system for interpreting behaviour that considers environment and organism as separate and independent entities, acting on each other from the outside, rather than as a system of mutual transformations.

9 On how to explain the particularly dramatic effect of one or more ants being crushed, especially on a trail, on the behaviour modifications of their nest-mates

One question to be conveniently raised before the end of this chapter is why, among all interventions carried out during this investigation on the ants' habitual environment, the crushing of one or more of their nest-mates, or the presence of their remains on a trail gave rise to the most dramatic behaviour modifications among the remaining ants. I must admit this is a difficult question, about which I can only venture some considerations in the way of hypotheses.

Under preceding topics in this chapter, I have developed some arguments to demonstrate that the behaviour exhibited by *Paratrechina fulva* on a foraging trail was the result of an underlying mechanism made up of three phenomena exhibited by them upon their repeated exposure to a behaviour situation: a mnemic record of their previous experience with the situation, a preparation, made possible by this record, enabling them, upon coming across each aspect or element of this situation again, to assume as imminent and inescapable the presence or occurrence of the aspect or element that, in the past, had regularly followed the element or aspect now being found again, and, finally, should the ants be properly motivated, their heading towards this aspect or element even before these are actually present as stimuli. These three phenomena would be the essential steps in purposeful, psychologically mediated behaviour – behaviour directed towards a goal apparently in the future, but which has in fact been retrieved from the past. The creation of this action mechanism would reveal, I think, how the evolutionary process, on the basis of an animal's repeated experiences with a given environment, could make this animal, upon a renewed encounter with this environment, not only consider the aspects and elements actually perceived on the occasion, but also prepare for those he had learned or got used to perceive as regularly following the same stimuli acting at that moment, and head towards them even before they were present, and from these to the next again and again, until the desired and expected outcome is finally attained. This action mechanism would be, I think, the outcome of natural selection over a probably long evolutionary period which eventually complemented the action repertoire of many animals, adding, to the mechanisms of reflex and fixed-action patterns, that of purposeful psychologically-mediated action.

Under this assumption, it should be pointed out that, since natural environments are not stable, it may so happen that on a given occasion an altered behaviour environment may be similar enough to the one that gave rise to this mechanism, and trigger it again, in which case an erroneous retrieval will take place some time. The observations on the behaviour of ants in this work show that a number of courses of action were possible at the moment. In some cases they might change their course (for instance, by taking a detour at some point in the environment when a small object obstructed their way), or be hindered in their march and either lose their bearings or return, or, still – as seen, for instance, when they came under a patch of light or shade on the trail – hesitate upon entering the altered area a few times, until the establishment of a new record of the altered environment, allowing them to proceed without hesitancy.

Well, my favourite hypothesis for explaining why crushed ants or their remains had a far more dramatic effect than other alterations in triggering disturbed behaviour is that, since ants are highly sociable creatures, their nest-mates are probably the most familiar objects in their behaviour environments. Inside their nests, ants frequently touch each other with their antennae, lick each other, and exchange food through regurgitation. I do not think it unlikely that a memory derived from these interactions, however far back in time, is a part of their experiences as they go on along a trail, as well as, probably, a memory of the repeated encounters with their nest-mates along the trail. Therefore, it seems to me that crushing an ant is a particularly effective way of altering their nest-mates' behaviour environment, since it places an obstacle or intrusion in a previously unblocked path, a still object where there had been movement, and replaces familiar with altered and unfamiliar – apparently repulsive – odours. Strictly speaking, I do not know whether the ants could recognise a crushed body or remnants of it as those of a nest-mate, but, if they did, this certainly would, given the set of alterations it would represent, help explain why this alteration, more than the others carried out in this investigation, hinders the use of an acquired memory of a previous behaviour situation. Natural selection may have endowed ants with an attitude of avoidance and flight in the face of this alteration, which definitely indicates a probable threat to their lives.

Of course, a second hypothesis might be ventured at this point. Most myrmecologists now working would say that their response to the crushed body or remains of a nest-mate is caused by alarm pheromones, released as the ant was crushed. I do believe this could be so, but then, we would have to admit, in opposition to what these researchers say, that the behaviour supposedly triggered by these substances is not necessarily made up of dramatic alarm responses, automatically elicited, and not modulated by any other fact or condition. And this because, as already shown in this work, when the crushing takes place at a distance of only 0.5 cm from the trail, the behaviour modifications exhibited by the ants on the trail are considerably less dramatic than when the crushing takes place right on the trail, and this is incompatible with the property these researches ascribe to alarm pheromones: that of being quickly and widely spread in the air round the area where they are released. In this way the pheromone emissions would reach the ants on the trail with full force, and, as we have seen, many of them turned towards and even approached the crushed bodies and remains on noticing them. It should also be mentioned that, besides the results from a number of early observations in this research, showing that alarm pheromones are not *necessary* for the occurrence of alarm responses in *Paratrechina fulva,* the results from Observation 20, in which ants were crushed on one of the branches of a doubly-bifurcating trail, led to another major conclusion: that these substances – should they actually be present – are not *sufficient* for this, at least in the absence of other conditions. On the other hand, the realisation that there was an alternative for action, that is, another, unaltered trail in the behaviour environment in this observation, or one single trail, unhampered and unblocked by crushed ants nearby, certainly favours the first hypothesis over that of an automatic action of alarm pheromones.

Finally, a third and last attempt to explain the issue under this topic is a hypothesis suggested by the findings and theoretical considerations of the Canadian psychologist Donald O. Hebb in his investigation of fear responses in chimpanzees (Cf. Hebb, 1946, and 1949, especially chapters VII and X).

In his investigation published in 1946 Hebb reported that a whole series of objects not employed before in their specific form, such as representations of animals, from reptiles to humans, with varying degrees of completeness and verisimilitude, gave rise to “fear responses” in chimpanzees, such as flight from the object, and other indicators of unusual excitement such as bristling, screeches, defecation, etc. He also reported that, of all objects employed, those representing primates with a conspicuous deformity or abnormal feature (as a chimpanzee skull with mobile jaws and detached from its body, a plaster mask representing a human or a chimpanzee, an anaesthetized chimpanzee, etc.), caused the most dramatic responses. According to the author, these results might be included in the category of “fear of the unknown”, together with other phenomena previously described by other scientists, such as fear and aggression in anthropoids when facing their usual caretakers wearing unusual clothing, or unknown people and objects, which can also be occasionally observed under certain circumstances in immature humans.

The new facts in the research were those related to the fear evinced by chimpanzees when faced with the adulterated bodies of humans and conspecifics. After further observations, Hebb could see that this fear did not originate in details in the procedure or objects employed, but seemed to be caused by the immobility or lack of parts in the objects, something apparently related to the avoidance of dead and mutilated bodies of conspecifics in humans.

This fear, according to Hebb, was "spontaneous": it was not learned, in the sense of being built through association with a further removed cause for fear, since it occurred when the organism was faced with the object for the first time; however, it was not innate, either, since it occurred upon the first presentation of the object only when the animal had already experienced "normal", unadulterated objects of the same class; in this sense, however, it was partially dependent on learning (or, rather, on the effect of previous experience). Also, this fear did not originate in a property of sensorial excitation, because it is obvious that a "physical absence" does not generate stimuli. Also, as already mentioned, emotional responses did not occur unless the animal had been exposed to the same class of objects, but in a normal state, that is, not before some central perceptions or ideas had been very specifically established. According to Hebb (1946, p. 274), these and other fears are not caused by a sensory event alone, since, in order to be so, one would have to assume a joint action of sensory and central autonomous processes. Consequently, it is not possible to clarify the nature of fear and generalise on its causes on the basis of stimulation factors only. Based on these considerations, Hebb concluded that the fear of mutilated bodies, as well as of unknown objects in general, occurs when an object, similar and dissimilar in many aspects to familiar objects, determines incompatible or conflicting processes in perception. The especially dramatic responses of chimpanzees (or humans) on facing dead or mangled bodies of conspecifics, therefore, would result, according to Hebb, from an exceptional familiarity with normal bodies of the species.

This is a generalisation that, I think, cannot be accepted in its entirety. Looking at domestic utensils deformed in some way – such as dishes and saucepans with altered shapes in an arts and crafts fair, manikins depicting people, animals, and ordinary objects in altered proportions – is unlikely to produce fear, but, rather, aesthetic responses. The sight of the injured body of a neighbour after an accident, someone frequently seen, but with whom we exchange nothing but greetings, will certainly be shocking, but, perhaps, not as shocking as the sight, under the same circumstances, of the injured body of a brother living far away and hardly ever seen during one's lifetime. Therefore, it seems that an interest in the object or its significance for the spectator will always be involved in some way with the response.

Returning to Hebb, for, having found out that, besides the perceptual conflict, other factors – of sensory deficit (such as a fear of the dark, observed in children with little exposure to environments under this condition) and, especially, constitutional and maturational factors – may also cause fear and anger, he considered (Cf. 1946, especially p. 268ff.; 1949, p. 147 ff., and chapter X) that a proper explanation for these behaviours could not be formulated only in psychological terms, and should make use of physiological concepts of brain activity. For this reason, Hebb undertook to formulate his own theory for addressing the question, stated in terms of reverberating traits or processes involving various circuits in the central nervous system. I think, however, that we might agree with Thorpe (1963, p.173) who said it was doubtful that the nervous system of insects might contain the multiple circuits claimed by Hebb to be found in the far more complex nervous system of chimpanzees.

The application of Hebb's hypothesis to the problem discussed here, leaving aside its neurological aspects, is clear: the especially dramatic nature of behaviour modifications exhibited by ants faced with the crushed bodies of their nest-mates, greater than any other alteration carried out in their familiar environment, would be caused by a perceptual conflict stronger than those observed in other cases, given the exceptional familiarity of the ants, eminently social creatures, with the normal bodies of their living nest-mates. Now, one might say the first hypothesis presented under this topic coincides with the one derived from Hebb's in that it is based on the assumption of a familiar-unfamiliar perceptual conflict. However, it should not be forgotten that, under the first hypothesis, this conflict caused behaviour disturbances in the ants not directly, but indirectly, by precluding their use of a mnemic record they had been keeping while acting their way through a given behaviour environment as they had habitually done before the alteration. For instance, in the observations under topic no. 5, when ants were crushed 0.5 cm away from the trail, behaviour modifications were far less dramatic than those exhibited when their nest-mates were crushed right on the trail, notwithstanding the fact that, in the former case, many ants would halt, turn towards the alteration, and wave their outstretched antennae at it, instead of fleeing right away, as in those instances when the ants were crushed on the trail. And this was apparently so because, in order to orient themselves and reach an objective, they had established a reliance on an olfactory track, rather than on what lay outside it. Similarly, as seen in Observation 20, ants crushed on only one of the branches of a doubly-bifurcating trail caused behaviour modifications which were far less dramatic not only in comparison with those on the unaltered branch, but also with those in which a single trail was employed. And this was so because, as already shown, many ants on the adulterated branch of this doubly-bifurcating trail were not as dependant on the olfactory track they were following as the ants on a single trail. This was so because they had a mnemic record of a nearby branch of the trail, so much so that they would start from a spot on the wall, go through a trackless space, and reach the other branch. As for the hypothesis based on Hebb's claims, which does not postulate the use of an acquired memory of the factors that the ants had become used to finding on the trail, it would be difficult to explain the facts in this observation. These findings are one reason why, among the three hypotheses presented, the first is probably the most well grounded, even though still in need of further development and a better demonstration.

CHAPTER IV

ON THE FORMATION AND TEMPORAL EVOLUTION OF FORAGING TRAILS IN *PARATRECHINA FULVA* ANTS AND THE PROBABLE FUNCTIONS OF TRAILS IN GENERAL IN THEIR LIVES

1 GENERAL OBJECTIVES OF THIS CHAPTER

In this chapter I am going to expose some observations that I think have allowed me to find out events and also trends and capabilities in virtue of which *Paratrechina (Nylanderia) fulva* Mayr (1862) and other ant species a) form foraging trails for their colonies, and, b) over time, effect transformations in the trails and in their own behaviour while on them, which generally result in a more efficient exchange with their environment. Finally, I also intend, on the basis of these observations and others previously reported, formulate some hypotheses on the functions that trails, not only foraging trails, probably have in the lives of these insects and which would probably be the reason for their advent in the course of evolution.

2 OBSERVATIONS ON THE FORMATION OF A FORAGING TRAIL IN *PARATRECHINA FULVA* AND SOME OTHER SPECIES

I had often noticed that placing a food item favoured by ants in the vicinity of their nests or other areas frequented by them was enough to induce the establishment of a trail. Generally, one or more ants, having found and ingested the food, returned to the nest and in some way induced nest-mates to head towards the site, either on their own or following the discoverers. Since, however, the presence of several ants in these places posed difficulties for the observation of what was going on during the establishment of the trail, I decided to select another site, unfrequented by the ants of a given nest.

To induce the formation of a trail under these conditions, it was necessary that some ant would head straight back to the nest after ingesting the food selected as an incentive. To do so, I relied on one of the following procedures: place a favoured food item in front of a worker outside the nest, wait for it to climb it, and then carry both to the selected site; or, differently, capture one or more ants found roaming round the terrain and take them to the site of the bait. The latter was used more frequently, since it precluded the risk of leaving signs of food that might compete or interfere with the establishment of a trail starting at the selected point.

In order to capture an ant walking in the vicinity of the nest I generally placed on the substrate, as already mentioned, two strips of paper – afterwards replaced with two pieces of cardboard the size of a business card, more appropriate for the function – before and behind the ant. What generally happened was that, while trying to avoid the piece of paper or cardboard in front, it would climb the one behind, and then I would carry it to the bait.

Not all ants captured in this way remained on the piece of paper or cardboard. Some of them, as soon as they found themselves on it, would start rushing around and fall to the ground. In these cases, I found out that as much as I tried, it was generally useless trying to recapture them, for, as soon as I did it, they rushed to the edge and, rather than fall off the trap, would deliberately jump to the floor. Most of them, however, either did not run or slowed down, and walked as if in search of their previous substrate; I then directed the piece of paper or cardboard, tilting it towards the bait as the ant approached one of the edges, in order that it could notice the bait and climb it. One or other ant would rush over the bait without noticing its nature. Most of them, however, approached the bait, paused, and while still on the piece of paper or cardboard, started sucking the solution contained in it by protracting and contracting their glossae. On these occasions, they suddenly seemed to be in a sort of trance, and so absorbed and concentrated that they apparently did not notice the slight oscillations of the paper or cardboard I involuntarily produced while holding it. They did not even react on being touched with a straw dipped in white paint, which I sometimes used to mark them, unless it touched their antennae or cephalic area.

A problem with both procedures was that these forced discoverers would hardly ever return to the nest without facing a number of incidents along the way, and those that managed to do it, could rarely return to the incentive. These difficulties were natural, since they had not reached the food through their own efforts, and were not familiar with the site where it had been found. Another problem was the difficulty evinced by the ants, on being warned by the discoverers, to follow them from the nest, or whatever place they happened to be, to the site where the incentive had been placed, which was due mainly to the insufficient tracks left by the discoverers, and also to their insufficient or non-existent experience with the area in which the food had been placed. This is what I will try to show by reporting a few complete observations and, for the sake of brevity, parts of other observations that revealed punctual difficulties; all of these were carried out in a single location: a patch in the garden of a rented house where I once lived and devoted myself especially to the study of trail formation.

The central feature in this location was a tap on a wall, on which I would sometimes lay a food incentive. It stood 60 cm above the junction of the wall and the cement floor, along which were frequently seen *P. fulva* ants belonging to two associated nests: N_1, the main nest, with a 15 cm long opening on the wall, extending from a point in the junction of the cement floor and one of the two beds comprising the garden, the one nearest to the house; and $N_{2,}$ under the water metre cabinet, in the other bed. The two beds, partially covered with grass, were separated from the cement floor by a 5.5 cm wide and 1 cm high concrete ridge. Figure 49, below, is an approximate representation of the scene.

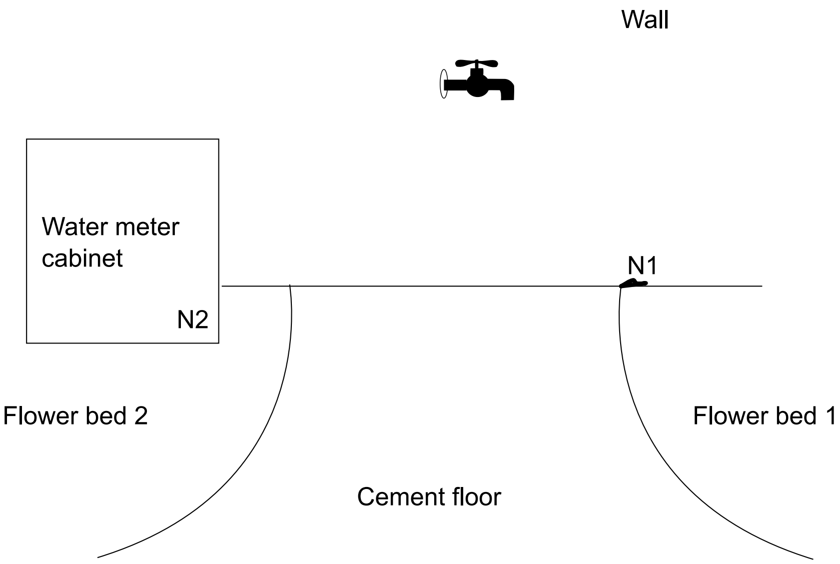

Figure 49: Approximate representation of a patch in a garden where observations on events involved in trail formation were to take place.

Legend:
N_1: Main nest
$N_{2:}$ Secondary nest

The observation below is reported in order to illustrate the difficulties mentioned above.

- *Observation 38– On an attempt to induce the formation of a trail of* Paratrechina fulva *extending from a tap on a garden wall to a nest in the same wall opening up close to the soil of a flower bed.*

The first worthwhile observation of how *Paratrechina fulva* ants establish a trail was carried out in the area described above on a day with intermittent drizzle, after three successive rainy days. The ants had disappeared for a few days, and their nest had been occupied by a colony of *Solenopsis saevissima* Fremont Smith, 1885, which I had seen leaving the bed some three days before. The *P. fulva* ants – if they were really the same – had apparently reoccupied the nest. Considering the succession of rainy days, I thought they should be highly motivated towards food, and, therefore, in an ideal state for a study of how they would form a foraging trail. At 7:30 p.m., I placed a piece of a fresh sweet with a topping, both of them wet, on the tap on the wall. At 7:43 p.m., as the drizzle abated, I captured an ant near the nest on a piece of newspaper and carried it to the incentive. The ant hesitated on the edge of the paper, placed its forelegs on the piece of sweet and started feeding; it was so intent on the activity that it would not even pause as I slightly dragged it while trying to remove the paper; finally it left the paper and climbed the bait. Its gaster became gradually bloated and transparent, and soon exhibited alternate yellow and brown bands. It then walked on the bait, "smelling" it and the tap; it stepped onto the tap nut, returned to the bait and again to the tap, but now to the spout, where it remained for quite a while; then it left, returned, and left again, climbed the nut and went back and forth round it; it left for the wall, circled the bait, returned to it and then to the tap, where it climbed the shaft and went round it a few times, until leaving again for the wall, where, upon being attacked by a sort of gnat , it rushed in the direction opposite the nest for a few centimetres, and started going down the wall. There, it met a nest-mate, and they touched each other's antennae and locked their jaws for regurgitation. I thought the ant receiving the regurgitated food might be one of the workers that had been on a trail formed 67 days before, walking towards a dried-up piece of sweet left on the tap nine days before, which had then been soaked during a heavy shower. I had not been able to see the formation of that trail. However it was, during all that time, I had not seen any ant on the wall and under the tap.

After four minutes of regurgitation, the discoverer of the food started down the wall, but returned for a few centimetres to touch its nest-mate; the latter, which could be distinguished by the absence of bands in its gaster, went up the wall, above the area covered by its mate, but not exactly following the same route, which I had marked with a pencil: it stayed 5 cm away from it, sometimes intersecting it by going back and forth, and walking in circles, going as far as some 20 cm beside the pioneer's track, some 20 cm above the tap and 30 cm to its side; then it came down to almost ground level, and resumed its march upward, nearer the pioneer's course, but independently from it, going up to 5 cm above the incentive, until it found the sweet close to the wall and climbed it. These facts made me think that the discoverer of the bait, not knowing where it was, probably did not mark its return path with an intentional scent track, but with the track it would invariably always leave during its normal march.

The "discoverer" spent sixteen minutes to return to the nest. At 8:10 p.m., two ants left the nest and walked along a stretch containing the probably unintentional tracks of the discoverer, exhibiting a behaviour identical in all aspects to that of the ant that had first followed the discoverer, sometimes downwards, sometimes upwards, but always near the pioneer's track. One of them apparently gave up, whereas the other found its way to the bait, reaching first the sweet sticking to the wall. At 8:15 p.m., as this ant reached the incentive, two other ants started up the wall along the 18-20 cm stretch holding the tracks of the discoverer; they proceeded by going back and forth over it, and would frequently roam around or retreat, distancing themselves from each other as far as 20 cm, until they got together again and went ahead, now one, now the other at the front; one ant reached the topping, while the other reached the sweet, after a 3-minute march. At 8:21 p.m. two ants left the incentive, going down the stretch containing the original track, not using it for their orientation, however, whereas the third ant on the incentive left it by first going up the wall. At 8:23 p.m., apparently after the arrival of the returning ants in the nest (I did not witness it), a group of six ants went up the wall, following the course taken by one of the returning ants, a path which I had marked, and reached the bait. A group of three ants came from lower down, but one of them returned. A heavy drizzle started, and I could not take notes in the site. At 8:30, a trail was practically established on the wall.

In short, this observation revealed that there was a general, though not strict, dependence on the tracks of preceding ants, either up or down the wall. There was, as it were, some dislocation along the strip of terrain containing the track of a nest-mate as a dominant feature, but the ants did not blindly follow the track in all its details, either when going down or up. The various ants did not follow one single track, but proceeded “on their own”, going in circles and exhibiting different kinds of dislocation.

A very interesting fact is that most of the ants coming from the nest (nest no. 1, Figure 49) along the cement floor, following its junction with the wall, missed the spot where they should go up and reached the ridge bordering the second bed and followed it for distances of 5cm to 35 cm. They would then go back and step up the wall at the same spot, except for a few that went straight back to the nest. If they had been following specific tracks left by ants returning from the bait, why should they go astray and cover distances varying so much from individual to individual, instead of going straight up the wall on reaching the right spot for that? Could it be due to a factor in perceptual organisation such as the one originally named by Max Wertheimer as the “law of good continuation” (Cf. Köhler, 1929; Koffka, 1935, p. 153, *passim*)? This factor, natural in the constitution of human beings, would lead them, for instance, on seeing two lines crossing at a given point, to perceive the line they had fist happened to follow – usually the longest – as being whole and, on being intersected by the other, as proceeding in its original direction, rather than as a line deflected on reaching the intersection point and having the intersecting line as its continuation. I believe that their missing the turning point from floor to wall might also be due to the habit the ants had probably developed of frequently going over the path along the junction of floor and wall, sheltered from water, extending from the main nest to the secondary nest, and the point in question would eventually be found on their way back because, after their mistake, they would be continuously intent on finding it.

The paths followed by the ants soon after reaching the location of the bait and before they became linear are approximately represented in Figure 50, below.

The return path followed by the second ant returning from the bait to the nest was preferred to those followed by other ants.

At 9:15 p.m., the vast majority of the ants going towards the bait went straight up the wall; only a few would go on for a while and then return to the point where climbing started. An interesting fact was that many ants would now go into and out of an orifice (represented by "O" in Figure 50) in the wall and next to the floor, some 40 cm away from the hole used before, and part of their way was now sheltered and out of sight.

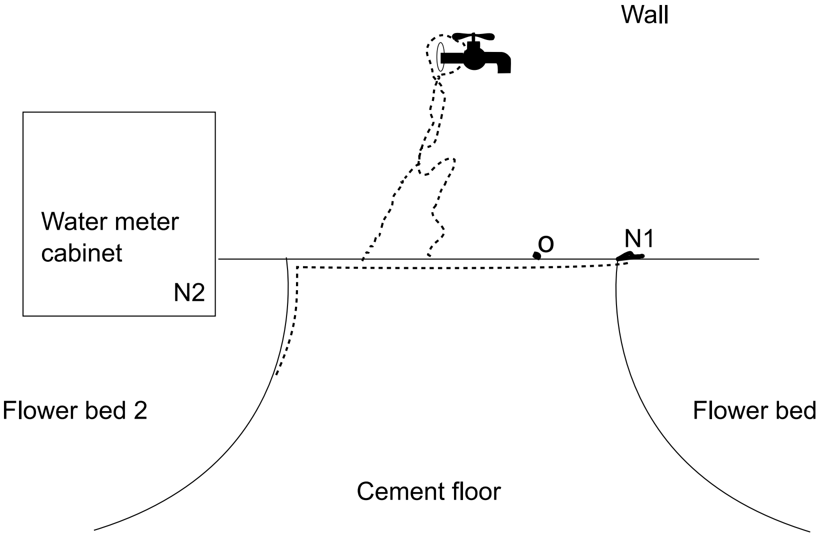

Figure 50: Representation of the path established by the ants after finding the food and before it became linear.

Legend:
Dashed line: trail
N_1: Main nest, the only active one at the time
$N_{2:}$ Secondary nest
O: Orifice serving as exit and entrance to the nest by the end of the observation

I now offer an account of other punctual difficulties faced during the attempts to establish a trail in areas not habitually frequented by the ants. The most common difficulty was when the discoverer of the incentive on the tap fell off the wall to the ground. The fall caused an interruption of its track over a stretch extending from a spot on the wall to another one on the cement floor. Finding the latter spot prompted the scouts coming from the nest and surroundings to look for its continuation on the floor and even, though more rarely, on the area of wall next to its junction with the floor, but this was not enough for locating the rest of the track. The search for the incentive took a few individual ants several minutes and sometimes, perhaps because of severe food deprivation, about two hours, and on these occasions they would cover the area of the cement floor next to the wall, the ridges separating the beds, and, finally, the soil and grassy area in the beds, even though they were very distant from the discoverer's track. As for the discoverers that fell off the wall, after entering the nest and returning to the vicinity of the wall, they seemed at a loss on how to climb it and eventually gave up the search. Most interestingly, on their return to the nest they went through a strip of the terrain containing their own tracks, which, however, they did not follow; the impression was that they could not perceive them.

One common difficulty in the establishment of a trail was the fact that some ants, even when in search of the continuation of a discoverer's track interrupted by its fall, could not find the food incentive, even when I collected them on a paper and laid them straight on the discoverer's path, marked on the wall with a pencil. Even though they proceeded along this path, perhaps because of tracks left by the discoverer, they would soon turn either right or left and move away and lose track of it, sometimes returning to the floor and leaving the wall for good. One of the ants I placed in this way proceeded along the discoverer's path without many mistakes and reached a spot 4 cm away from the incentive, when it then went down the wall without noticing it. Another ant, placed in the same way, after going down the wall for a while, reached the discoverer's path and followed it somewhat more thoroughly and at a slow pace, sometimes moving some 3-4 cm away and then returning; it eventually found the bait, a piece of wet sweet, but could not climb it since this was not contiguous to the wall. It roamed about and further away from the finding, went a full circle and then reached the discoverer's path and went down, a move I found not quite clever but that seemed to make sense for the ant. Then, some 40 cm away from the bait, roaming round apparently in search of it, the ant ended up on the floor, where I lost it among the others. I placed another ant on the discoverer's track, 10 cm below the incentive. After going downwards for a while, this ant, like the one before it, started going back towards the bait, following quite thoroughly the discoverer's path, but with pauses and brief lateral excursions, as if probing for the objective. It walked behind the incentive, at a distance of 1.5 cm, apparently without noticing it, and then went ahead, roughly following the circular piece of the path marked on the wall, as seen in Figure 51 below, and finally reached the piece of sweet, which, after my intervention, was no longer contiguous to the wall.

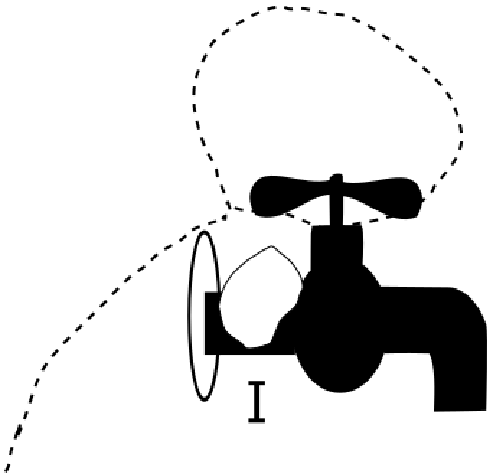

Figure 51: Illustration of part of the path of an ant that had discovered an incentive on a garden tap.

Legend:
I: piece of wet sweet used as an incentive
Dashed line: the first ant's path, marked in pencil.

Another flaw on the discoverer's way back to the nest was due to an instance of predation. An ant I had placed on the bait fed on it and was walking along the wall, when I had the impression that it was trying to enter an orifice. I soon noticed my mistake; the ant had stepped on a thread, part of a small web spun from the orifice and was being dragged inside by a small spider, probably an *Agelena*. This is a small spider that covers the front and inside of cavities with a blanket-like web, made with the sticky threads extruded from its spinnerets. When I tried to pull the ant out it was already dead.

This may seem a rare event, but it is not. On another day, in an orifice among a number of them on the same wall, I saw a small spider of the same species about to jump at an ant I had placed on the incentive on the tap and was now returning to the nest; I barely had time to block the spider inside the orifice with a piece of wet sweet. On another occasion, in a different place, I saw a black jumping spider approach a trail and then run away. Later, I saw another jumping spider, with a smaller, yellow body banded with black, and white palps, standing on a rainwater pipe, apparently intent on watching the procession of *P. fulva* ants on a trail on the wall near the pipe. Figure 52, below, illustrates the situation.

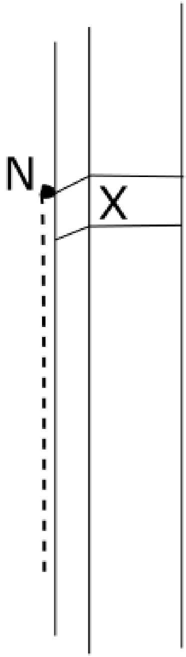

Figure 52: Representation of a trail of *Paratrechina fulva* (on a wall, beside a rainwater pipe) being watched by a jumping spider.

Legend:
N: ant nest in the wall
X: jumping spider
Dashed line: ant trail

The spider seemed to be paying close attention to the procession of ants next to the pipe, and, with quick movements, turned towards one or other among the many marching ants, especially those with plumper abdomens, and then looked as if about to strike. It remained like this for some minutes, perched on the pipe, turned towards the entrance to the ant nest, located on the wall, next to the pipe, and then moved to the surface of the pipe perpendicular to the wall, where it then resumed its watch. Twice it attempted rushing at ants larger than the average, but halted suddenly, as if frightened by other fast approaching ants. It came down the pipe and half hid at a spot further away from the trail, on the corner of two surfaces of the pipe – the upper one, parallel to the wall, on which the spider had settled, and the one perpendicular to the wall – apparently "on the lookout" for an approaching *Camponotus* ant, well larger than a *P. fulva*, which made it retreat and hide out of sight. As another *Camponotus* headed towards the spider, apparently by chance, the spider retreated as if "frightened", crossed the trail, and stood on the other side watching the ants. I was then called by someone and had to interrupt the observation. I think the spider would be successful in predating an ant if it happened to come across an isolated *P. fulva* just leaving an incentive it had been induced to discover.

As a conclusion to this topic, I will report again, in greater detail, another observation during which I was surprised at finding out another reason, in addition to those above, for *Paratrechina fulva* ants, however highly motivated towards colony provisioning, failing to establish a trail towards a food item that had been highly appreciated on other occasions.

- *Observation 39 – An attempt to induce* (P. fulva) *ants to establish a trail towards some refined sugar placed at some spots round their nest, the failure of which was apparently due to their having previously found a more appealing food item.*

One thing I was curious about was whether a trail of *P. fulva* was invariably formed, as I had observed, by some workers following an ant on its leaving the nest for a new visit to a food source it had previously found, or, differently, whether there was some more complex and refined form of communication involved. What I had in mind when considering this possibility was the amazing form of communication, discovered by Karl Von Frisch (1950), used by European honey bees to inform their nest-mates about the location of a food source they had found. This communication involved a ritualised dance in the hive, with genetically-fixed symbolic elements, indicating the direction and the distance to the food source, to be interpreted by the concentrated bees and used upon their leaving the hive. I believe that selective pressures on bees led to a more refined communication system than that of ants because following the discoverer of a food source in their case – involving flight and covering a few kilometres sometimes – is less likely to succeed than in the case of ants, which can find their food sources by walking not too far from their nests. I cannot say, however, why I thought this observation might reveal some more complex form of communication among ants. However, I report the observation because, as we have already seen, an observation like this, even when badly planned, can teach us a few things.

In a relatively cold evening (about 15° C), in order to attract the ants, I placed four low mounds of refined sugar in the scene represented in Figure 53, distributed in the following way:

1. On the concrete ridge separating the first bed from the cement floor, at a 90° angle to the wall, taking the centre of the nest entrance as a reference;
2. On the cement floor between the two beds, 60 cm away from the entrance to the main nest, at a 110° angle to the wall, taking the centre of the nest entrance as a reference;
3. On the same cement floor, 80 cm away from the centre of the entrance to the main nest, at an angle of approximately 140° to the wall, taking the centre of the nest entrance as a reference; and, finally,
4. On a thin wooden strip with the corners covered with cotton and placed on the garden tap.

Figure 53, below, illustrates the situation.

The ants in the main nest were active and marched on the floor, next to the junction with the wall until they reached the corner of this wall and the concrete ridge bordering the second garden bed; thence, already joined by ants from the secondary nest, they headed towards a piece of a spongy sweet in the second bed, probably thrown in from the street. I knelt down on the cement floor opposite the tap, at a safe distance from the incentives so as not to interfere with the activities of the ants that happened to reach them.

At 8:40 p.m., a *P. fulva* ant reached incentive no. 2, climbed it, came down, circled it, reached one of my shoes, came back to the mound of sugar and headed for the main nest noticeably faster than the ants on the trail next to the wall. At 8:50 p.m., since no other ant had visited the mounds of sugar, apparently because they were totally absorbed by the sweet in the flower-bed, I removed it so as induce them to give up this route and develop an "interest" in the other incentives on coming across them. I also dug up the soil where the sweet had been in order to suppress any remains and keep them away from arriving ants. There was no *P. fulva* near the four baits I had set.

At 8:53 p.m., two *P. fulva* ants, moving in circles, passed between incentives no. 2 and no. 3 without noticing them. One of them returned to the nest in three minutes, and the other in four minutes. At 8:56 p.m., a *P. fulva* zigzagged past incentive no. 2, reaching as far as 1 cm from it. Two minutes later, another *P. fulva* also went past the same incentive, at a distance of 1 cm, reached one of my feet, went back towards the incentive, almost rubbing against it, and then went to nest no. 1.

At 9:00 p.m. a *P. fulva* climbed incentive no. 1, on the ridge bordering the first flower bed, and remained there, apparently feeding. Three minutes later, another one reached incentive no. 2, circled and then stood on it. At 9:04 p.m. an ant went over bait no. 1 and a little further ahead, waving its antennae, as if in exploration, and then returned to the bait it had gone over, at the same time as the ant that had been on it returned to nest no. 1. One minute later, the ant on the second mound left towards the nest, but halted on the way and returned; it walked on the mound where it had been and circled it at a distance of about 10 cm, returned to it, walked towards the nest, and then returned towards the bait, reached one of my feet after coming across and touching another ant, that went past the bait and away. The ant on the first bait, in its turn, left it and went the direction opposite the nest. Figure 53 illustrates the situation.

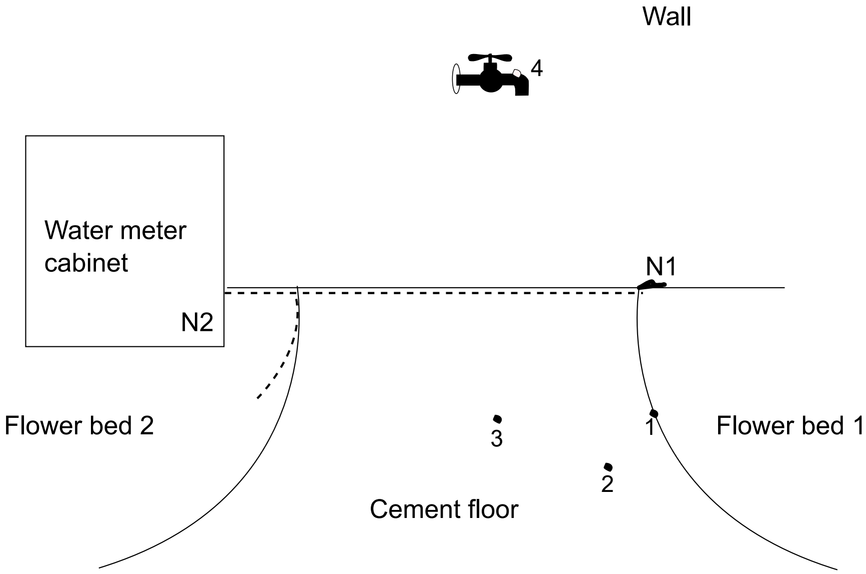

Figure 53: Approximate situation before Observation 39 in a piece of garden.

Legend:
Dashed line: trail already established before the observation
1, 2, 3, and 4: mounds of refined sugar used as baits to attract ants and induce the establishment of foraging trails

At 9:10 p.m. the ant on the second bait walked round it, covered about 20 cm towards the nest, and then I lost it among the other ants. Apparently it did not return to the nest. Another ant went past the first bait, at a distance of 3 cm from it, and did not halt.

At 9:15 p.m. there was a *P. fulva* on incentive no. 1 and another one on incentive no.2. The ant on incentive no. 1 returned to the nest; that on incentive no. 2 came near my feet without a stop, returned to the bait, and covered a 10 cm-radius circle round the bait, came near my feet again, going further away from the nest until I finally lost sight of it. Meanwhile, the trail between the two nests and close to the wall persisted.

At 9:18 p.m., a *P. fulva* went as far as 3 cm from the first incentive and stood still for two minutes, moved slowly, and stood practically still and away from the sugar for another two minutes. At 9:22 p.m.

another ant climbed the third mound, went near my feet, and then returned to the third mound. As for the first ant mentioned above, it remained still in the same place. The ants on the first and second mounds returned to the main nest. At 9:25 p.m. the ant that had stood still by the first incentive went back to the nest without touching it. Now there were several ants walking between the main nest and the second and third incentive, but they soon moved away.

These scenes were repeated until 9:36 p.m. Since the sugar mounds had been placed round the main nest 56 minutes before, time enough for one of them to originate a foraging trail, I wondered if this was because they were still searching for the probably more appealing spongy sweet. At 9:37, in order to ascertain whether this was the case, I placed a cardboard circle holding a bit of the sweet on the concrete ridge next to the first bed, 20 cm further away from the main nest than the first mound of sugar.

One minute later, a *P. fulva* went past the first incentive till it was 5 cm ahead of it when it then returned for a while, entered the bed and followed the ridge until it reached and climbed the sweet. Another ant, walking on the ridge, away from the nest, also found and climbed the sweet. There were practically no ants between the three mounds of sugar on the floor and the nests. At 9:40, a third ant climbed the sweet as one of the two ants already there left for nest 1, going slowly over the first mound without stopping. At 8:43 p.m., four ants, roughly aligned, left the nest and followed the inner surface of the ridge next to the first garden bed until they reached the sweet. At 9:45 p.m. another ant followed the same route used by the preceding ants and reached the sweet. At 9:46 p.m. an ant returned from the sweet to the nest as another ant hesitatingly approached it. Scenes like these went on until 9:53. I provide below a minute by minute account of the number of ants coming from the nest to the sweet and from the sweet back to the nest, all of them following the inner surface of the ridge bordering the bed. The symbol > stands for coming ants, and < for returning ants:

- 9:55 p.m.: > > < < (1 halted when on the sugar)
- 9:56 p.m.: > > > > <
- 9:57 p.m.: > > > > > > > > > > > > > < (all coming ants did it as part of a single group)

- 9:58 p.m.: > > <
- 9:59 p.m.: > > > > > > > < < (The ants came in groups of 2 or 3). (Some proceeded in circles; one of them arrived from a direction opposite the nest)
- 10:00 p.m.: > > < <
- 10:01p.m.: > > > > < (I gave up observing the other incentives)
- 10:02 p.m.: > > > > > < < <
- 10:03 p.m.: > > > > < < < < (The last returning ant, after a while, went back towards the sweet)

Twelve minutes later, 59 ants had come to the sweet, and 41 had returned to the nest, six of which coming back to the bait after covering part of the way to the nest. Some of those reaching the sweet would walk round the bait or run to and fro, apparently very excited. Meanwhile, only two ants remained on the first mound of sugar. The trail went past the mound at a distance of 1 cm, but no ant would stop. I scattered the sugar on the ridge, on the ants' path, and also on the soil in the bed, so that the ants visiting the sweet could not help finding it. Consequently, some ants going to the nest or from it would stop and linger for as long as two minutes. Although ants started to gather at this point, the trail towards the sweet was established again and the ants showed a clear preference for it. It should be noticed that the former incentive, the scattered sugar, was in a better position in terms of distance to the nest and ease in marking a path.

I think their preference for the sweet over the sugar was the fact that it was damp whereas the sugar was not, since the food ingested by *P. fulva* is generally restricted to liquid or viscous substances, even when they feed on dead arthropods. At 10:35 p.m. there were no ants on incentives no. 2 to no. 4, and the sweet was visited by five times more ants than the sugar on the ridge and the soil in the bed. Apparently, as the sweet gradually dried it lost its attractiveness to the sugar as this was gradually dissolved by the damp soil. The trail between the two nests persisted, but not as crowded as those towards the sweet and the sugar from the first mound.

I think the most curious fact in the observation was that a practically collective memory of a food item preferred to another, less distant and perfectly acceptable on its own for foraging, discouraged for a long time the establishment of trails towards the latter. *Paratrechina fulva* ants are, like all ants, as myrmecologists always say, instinctive creatures, but also heavily influenced by their individual past histories.

To finish this topic I will relate an observation carried out in a place apparently unfrequented by ants and not conducive to the preservation of tracks left by them during their normal march.

- *Observation 40 – On the behaviour of* P. fulva *ants from a newly-established nest when forming a trail from scent deliberately laid on the substrate.*

The scene for this observation was the same as that in Figure 41, in which I attached two different incentives to a tiled wall using strips of sticking plaster: first, a cotton swab dipped in a solution of water and sugar, and, next to it, a cockroach that was being preyed on by ants on the floor, near a nest of *P. fulva* in a crevice in a doorpost. It must be said that for quite a few months before the observation I had never seen any ant either near the doorpost or in the bathroom in which it took place; therefore, I thought it had been recently established.

The observation started at 1:10 p.m., about one hour and twenty minutes after unsuccessfully trying for two hours and twenty minutes to induce the formation of a trail on the tiled wall of the bathroom. I had tried to do so by placing eight ants on the cockroach; they were captured on the floor near the nest, one by one, at a spot where some mucus left by the dead cockroach was still visited by ants. Seven of them, after hurrying over the cockroach, fell either off the paper I had employed to carry them, or off the wall.

I marked the thorax and abdomen of the eighth ant, and, with some difficulty, put the notebook I had used to transport it and placed it next to the cockroach on the wall. I had already marked an ant before as it was leaving the cockroach, but it had fallen on the floor and I had not followed it. Returning to the eighth ant: it spent quite a while cleaning its legs and antennae, then walked, halted by the cockroach and climbed it. It then fell off. I caught it and put it again on the cockroach; it walked on it, cleaning its antennae once in a while; as it left the bait I marked with crosses the spots in which it changed directions in its course. It turned right to the doorpost in a very irregular course and then down towards the nest. Seventeen minutes later, a heavily marked ant left the nest; I thought it was not the ant that had come down the doorpost to the nest, but the other ant, that had fallen off the wall. Three other ants left the nest and went to the mucus left on the spot where the dead cockroach had been found. Looking for the marked ant again, I found it near the nest, where a worker caught it with its jaws and dragged it inside without lifting it. After some time without any ant being seen near the nest, I left the scene for lunch. I came back one hour and twenty minutes later. During the time I observed the ants, I saw that none had been to the cotton wad dipped in the solution of water and sugar.

When I returned, at 1:10 p.m., I carried another *P. fulva* to the cockroach. The ant walked on it, nibbling it, and then left it, turned left along the tiled wall, apparently disoriented and lost. I left it in order to follow a fat worker, its gaster showing alternate dark and yellow bands, which I then noticed near the baits and had probably fed on one of them – most likely the cotton wad dipped in the sugary solution – since none of the ants that had nibbled the cockroach on the floor and the wall exhibited gasters as transparent and large as this one. As this ant returned to the doorpost, touching the surface o the wall and tiled column with the tip of its gaster at intervals, I took a pencil and lightly marked the stretches it covered. The ant reached the doorpost, lowered its gaster, and pressed its tip more vigorously against it, and forthwith went down the doorpost along a narrow line or groove towards the nest. It reached the skirting board and repeatedly tried to go into a tiny crevice 10 cm away from the true entrance to the nest. It spent a long time trying to do this, walking to and fro and returning to the crevice; it finally went down and reached the entrance at 1:30 p.m. Figure 54 shows the path taken by the ant from the bait to the nest.

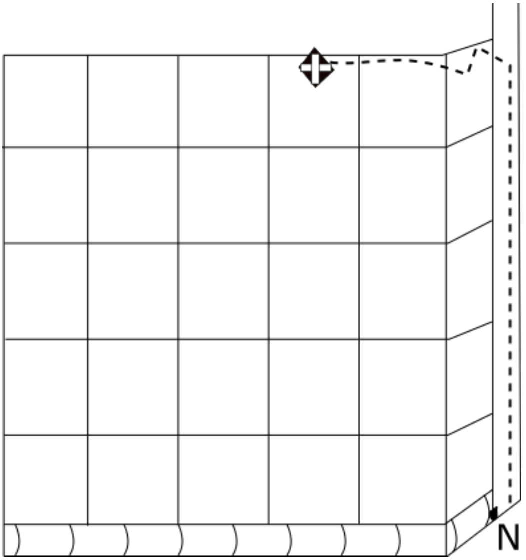

Figure 54: Approximate representation of the course taken by an ant, with scent deliberately laid on a wall and a column, both of them tiled, and a doorpost, to its nest, in the base of the doorpost.

Legend:
N: entrance to the nest
Rhombus: dead cockroach and cotton swab dipped in a sugary solution under strips of adhesive tape
Dotted line: the ant's path after ingesting the sugary solution

Forty seconds after the returning ant entered the nest, another one left it towards its tracks and soon reached the cotton swab dipped in water and sugar. Four aligned ants left the nest, three of them right on the heels of the one in front; two of them missed the left turn of the track and lost their way up the doorpost. The other two turned left, not strictly following the pioneer's track, and reached the bait. Two ants left the nest, went some way up the doorpost, and then returned.

Then I saw two ants leaving the bait and heading towards the nest, the first to do it: they tended to let themselves go with gravity, and did not exactly follow the discoverer's tracks. Eventually, following a slightly sinuous course, each of them on its own route, they reached the doorpost and followed the pioneer's tracks back to the nest. At 2:05 p.m.

many ants had already reached the bait. Others went slowly upwards, their march punctuated by brief, sinuous irregularities; depending on the direction they tended to go, they outstretched the antenna on that side; moving on with their bodies lowered, oscillating from left to right and back was more noticeable on smooth and unmarked stretches on the tiles. While walking, they had their quivering antennae outstretched and close to the surface, gradually advancing in fits and starts, covering not more than 5 mm in each burst. Their abdomens were lightly raised, and the front part of their bodies lowered from the thorax. During this oscillating march one ant fell off the wall. Mistakes occurred at the turning point where the track went towards the tiled columns, even though it had been more heavily scented. Some ants missed the turn, went on for a few centimetres, and then returned and found the track again; they proceeded with turns now to one side, now to the other, as if skidding left and right, precisely in the areas I had marked to follow the course taken by the discoverer. They went towards the bait in groups of 4 or 5, sometimes 5 or 6; those in the rear would sometimes stumble on the ants in front, and wander and redirect their course with them; once they started walking faster, which apparently occurred when the scent trail was strong, especially along the grooves between the tiles, those in the rear would overcome the ants in front as they paused for a while. At 2:13 I counted 17 workers on the bait, many of them with pointed abdomens and with visible yellow and brown bands. Some ten minutes later the ants were no longer coming in groups, but each on its own. The path to the bait was generally observed. On the way back, however, they would either follow the same route, which was not very frequent, or walk from spot to spot until they reached a groove between two tiles and then the doorpost; once there they followed the pioneer's track to the nest. Figure 55, below, illustrates the paths taken on the occasion.

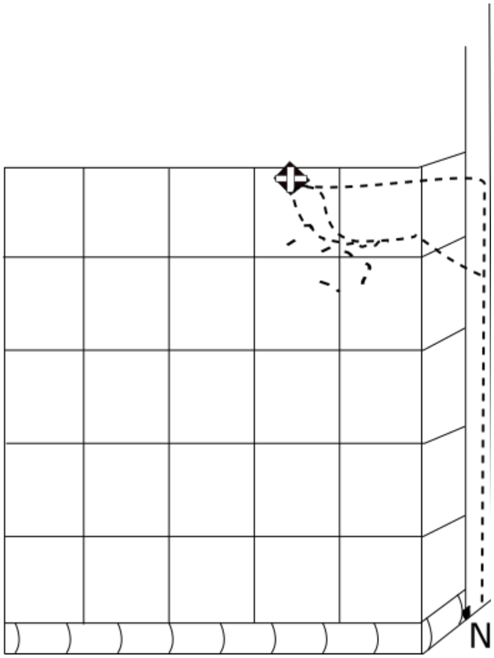

Figure 55: The paths most evidently taken by the ants coming from the bait to the nest and some disoriented ants below them at 2:23 p.m.

At 2:25 p.m. I saw three instances of regurgitation on the trail, unusually involving three instead of two ants: 2 aligned *fn*.s regurgitating the food and 1 *fi* receiving it (Cf. illustration in Figure 56, below).

Figure 56: 1st drawing: ordinary position of an ant regurgitating food to a nest-mate.
2nd drawing: two ants coming from an incentive regurgitate food to a nest-mate coming from the nest.

At 2:30 p.m. there were apparently more than a hundred ants on the doorpost and the wall. There was not a clearly defined trail, except, partially, among *fi.*s. However, they increasingly tended to take a shortcut along the wall using the path followed by the *fn.*s, which, however, would yield to gravity and sometimes go astray. The *fn.*s seemed always ready to give away the ingested solution to *fi.*s; regurgitation was frequent, and pairs of ants would stop here and there with the front part of their bodies raised from the petiole. Whenever I watched them there were four or five instances of regurgitation among them. I estimated there were about 30 or 40 workers on the bait, but it was not possible to see them all, as many of them would crawl under the bait and the sticking plaster. Sometimes the *fn.*s would slip a little, apparently because the tiles were too smooth. Oscillation in the march both of *fn.*s and *fi.*s never totally ceased, but lowered bodies and alternate shifts from left to right did. Their progress, however, was always sinuous.

At 2:48 p.m. regurgitation among the ants I could see had practically ceased. One or other ant went towards the cockroach. The *fi.*s were no longer thin and seemed twice as large as they had been at the start of the observation, suggesting that the colony had been severely deprived of food. My daughter started playing the guitar in a room next to the bathroom, and I noticed that, whenever there was a stronger chord, the gasters of *fn.*s would quiver ventrodorsally, a movement a little like a jolt.

At 2:55 p.m. the distribution of ants on the wall had completely changed. A number of them were as far as 1.25 m above the bait, while a smaller number went up to my right towards the junction of the wall and the column, and a larger group on my left seemed to extend the trail further up and beyond the bait. Figure 57, below, illustrates the situation.

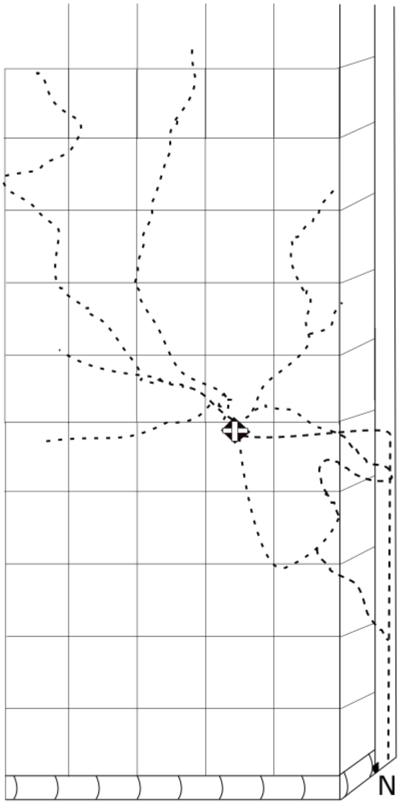

Figure 57: Distribution of ants 55 minutes after the trail was formed.

Legend:
Trapezoid: cotton wad dipped in a sugary solution and a cockroach, both attached to the wall with adhesive tape.
N: entrance to the nest in the base of a doorpost.
Dots and dashes: ants

The march of the ants to the left of the bait seemed to be continuously reoriented, with relatively wide oscillations in their course, in contrast with the constant oscillations at short intervals seen before. These were ants that apparently had missed the trail and were now disoriented, in a state that Cornetz (1914) called "foraging state", having probably been stimulated to leave the nest after being warned of a discovery of food outside. Figure 58, below, illustrates part of the path followed by one of the ants. If one of them happened to come across some *fn*, it would be given regurgitated food, an event that no longer happened on the more regular trails between the nest and the bait. In order to ascertain whether the disoriented ants in this area of the wall were really *fi.*s, I placed a new cotton wad dipped in the same solution used in the main bait on a utility knife, and set it about 2 mm away from the wall and 0.5 cm in front of one of the ants. The ant got near it. I then rubbed the bait against the wall, leaving some moisture on it, and then took it away. The ant ingested some of the wet remains on the wall. I placed the bait on the utility knife 0.5 cm away from two other ants; they reached the wad and started sucking it, sometimes walking on it for a while. After a few seconds bands were clearly visible in their gasters. On coming across other ants, they positioned themselves front to front, raised their heads and thoraxes and stroke each other with their antennae, and moved their mandibles closer, as if they were about to regurgitate. The same thing happened whenever they met. They were always ready to regurgitate. On resuming their walk, they would always strike the tips of their abdomens against the substrate, in a more perceptible way than *fi.*s, which, however, did the same. In order to attract the ants to the bait on the utility knife, I had to place it right before them or almost touch them with it: it was not enough to place them 0.5 or 1 cm away from them.

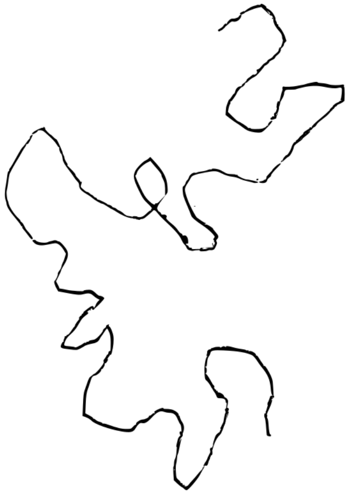

Figure 58: Course taken by a stray ant in the same group depicted in the previous figure, followed step by step.

The failure of stray ants to perceive objects not placed in front of them seemed to be due to their being intent on searching for the bait and tracks of their nest-mates on the substrate just ahead. In order to ascertain this I placed the utility knife with the bait 3 cm ahead of an ant slowly walking down the wall, 1.5 m away from the bait. It went to the right for a while, then turned left a little faster, went as far as 0.5 cm from the wad, and, after some oscillation, finally headed towards it. Before accelerating, it half raised its body and "smelled" the space ahead (its outstretched antennae repeatedly vibrating in a parallel position). I placed the bait beside another ant, 3 cm away. The ant half raised its body, made "sniffing" motions (moved its outstretched antennae up and down three times in a row) and moved away in an oscillating march. I tried placing the bait 1 or 0.5 cm above the ant: since its antennae remained continuously bent down, it was apparently unable to perceive the bait in this position. I placed the bait 1 cm above some ants. Generally, they started moving round more often, moving their lowered antennae, as if intensifying their search. Sometimes they halted and cleaned their antennae (sliding the gap between the spur and the tibia of each of its forelegs distally along the funiculus). However, they did not raise their antennae. The same happened when the bait was hung just 0.5 cm above the ants. As I wrote then, they were like pigs, oblivious to anything taking place just above them. Then I placed the wad in front of another ant, 1 cm away. The ant went straight to the bait, and touched it with the forelegs just as I removed it. The ant was not upset: it joined the tips of its antennae, stretched them towards the moisture left by the bait, and started sucking or licking it. As I touched one of its antennae, the ant would raise it and tried to grab the bait with its forelegs. The ant could be conducted in this way. However, if the bait was raised 0.5 cm, the ant could be made to clean its antennae and strike the ground with them more vigorously; however, it would not necessarily remain in the area; it could even move away.

As a general conclusion, it might be said that the great mobilisation of the ants in this colony was apparently due, for the most part, to the high level of food deprivation and the strong scent deliberately laid by the discoverer along the path from food to nest; the scent was strong enough to persist on surfaces that would not hold it under normal marching conditions. This form of depositing scent marks is only employed, I think, when the scout that found the food did it on its own and knows reasonably well the way back to the nest. However, during this specific provisioning instance, an efficient and sharply defined trail was never really formed. I think this was the case because of the following reasons: a) the ants' unfamiliarity with the terrain; b) the slipperiness of the tiles, which made the returning ants skid on their surface and prevented them from depositing a relatively continuous scent track serving its usual purpose, that of leading the ants coming from the nest towards the bait; c) the relative imperviousness of the tiles, unfavourable to the preservation of the scent track left by the ants; and, finally, d) a state of apparently severe food deprivation in the colony, which made the workers, as it were, to rush around the neighbouring space after food, even in the absence of adequate direction markers.

As a conclusion to this topic, it must be mentioned that I have not seen among *Paratrechina fulva* any other forms of warning and prompting nest-mates towards a food source other than depositing a scent track and regurgitating food to ants found on the way or inside the nest. However, myrmecological literature points to other ways of recruiting nest-mates in other ant species. I have observed a quite different form of warning among *Pheydole oxyops*, a predominantly insectivorous species. Observation 41, below, reports the behaviour of ants from two nests of this species as I placed a dead cockroach near one of the nests and a wounded cockroach near the other.

- *Observation 41 – On the behaviour exhibited by workers from two nests of* Pheidole oxyops *Forel (1908) as cockroaches were placed in their vicinity.*

I found two nests of *Pheidole oxyops* in a cemetery; their characteristic form made them easily recognizable: a wide slit in the soil with an entrance with a diameter of 1 cm. Tens of workers carried soil or walked by the entrance of the first nest. I laid a dead cockroach on the ground, some 40 cm away from the nest. On coming across it, a worker tried unsuccessfully to drag it away, and returned. It went past two nest-mates without any unusual action. As soon as it entered the nest, turmoil began: some twenty ants came out round the nest and headed in the direction the scout had come from. Soon there were two hundred or more ants briskly moving and, walking rearwards, they dragged the cockroach away. Two larger big-headed workers, or "soldiers", helped to move it.

A little later, I found another nest of the same ant species and laid a wounded cockroach about 50 cm away from it. The worker that first came across it pulled and nibbled it, but, as far as I could see, held no piece of it in its mandibles on returning to the nest. While going past two nest-mates in succession, it looked as if it had suddenly had a nervous attack: it raised the frontal part of its body, that is, its head and forelegs, and repeatedly shook it from left to right and back, whereupon the two others started running in a sinuous course. As soon as it reached the nest, the discoverer repeated the same movements and started running. There was a lot of excitement. Other ants seemed to do the same motion as the scout. Soon a worker left the nest in a sinuous course, followed by some ten ants, right behind or beside it, in a course not as markedly sinuous: they followed practically the same course as the discoverer, as if following its track, not strictly, but within the bounds of a strip.

Their heading towards the food following the same course as the scout could be due, according to a study by H.G. Fowler (1967), to its having marked the course with a trail pheromone. As to the speed and the great number of ants involved, these seemed to be an adaptation to the short-lived activity of the pheromone – about 5 minutes, according to Fowler – and the need of many ants for moving the prey to the nest.

In the first observation reported above, I could not ascertain whether the movements of the discoverer exhibited in the second observation, apparently serving communication, had also occurred. If so, they took place inside the nest. A third observation, carried out before these I have just described, led me to think that, if they occurred in these observations, their purpose was not only to drive them towards the food, but to attract them out of the nest, and, if not, that they were not the only way of attracting them out of the nest. This third observation took place in a vacant lot, where I found a nest of *Pheidole oxyops*; there were about half a dozen ants in the vicinity, and about the same number under a stone I lifted nearby. Soon, however, perhaps because the latter were somewhat upset on returning to the nest, hundreds of them came out of it and roamed around in all directions. In this case, would a scent track deliberately deposited not be enough for them to follow? Movements such as those seen in the second observation, as well as other signs of excitement exhibited by a worker from that nest, would only serve the purpose of attracting its nest-mates out of the nest, whereas the discovery of a food source would be conveyed by a clearly marked scent track leading to it.

3 THE TRANSFORMATIONS FORAGING TRAILS UNDERGO OVER TIME AND THEIR OUTCOME

While studying ant trails, especially those of *Paratrechina fulva*, I could see that the workers of this species have abilities that, over time, allow them to alter some aspects and behaviours prevailing while on trails, thus increasing their adaptive effectiveness. After some time, these alterations include changes in their attitude towards their nest-mates on the trail and an enhanced spatial orientation.

3.1 SOME CHANGES IN THE RECIPROCAL ATTITUDES OF ANTS ON A TRAIL OVER TIME

In one of my first observations, since I was interested in finding out whether *P. fulva* had any gestures serving communication, I used a magnifying glass to observe a trail marching on a wall. I noticed that the ants going towards a food item used as an incentive and those returning to the nest, on coming across each other, would either immediately turn aside or halt and repeatedly strike each other's antennae, touch each other's heads, and seemed to bite each other. What I failed to notice during this first observation was that their joining their mandibles was usually followed by regurgitation of part of the sugary solution ingested at the bait by the returning ant to its nest-mate. I noticed, however, that this behaviour was rare on established and crowded trails: in these cases, they usually touch each other's antennae and move aside. Now, it should be pointed out that the food provided to an animal is considered by Experimental Behaviour Analysis advocates as reinforcing the ensuing behaviour and making it increasingly more vigorous and frequent. However, how would one explain the fact that instances of ants going towards the bait soliciting regurgitated food decreased over time, or of ants turning aside more frequently from nest-mates coming from the opposite direction? It was clear that there should be another explanation. On a trail formed nine days later on the same doorpost of the preceding observation, I noticed that whenever an *fi* met an *fn* face to face and paused to join its antennae and mouthparts to those of the *fn*, the latter would also pause and raise its head, ready to regurgitate. However, if the trail had already been established for a while, this action would, in most cases, serve only orientation purposes and enable the *fi* to ascertain whether the *fn* carried any food and, if so, what kind of food; frequently, regurgitation did not occur. The *fi* would then resume its march, turning slightly left or right and then, accelerate its march, and head straight to the incentive. Sometimes this "mouth-to-mouth" contact did actually take place, as well as brief, light regurgitation, and then the *fi* would quickly proceed. Apparently, *fi.s* would always take the initiative of directing its mouthparts to those of the *fn.s*; the latter, however, seemed always willing to regurgitate and would actually do it when the *fi.s* paused long enough. Some minutes later, instances of actual and prolonged regurgitation still took place, but they were less intense than they had been nine days before, perhaps because now the ants were not as seriously deprived of food as they had been. The ants had certainly been feeding on the fat they could find in the soap in the bathroom and in the nearby kitchen.

In this observation I noticed that as I crushed an ant on the trail, ants walking in both directions would retreat, apparently in a response of avoidance and flight: they would touch one or other ant coming from the opposite direction and many of them would return in a hurry, almost as excited as when they had come across their crushed nest-mates. And all the ants in this part of the trail, which was very crowded, were returning to the nest; some ants going up the wall or about to do it, would touch returning ants, but would retreat only after going ahead for a while. Apparently, the alteration in the posture and movements of the returning ants, as well as the touches occasionally received, were not perceived by the arriving ants as indications of a threat. I noticed, as mentioned in the beginning of this writing, that some ants, having gone past the dead ant, would raise their bodies towards a small black dot on the wall, or run away from it, or "cautiously" go past it, that is, hesitating only at this point: a clear indication that they were prey to something like fear; however, this condition was not enough to prompt the ants going up to return – perhaps because they were highly motivated to collect food.

Returning to the consideration of what happened during the encounters of *fi*.s and *fn.s,* I noticed that, during the initial stage of trail formation, sometimes the former, sometimes the latter, would turn aside;

it was *fi.s* that seemed to look for *fn.s*, but they also seemed to turn aside more often. On forceful frontal encounters, *fi.s* would always be the ones to go back, even though with some resistance: this could be noticed by the reduction in speed of *fn.s*. In such cases, *fi.s*, being quicker at reorienting, would always take the initiative of turning aside.

After some time, frontal encounters practically ceased. Since by then the ants were normally walking at a uniform speed, though slightly sinuously, ants going in one direction would come across those from the opposite way and proceed by going sideways, choosing the side that was less crowded or presented the least resistance. On already stabilised trails, it was not infrequent that a single path was taken by each of the groups, *fi.s* and *fn.s* going either left or right, thus offering no obstacles to their march. Thus, for instance, on a stabilised trail following the junction of a ceramic mosaic floor and a wall, as I counted how many ants going both ways would turn aside, I found that, in 15 encounters, *fn.s* turned right towards the junction, whereas *fi.s* also turned right, but further away from the junction; there were no cases in which both would choose the same side of the floor. Later, without counting them, I observed that this continued to be the general rule for the trail.

3.2 ON THE TENDENCY OF ANTS ON A FORAGING TRAIL TO USE HETEROGENEITIES OF THE ENVIRONMENT FOR ORIENTATION, AND TO TAKE SHORTCUTS

While establishing trails, not only *Paratrechina fulva*, but also ants in general evince a tendency to make use of heterogeneities in stimulation in their environment – such as the junction of different surfaces, furrows, cracks, cavities, and grooves – to orient their course and take shortcuts to their objectives. The reader will notice this by examining illustrations of *Paratrechina fulva* trails already presented and the reports to follow.

- *Observation 42 – On the trails of Labidus coecus* (Latreille), *a species of Dorilynae.*

Labidus coecus is one of the ant species known as "army ants" or "legionary ants", described by Wheeler (1910, p. 246) as "the Huns and

Tartars of the insect world" for being specialised in surprise raids against small animals, especially insects and other arthropods. We owe to T. C. Schneirla (1949, 1955, 1956, 1957, 1958, etc.) most of the knowledge we have on Dorylinae ants, especially those from the Nearctic realm, such as *Eciton hamatum* and *Eciton burchelli* from the forests of Guatemala. According to his investigations, the latter can form swarms of up to 1,700,000 polymorphic workers. During their raids, *Eciton burchelli* relies on fan-shaped swarms, which at their peak form rectangular masses some 15 m wide and 1-2 m deep in the vegetation, and perform outflanking manoeuvres every 5-20 minutes. Among other species, such as *Eciton hamatum*, the raids are carried out in columns or lines branching out at intervals, with medium-sized and small workers hurrying up and sometimes colliding with the larger, slower workers. These collisions play a part in originating these branches.

At the end of their raids, near dusk, these ants, and Dorylinae ants in general, build a bivouac – a kind of nest for the night. The bivouac is formed by their interlocked bodies, hanging in a bunch in a safe place such as a hole in the ground or hollows in trees. The raids comprise two distinct phases, called by Schneirla *nomadic* and *statary.* During the nomadic phase, the colony establishes the bivouac every day in a different area for 13-15 days, whereas during the statary phase, they keep a single stationary bivouac in the same area for 16-20 days. Using the bivouac as the centre for their raids and going each day in one direction, the ants in this phase systematically explore the surrounding terrain. This second phase occurs when the queen is physograstric, and therefore unable to cover 100 to 300 metres every day, and ready to lay thousands of eggs which will require more effort by the workers to hatch. The nomadic phase begins with the emergence of a great number of inexperienced workers, the presence of which will prompt older workers to more vigorous daily raids, by the end of which the bivouac will have been moved to a new location and the colony migrated to a new area.

Among *Labidus coecus*, the species considered here, these dislocations generally occur underground or under fallen leaves, but in cool or cloudy days they may occur on the soil. The reason, or the consequence of this, is that they are averse to being exposed to the sun or high temperatures. Once, as a column of these ants entered a country house, I collected some of them on a newspaper to see how they would react on being taken out of the migratory flow, and released them on the soil in a sunlit area. This was in the morning and the soil was not yet very warm, so much so that leafcutters and other ants roamed around naturally. As soon as they were released they had convulsions, and within seconds they had contracted their bodies and died.

Once, at 6:00 am, after a rainy night, I found on a cement floor with some cracks and holes, a trail of *L. coecus* connecting a piece of beef suet they were feeding on and two orifices in the floor and next to the wall. Figure 59, below, illustrates the situation. The two orifices were about 1.20 m from each other and crowded with ants with their bodies interlocked. The branches going left and right from the incentive towards the orifices were about 1 m long.

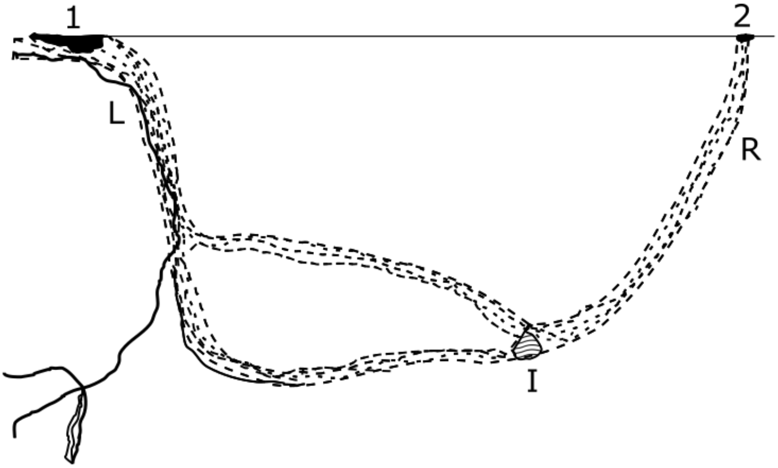

Figure 59: Approximate representation of a trail of *Labidus coecus* on the cement floor of a backyard.

Legend: 1 and 2: orifices in the floor, full of ants (probably bivouacs?)
I: Incentive (beef suet)
Whole lines: cracks and groove in a cement floor
Dashed lines: trails or columns: left and right branches of the trails, coming from the nest to the incentive and vice-versa.
L and R: left and right branches of the trails, coming from the nest to the incentive and vice-versa.

The trail apparently included thousands of ants of a reddish--brown colour, most of them small, their sizes varying from tiny 2 mm long workers to big-headed black "soldiers" 1 cm long. I could see some newly--emerged workers of an orange hue. Workers in this species have no eyes or, when they do, they are either minute or malformed. Although numerous, they did not take much room, suggesting that they favoured underground dislocation and most had not come to the surface. They walked quickly, following a somewhat sinuous course; the impression was that they were very excited. All of them had long legs, an extremely thin petiole, and pointed sickle-shaped mandibles, to be used not in cutting, but in nipping, piercing, and pulling. I noticed that neither *Solenopsis saevissima* nor *Paratrechina fulva* had formed any trail that day as they had usually been doing.

I crushed some ants on both the left and right branches of the trail. Agitation increased; their march near the dead ants became more sinuous, and traffic was jammed; however, ants going either way would only exceptionally reverse their course.

I returned at 11:00 a.m. The trail looked a little different, as shown in Figure 60, below. It still followed cracks and a groove in the cement floor.

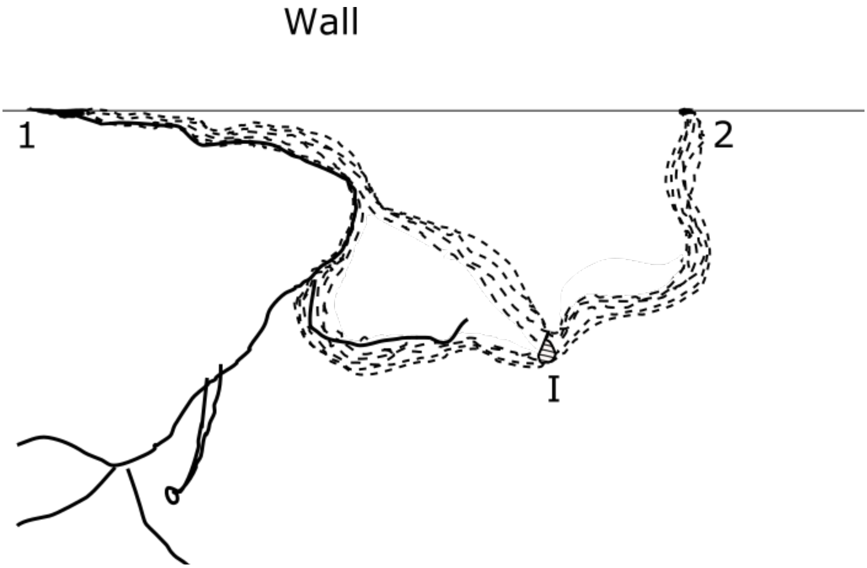

Figure 60: Representation of a trail of *Labidus coecus* 5 hours after it was found.

Legend:
1 and 2: initial and terminal points – perhaps holes – of the trails on the cement floor next to the wall
I: Incentive (beef suet)
Whole lines: groove (thicker line) and cracks in a cement floor
Dashed lines: trails

At 11:30 a.m. I had another look at it. The left branch had changed a little and extended partially downwards, below the area in which the ants turned towards the incentive. The reason for this was that some ants, one by one, proceeded for a few millimetres along the longest crack, as if in exploration, and apparently left a long-lasting scent track, followed by other ants.

One hour later, this extension of the left branch of the trail had already disappeared. At a certain point of the trail I saw some ants surrounding a small worker of another species – probably a *S. saevissima*. They stood on their hind legs and repeatedly projected their abdomens towards the victim; I do not know whether they were hitting it with their stingers, discharging some sort of secretion, or both. Meanwhile, another ant held the intruder with its mandibles. While "shooting", their mandibles were abducted. Later, I saw a conspicuous mass and witnessed the same operation carried out against another *S. saevissima*.

I laid a dying ant, a larger, big-headed *L. coecus* worker on the trail. It still bent ventrally, bringing abdomen and head closer together, and then feebly moved its abdomen. It was immediately pulled some 3 mm away from the trail. I placed it on the trail again. It was again dragged away. A medium-sized worker started dragging it; others hesitated before proceeding; only rarely would an ant return; a good number stepped on the ant, their abdomens raised between their hind legs and pointed towards it, more specifically towards its head and abdomen. Its motions decreased even more.

I pressed with my finger a *S. saevissima* and placed it on the trail; though its mobility was reduced, it walked for a while on the trail. It did not arouse much interest. One or other small worker halted to examine it, shaking their antennae or standing with their abdomens turned towards it. Then, the ant lay there, some 3 mm away from the trail without being disturbed again.

I placed a *Camponotus crassus* on the trail; its abdomen was ruptured, and the smell of acid was very strong. It definitely aroused more interest. No larger ants ("soldiers") halted, only small ones. Some directed their abdomens at it, while others pulled it with their mandibles.

At 7:10 p.m., I noticed there was a bit of some green vegetable on the right branch of the trail; the ants bit it and sometimes raised their bodies, with their abdomens toward it, as if they were dealing with an intruder. The problem was that I had the same impression when they moved their abdomens while on the incentive.

It should be said that the size of these trails increased over time. On the following day there was another irruption of these ants, formidable in numbers, towards the square platform supporting a rubbish bin; they came from the junction of the floor and wall next to the kitchen, and also from the opposite side, where *S. saevissima* used to walk before. These visiting ants tended to go into orifices, some of them possibly entrances to nests of other ants. I also saw trails next to the doorpost of an outhouse, sprinkled with fresh sawdust. That day the ants carried cooked rice grains to a hole next to the platform supporting the rubbish bin. I think they did it because the rice, before being cooked, had been fried in fat, a food item favoured by them – this might also explain why many ants are attracted to dissolving soap. During another observation of *L. coecus* I saw them carrying fragments of vegetables with oil dressing and bits of bread and butter; they also licked remains of butter in a can found in a box filled with rubbish.

In this observation the reader should have noticed how these ants rely on heterogeneities of stimulation, in this case cracks in a floor, for their orientation, as well as their tendency to take shortcuts.

I proceed now to a new observation with another ant species.

- *Observation 43 – On a trail of Tapinoma melanocephalum* (Fabricius, 1793) *on tiled walls.*[31]

Tapinoma melanocephalum is a tiny monomorphic ant in the Dolichoderinae subfamily. It is very thin, and its length varies from less than 1mm to 0.5-2mm; it has no stinger and its petiole has only one node which is generally not visible when the ant is seen from above; its head and thorax are dark brown, and its abdomen and legs are creamy, almost transparent, hence the popular name of "ghost ant". In the US it is also known as "tramp ant", probably because of its brisk and erratic movements when not on a trail. Its origin is unknown; it is a cosmopolitan species, introduced in many countries. It is a household pest and frequently a major transmitter of microbes in hospitals. When crushed, it smells like rotten coconut or carrion. A single colony in a house generally has many nests, with many queens and mutually tolerant workers. A basic condition for their establishment is humidity; therefore, they are commonly found in kitchens, bathrooms, and laundry areas. In houses they generally nest in door frames and posts, hollows in shelves and tiles, inside radio and television sets, etc., with many subsidiaries since they move from nest to nest quite often; they enjoy honey, sweets, dead insects, and pet food. Outdoor nests are generally found in grass tussocks or under the humid bark of trees and bushes; in these environments they generally feed on dead arthropods and the honeydew produced by sap-sucking insects.

The trail considered below was established in the laundry area of my flat, and connected a rubbish bin to two nests in tiled walls. There

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[31] I am indebted to Dr. Carlos Roberto F. Brandão, The Zoology Museum of the University of São Paulo, for the identification.

were hundreds of them and they clearly used heterogeneities of stimulation to orient themselves along a ceramic floor, a door frame, and the walls, except for a short stretch, in which they took a shortcut; a scent track – and, perhaps, the view of their marching nest-mates – also served as an aid for their orientation in open areas. The trail was about 5 m long. Figure 61 illustrates the situation.

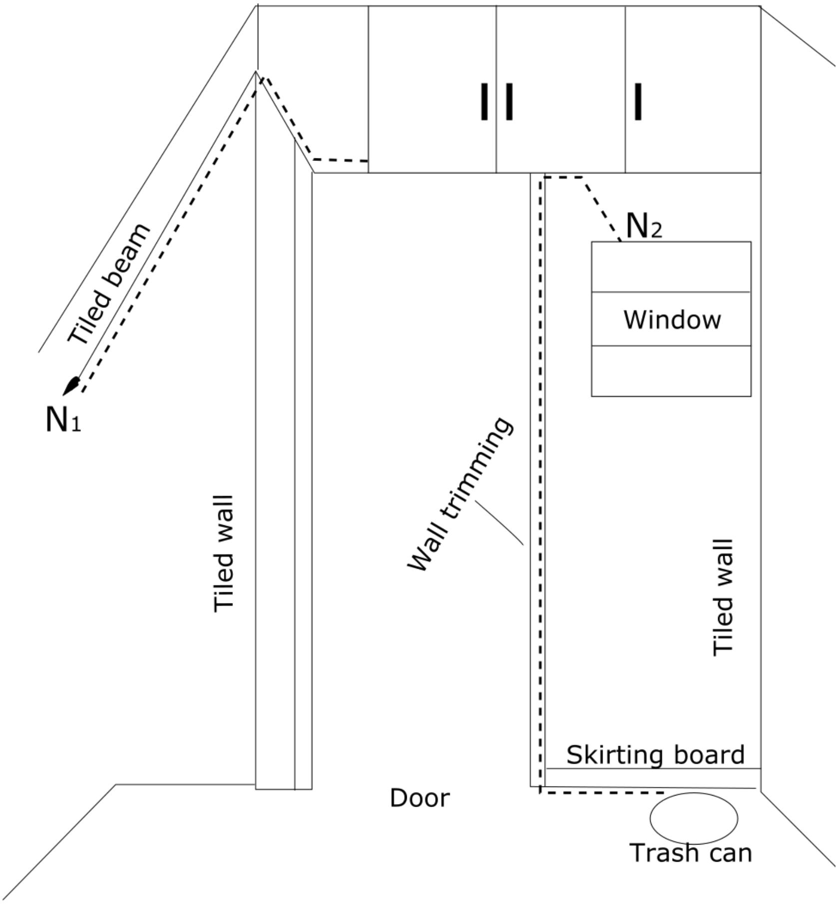

Figure 61: Illustration of a trail of *Tapinoma melanocephalum* on a ceramic floor and two tiled walls.
Legend:
N_1 and N_2: nests or subsidiaries
Dashed line: trail

I am going to describe their course from the provision source to the nests, but obviously there were ants walking in both directions. The trail came out of a rubbish bin and followed the junction of the ceramic floor and a tiled wall for some 60 cm and then reached a door frame. It then followed a straight upward course, walking now on the tiles, now on the frame, for about 2.10 m. The trail then split: one branch went upwards and under an iron cabinet attached to the wall, while the other turned right, following part of a groove between two tiles when it then suddenly made a 45 degree turn to the right. This branch went towards a recess in a wall at the end of which there was a window; this recess gave access to a secondary nest. If route marking were the sole factor involved in their course, the ants would tend to take the groove between two tiles and then follow this downwards to the upper level of the window, and then go back to N2. Going back, however, is not something that ants naturally or spontaneously do. Their past experience apparently allows them to remember the spatial orientation of the nest in relation to the rest of the trail, for they interrupted their march along the groove to change their orientation. The angle taken shows that their orientation involves a perfect balance of these two tendencies – marking their route efficiently and taking the shortest distance – by making the most of external directional support and saving effort. It can be seen, therefore, that ants do not walk in a purely physical space, but in a representational, that is, mnemic, environment, in which events are projected on the basis of past experience.

I noticed that scent tracks become a directional support when the physical environment does not provide one. And more: facts show that ants prefer more conspicuous markers or stimulation heterogeneities – for instance, the junction of two flat surfaces, or the junction of a door frame and a wall is preferred to the shallower and less conspicuous groove between two tiles.

The branch of the trail going underneath the iron cabinet on the wall was not interrupted. It followed the uppermost part of the door frame until it reached another tiled wall, perpendicular to the wall holding the iron cabinet. Then it went upwards again in a 45-degree angle until it reached the junction of the wall and a tiled beam next to the ceiling of the laundry area. The trail proceeded along the surface of the beam facing downwards for about 1.52 m towards a large gap in the wall, used for the passage of electricity wiring. This gap was their main passage when going out of the main nest.

One point should be stressed. The ants' marching styles were different on the stretches in which there was no other directional support but the scent track. In these areas some ants proceeded by fits and starts, that is, their progress was interrupted by brief pauses. Some of them even circled for a while, as if looking for the scent track, especially when I breathed on that stretch. My breath, however, had practically no effect on them when they went along junctions and grooves. On unmarked stretches, ants overcame each other more frequently than on stretches along junctions and grooves. I think it is easier to interrupt or destroy trails on stretches devoid of external orientation, where their routes become less evident. This provides a reason for their preference for marked routes.

The observation above was carried out in the morning. I resumed it at 5:40 p.m. and noticed that there were groupings of 4-8 ants on the trail marching on the ceiling and the door frame. Using a magnifying glass I saw that they were half-full; their abdomens were flat surfaces, or the junction of a door frame and a wall is preferred to the shallower and less conspicuous groove between two tiles.

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The observation above was carried out in the morning. I resumed it at 5:40 p.m. and noticed that there were groupings of 4-8 ants on the trail marching on the ceiling and the door frame. Using a magnifying glass I saw that they were half-full; their abdomens were white, with a light yellowish hue, and they licked or turned towards a much larger ant, also half-full, but with several conspicuous bands in its gaster – differently from the smaller ants, whose gasters were turgid and transparent, but showed no bands. Some ants, generally two or three, were visibly licking an ant twice their size, apparently a queen. I tend to think that, as I had noticed in the case of *Paratrechina fulva*, when foraging is particularly intense, queens come out, perhaps affected by the excitement of workers; this also happens when ants move to another nest and prevents queens from being left behind.

A conspicuous and differentiated heterogeneity of stimulation in the environment tends to be preferred to one that is not. However, what turns heterogeneity of stimulation into an orientation aid is the fact of its being oriented towards the nest or the food source or of its serving to help the ants to reach them. Therefore, it is the need of an aid to orientation and the attainment of their goals that leads ants to use them; the greater their orientation support, the more so.

It should be noticed that the stretches lacking external orientation aids are those in which ants transform trails more often, when linear trails become columns or widen out into broader strips. I had seen *Tapinoma melanocephalum* ants in my flat for a long time, certainly for more than a year. As for the trail considered here, it might have been going on for a few hours. I had been travelling with my family for five weeks and returned eight days before. Meanwhile, our maid had been to the flat twice, but probably had not provided any food to this colony. These ants had perhaps taken some days to find any usable rubbish; this might perhaps account for the greater magnitude of this trail, as well as for the coming out of the queens, soon blocked by their attractiveness to the workers.

It is evident that many heterogeneities in the environment, such as junctions of floors and walls, ridges, gaps, and cracks in a substrate, could act as directional supports for the ants, due not only to their sensorial effects on them, but also to their physical and mechanical effects. The observation below was planned in order to ascertain what effect a long object, posing no physical constraints to the ants, but producing stimuli perceived by their senses, would have on them.

- *Observation 44 – Ascertaining whether a long object placed above a surface on which ants moved might serve as an orientation support for them.*

This observation was carried out in a place mentioned before: a garden with two flower-beds and a tap in a rented house. I placed a thick, coarse, rectangular cardboard sheet, 1 m long, 70 cm wide, on the cement floor between the two flower beds, some 12 cm from a wall. The nest of *P. fulva* active on that day was on my left, under a water meter cabinet on the flower bed. I placed an incentive on the cardboard, a cotton wad dipped in sugary water, 40 cm from the edge of the cardboard closest to the wall, 52 cm from it and 45 cm from a cement ridge. I placed a 46 cm long, 4 cm wide, 1 cm thick damp pine batten with some earth on it almost perpendicularly to the wall, supported by two lumps of putty that raised it 1 cm above the floor and 0.5 cm above the cardboard, near the incentive. Then I positioned a 1.40 cm long cylindrical rod (a broom handle) across the cardboard, over the corner near the wall and closest to the nest, but not leading to the incentive. The piece of putty closest to the incentive was about 1-1.5 cm away from it. Figure 62 illustrates the situation.

This observation took place on a cold, windy night, with intermittent drizzle. I captured six ants with a piece of paper and placed them one by one on the incentive. Some of them did not remain there. They tended to walk in full or half circles round the incentive in order to return to the nest. They went in many directions, but especially to my left, which was nearer the second flower bed. They walked for a while towards it, on the putty, under the batten, and on the broom handle, coming and

going round, but not too far from it: 20 or 30 cm at most. Some 30 minutes later, there was an increase in the number of ants

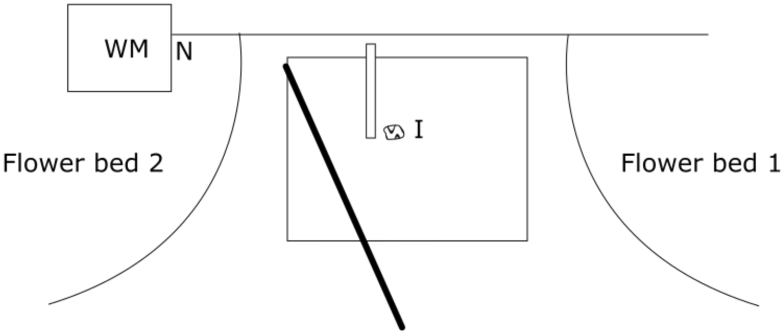

Figure 62: Representation of the situation in Observation 44.

Legend:
Straight line: wall
Large rectangle: cardboard on cement floor
Smaller rectangle: damp pine batten with earth on top
Thick line: broom handle
N: nest
WM: water meter cabinet
I: Incentive

This observation took place on a cold, windy night, with intermittent drizzle. I captured six ants with a piece of paper and placed them one by one on the incentive. Some of them did not remain there. They tended to walk in full or half circles round the incentive in order to return to the nest. They went in many directions, but especially to my left, which was nearer the second flower bed. They walked for a while towards it, on the putty, under the batten, and on the broom handle, coming and going round, but not too far from it: 20 or 30 cm at most. Some 30 minutes later, there was an increase in the number of ants on the concrete ridge to my right, on which I had laid, and later removed, a similar incentive; the ants seemed to be in active search.

I placed two other ants on the incentive. Since the edge of the cardboard did not touch the floor, I secured it with strips of adhesive tape.

Two hours and twenty minutes after the situation had been prepared, I returned to the site. The only ants stepping onto the cardboard sheet and out of it walked next to the batten or under it. There was no doubt: a good number of ants left the junction of the floor and wall near the batten, went past the piece of putty and over a piece of adhesive tape; they continued alongside the batten for 1 or 2 cm, then under it and then left it when they were some 2 cm away from the incentive. Despite the strong wind and the cold, they did the same on their way back. One or other ant would occasionally walk between the batten and the broom handle, but the number of ants following the batten was far greater. The trail was not perfectly straight, but was clearly determined by the batten. They went under its shade and left it without hesitancy. There was some hesitancy, however, among the ants returning to the nest. Some left this way at various points near the incentive, and proceeded in a slow, wavering march, coming and going, turning left and right, covering some twenty centimetres towards the nest; then, waving irregularly, they returned to the path under the batten. When I counted them, I found out that these attempts to take a short cut to the nest were far more frequent than I had thought: about half the ants, or nearly so, undertook it. As they went towards the incentive, however, there was no other possible route, but the one under the batten. As I saw them walking under it with their antennae stretched upwards, they looked like tiny trolley buses. Clearly, the control of the batten over the ants was not physical or mechanical, but sensory.

- *Observation 45 – On what was found the following morning, after some alterations had been carried out at midnight in the situation described in the previous observation.*

At midnight, when this observation was finished, I removed the cardboard sheet and placed the incentive on the cement floor. I placed the batten, its ends supported by lumps of putty, at a sharp angle in relation to the wall, as shown in Figure 63, below.

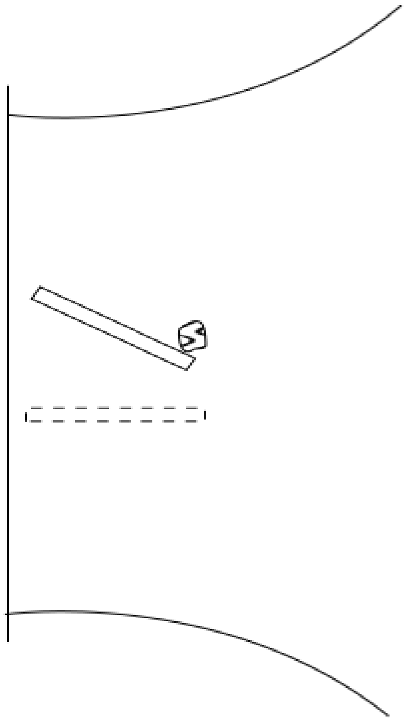

Figure 63: Illustration of the situation described in the previous observation, when some alterations were introduced after its completion.

Legend:
Straight line: wall on a cement floor in the garden.
Curved lines: 5.5 cm wide, 1 cm high concrete ridges separating two flower beds
Whole line rectangle: batten with its ends supported by pieces of putty
Dashed line rectangle: position of the batten in the previous observation
Small circle: food incentive

Under these conditions, the batten did no longer signalled a shorter way to the nest in flower bed no. 2 as it had done before; it pointed instead to a somewhat backward progress in relation to the nest. Now it was expected that finding the incentive would be more difficult, since the cardboard substrate had been removed and the batten was in a different position. The situation was different.

On the following morning, to my surprise, I did not find a trail of *Paratrechina fulva*, but a less crowded trail, some 20 cm long, of *Solenopsis saevissima*, coming out of an orifice in the cement floor, 1 cm away from the batten, and proceeding under it in a straight line; at a point 2 cm away from the incentive, the trail turned towards it. Figure 64, below, illustrates the situation.

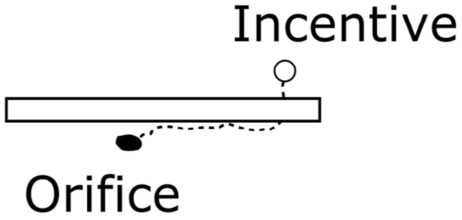

Figure 64: Illustration of a trail of *Solenopsis saevissima* found under the batten in the morning after the alterations carried out in the situation represented in Figure 64.

Legend:
Rectangle: raised batten
Black dot: orifice in cement floor, exit of a *S. saevissima* nest
Small circle: incentive
Dotted line: trail under a batten, following one of its edges

Undoubtedly, the location of the incentive and the batten were not favoured by *P. fulva,* but by *S. saevissima.* Twenty centimetres were certainly not a long distance to walk, especially with such a valuable marker pointing the direction to follow. I do not know what happened to the *P. fulva*: whether they could not find the incentive or had been repelled by the *S. saevissima.*

3.3 ON THE APPARENT USE BY ANTS, AS THEY MODIFY A FORAGING TRAIL, OF PREVIOUS EXPERIENCES WITH A GIVEN BEHAVIOUR ENVIRONMENT

Successful and attempted shortcuts seen on trails of *Paratrechina fulva* are certainly an evidence of the acquisition, on the basis of previous individual experience, of a spatial cognition allowing these ants, from the point of the environment where they are, to determine the direction to be taken to their nest or to the incentive they are visiting. In the two observations now to be reported I think one can also perceive their use of a record of previous experiences in a given behaviour environment to adaptively modify a trail undergoing a sudden modification that precludes or hinders its effectiveness.

- *Observation 46 – Behaviour modifications in* Paratrechina fulva *when faced with 3 nest-mates on a trail, crushed on one of the legs of an iron stand, their only access to a temporary nest and to the external environment.*

This observation concerns a trail coming from a hole in the soil of a planter (probably a temporary nest, since it disappeared a few days later), resting on a three-legged iron stand on a stone floor next to a flower bed. In order to reach or leave the planter, all the ants used one of the legs of the stand, which were 50 cm-long, 1 cm-thick. This was the only place where a trail was clearly noticeable, since the ants, while on the planter and the floor, followed a looser course. Figure 65, below, illustrates the situation.

I observed the trail for a while and took down the time the ants spent to cover this vertical stretch. It was a thin trail, with great variation in speed: to cover the 1 m stretch along the planter and the stand, ants going upward spent 31 seconds, while ants going downward 33 seconds, in a range of as much as 42 seconds; in 60% of their encounters, the ants touched each other's antennae. After this record I crushed three ants on the trail, at the point where the outer surface of the planter and the stand met, some 30 cm above the floor. Figure 65 illustrates the situation.

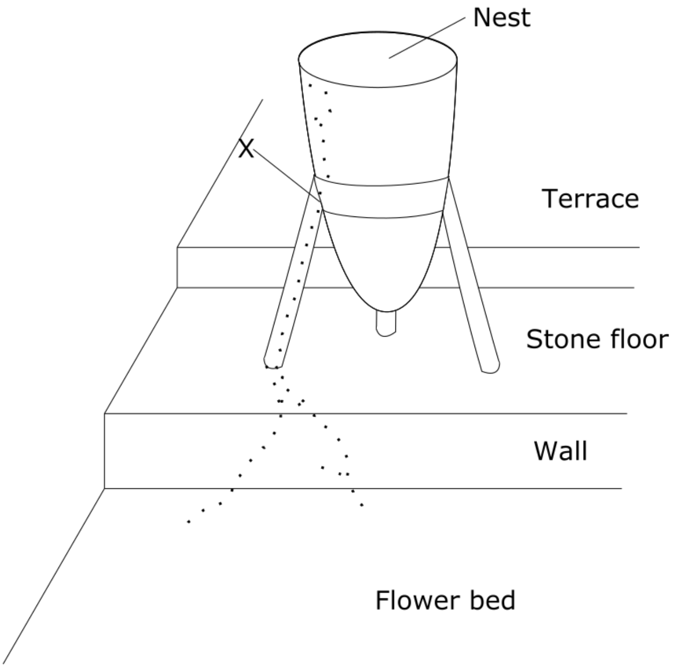

Figure 65: Illustration of the situation in Observation 46.

Legend:
Dotted line: trail
X: alteration point

I observed the behaviour of 22 ants near the alteration point: 9 of them going downwards, 13 upwards. Records were verbal and included only the way each ant moved in relation to the experimental alteration. Seven of the 9 ants going downwards returned when 1-10 cm from the alteration point. Their speed was greatly accelerated (in one case, unfortunately the only one in which speed was measured, the ant took only 5 seconds to cover the 70 cm to the top of the planter). Two ants tried to avoid the alteration point by going to the opposite surface of the leg, and then returned. Many ants returned to the nest on reaching the edge of the planter. Among the 13 ants going upwards, 4 returned as soon as they were from 2 to 5 cm from the alteration point; 2 made a detour along the unobstructed surface of the leg, 4 returned for a while and then tried again to proceed before either going all the way back or making a detour, 3 ants hesitated near the alteration point, tried an accelerated detour, and then set out along the surface of the planter in a random course, at least initially, away from the trail. What is important in this connection is the fact that, after the ants were crushed, the trail thinned out as another one was established along another leg of the stand, which eventually absorbed all the original flow. Unfortunately, I do not know how this new trail originated. It seems clear, however, that the ants – whether those going downwards of upwards, I cannot tell – may have relied on a mnemic record of another, previous path leading out and into the nest, in addition to the altered path.

- Observation 47 – *Modifications carried out by* Paratrechina fulva *in their course after being faced with two crushed nest-mates on their trail, established on a floor near their nest and traversed on a daily basis.*

This observation concerns a 1m-long trail in a backyard, established along the junction of a ceramic mosaic floor and a 5 cm-high cement step. This step led to a roofed area, also paved with ceramic mosaic, and leading to an office and a small bathroom. The trail extended from the entrance of a nest, next to one end of the junction mentioned above, towards an incentive (a cotton wad dipped in a mixture of water and already fermented sugar) at the other end of the junction, and the step, close to a wall. My original objective, frustrated, as it will be seen, was to measure the speed of *fi.*s and *fn.*s in each of four equal stretches of the trail; these stretches were marked with chalk on the backyard floor. Records were to be taken under two different circumstances: a control phase, with no alterations on the trail, and an experimental phase, when some ants would be crushed halfway along the trail. The ants from this nest would frequently roam about the backyard and the surrounding area and visit a rubbish bin on a raised cement platform as well as the area described above.

The incentive was placed at 1:13 p.m., and soon a trail was formed. However, it was hindered by intermittent rain, and at 2:20 p.m. it had disappeared. At 7:00 p.m. I replaced the incentive; at 8:40 p.m. I sat on chair in the roofed area to observe the trail. But, since it was difficult to see the ants on the backyard floor, I moved the incentive, which already had some ants on it, to a place with better lighting: on the floor of the roofed area, near the wall closer to the nest, 1 m away from it. I also captured some ants on the trail and put them on the incentive to speed up the establishment of a new collective path. Some of the ants went back to the nest following the junction of the wall and the floor of the roofed area, while others went up the wall, and then, after some hesitation, went back. Meanwhile, the ants coming out of the nest still went towards the place where the incentive had been. After some time, the ants tended to follow a variety of routes on the floor and the wall, and, therefore, there was no sense in trying to measure their speed. I returned the incentive to its original location.

The trail was re-established very easily, but now it was less crowded. At 9:40 p.m. I started taking down their speeds and then crushed two ants as they came past each other, at a point 50 cm away from both ends of the trail. Returns and accelerated detours were seen all over the path among *fi.*s and, at first, among *fn.*s, but the latter, after going back, would generally face the alteration again in order to reach the nest. Jolts, followed or not by a return, were common among ants going both ways. I waited for 12 minutes and again started noting their speeds whenever it was possible. The ants took some time to leave both the incentive and the nest; some of them returned to the nest right after leaving it. Traffic clearly decreased. Some courses outside the trail were now to be seen along the roofed area and the backyard, with wide detours that seemed possible only if the ants knew the direction to be taken towards their goals. An outstanding fact was that now part of the ants followed a straight line along the middle of the step, while another group went along the floor of the roofed area, apparently using its junction with the step as an orientation aid, both in coming and going. From 11:30 p.m. to 11:52 p.m., no returns occurred. At midnight it might be said that their probable familiarity with the area, combined with the orientation support provided by the junctions of the step with the lower and upper portions of the floor, helped them to make detours and reduced instances of return. These detours eventually stabilised into four other routes, used in both directions and replacing the original one, (1). They were as follows (Cf. Figure 66 below): trail (2) shared the first 35 cm of the first trail, then departed from it on a slanting course, going as far as 15 cm away, and then approached it again until it reached the incentive along this independent course; trail (3) went a long way along the middle of the vertical face of the step leading to the roofed area; when about 35 cm from the incentive, it went down and joined the original path and went ahead; trail (4) followed the upper border of the step and then its junction with wall 2 until it reached the incentive; trail (5) went into the roofed area, further away from its edge, to a distance of as much as 35 cm from the crushed ants; again, it gradually approached the edge until the point where it joined the final stretch of route 4. Figure 66 illustrates the situation.

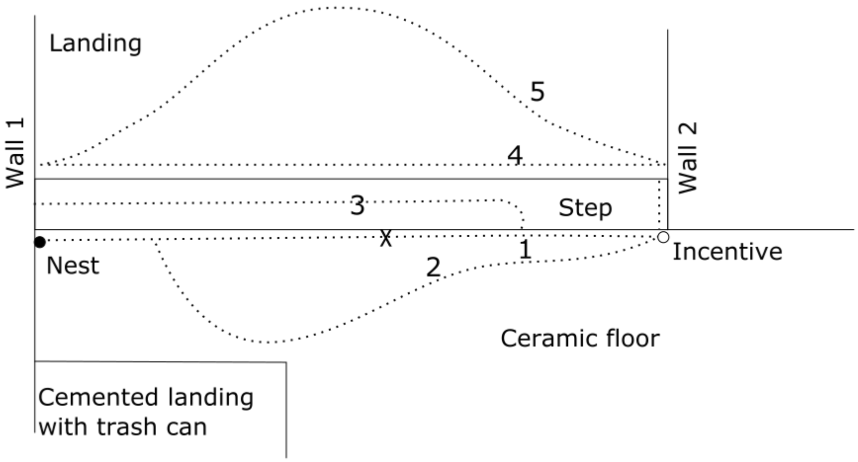

Figure 66: Representation of the four trails (2-5) that replaced the original one (trail 1) after two ants were crushed halfway along trail 1(See text above for an explanation).

Apparently, a mnemic record of their previous experiences with this environment allowed the ants to establish a variety of alternative routes and thus avoid their crushed nest-mates.

4 ON THE CHOICE BETWEEN INCENTIVES OF A SIMILAR NATURE, BUT WITH DIFFERENT NOURISHING VALUES AND AT DIFFERENT DISTANCES FROM THE NEST BY *PARATRECHINA FULVA*

We have already seen in this inquiry that a trail can become more crowded and the ants apparently more intent on using a cotton wad dipped in a sugary solution when the concentration of sugar is increased, or, if it is nearly or totally dry, when water is added to it; though the concentration of sugar is decreased, ingestion becomes easier and faster. This observation was carried out in order to ascertain whether the ants from a given nest, faced with similar incentives near each other, each with a different caloric content, would show any preference for those with higher nourishing value.

- *Observation 48 – On the behaviour of the ants of a given nest towards a set of similar food incentives (cotton wads dipped in water, and in water with different concentrations of sugar) laid near each other.*

This observation was carried out in the already familiar setting of a garden with two flower beds separated by a cement floor (Cf. Figure 53); its purpose was to observe the behaviour of ants from a primary nest located in a 15 cm long crack in a wall, next to the junction of the cement floor and the edge of a flower bed. I placed a short wooden board on the bed, some 35 cm away from the nest entrance, holding 6 incentives dipped in solutions with differing concentrations of sugar at 5 cm intervals. In Figure 67, below, these incentives are numbered from zero to five; zero indicates water without any sugar; 1 represents water with a single measure of sugar, whereas the others included water with two, three, four, and five times this single amount of sugar. They were placed in random order; number 2, the last in the sequence, was 70 cm away from the nest, incentives 5, 1, 3, 4, and 0 were, respectively, 65 cm, 60 cm, 55 cm, 50 cm, and 45 cm away from it.

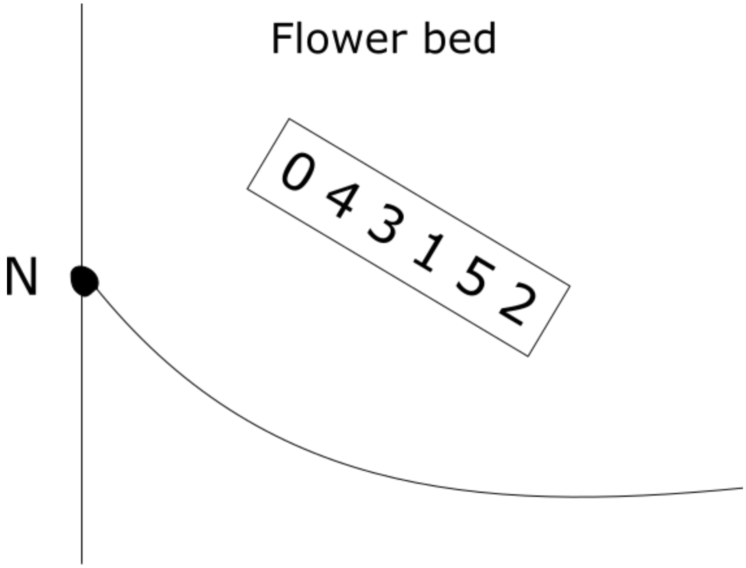

Figure 67: Approximate representation of the situation in Observation 48.

Legend:
Straight line: wall
Curved line: concrete ridge between a flowerbed and a cement floor
N: Nest
Numbered rectangle: short wooden board with six incentives (cotton wads dipped in a solution of water and sugar); the numbers indicate how concentrated the solution used in each incentive was.

At 5:40 p.m., twenty minutes after I had prepared the situation, as I remember, I counted how many ants from that nest were on each incentive. I found 1 ant on incentive no. 0, 25 on no. 4; 12 on no. 3; 1 on no. 1; 0 on no. 5; and 0 on no. 2.

Ten minutes later, I counted them again. There was no ant on no. 0; there were 22 on no. 4; 12 on no. 3; 0 on no. 1; 3 on no. 5; and 2 on no. 2.

At 6:00 p.m. I did not count them, but noticed that the number of ants on incentives no. 3 and no. 4 had increased.

I moved the board in 180 degrees, reversing the sequence of incentives and altering the distance between each incentive and the nest. Figure 68 illustrates the situation.

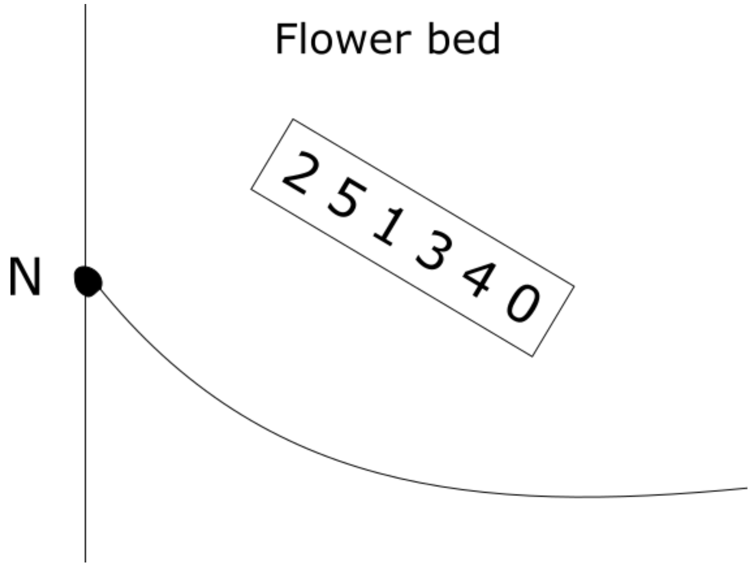

Figure 68: New situation as the ends of the board with incentives on it were reversed on the flower bed.

Legend: See previous figure.

At 6:18 p.m., again I counted the number of ants. I found 8 ants on incentive no. 2; 27 on no. 5; 1 on no. 1; 1 on no. 3; 3 on no. 4; 0 on no. 0. Then, at 7:30 p.m., as I finished the observation, I counted 15 ants on incentive no. 2; 27 on incentive no. 5; 0 on incentive no. 1; 3 on incentive no.3, 9 on incentive no. 4, and 1 on incentive no. 0.

If we analyse these data, we can see that their choices reveal a compromise between concentration of sugar and proximity to the nest. In fact, considering the sequence of incentives in the first situation, the two most visited among the four nearest the nest were those with higher concentrations of sugar. Incentive no. 5, with the highest concentration of sugar, being the fifth and last but one furthest away from the nest, was hardly visited, according to my two counts. In the second situation, with the sequence reversed, the result was the same in a certain way: among the four incentives closer to the nest, the most visited were the two nearest to it and with higher concentrations of sugar.

5 ON THE ATTACHMENT OF *PARATRECHINA FULVA* TO THE SCENT TRACK UNDERLYING A TRAIL AND THE ROLE OF ANTS COMING FROM EACH DIRECTION OF THE TRAIL IN ESTABLISHING THIS TRACK

Previous observations in this work indicated a tendency of *P. fulva* ants on a trail to preserve their contact with the scent track they had been following when this was suddenly interrupted by some object, such as a leather cigarette-case or a cardboard box. This tendency can be perceived in their attempts to crawl under one of these objects at the point where the trail had been cut off. These objects seemed to work on their perceptual organisation as *backgrounds* rather than as the perceptual *figures* in human perceptual organization, using the classical distinction established by Edgar Rubin (1917) and adopted by Gestalt scholars such as Kurt Koffka (1935) and Wolfgang Köhler (1947). The scent track, on the other hand, would act on the ants as a true perceptual figure, and, as such, as the most important part in their perceptual field. The observations below are intended as a clearer explanation of the ants' attachment to a scent track, and the consequences of this attachment to their behaviour.

- *Observation 49 – Behaviour modifications in* Paratrechina fulva *ants faced with a glass tube next to the entrance of their nest.*

I started the observation by placing a 20 cm-long, 1 cm across, transparent glass tube along the junction of a backyard floor and a low step leading to a roofed area. One of the tube ends faced the entrance to the nest referred to in Observation 48, above, at the end of the junction, next to the wall. It lay almost exactly above one short stretch of an ants' trail connecting the nest to a food source, most likely the honeydew produced by aphids and coccids feeding on the sap of some plants in vases. These vases were some metres away from the nest. Figure 69, below, illustrates the situation. My original purpose was to ascertain whether, as I anticipated, on the transition to another environment, that is, the end of the tube, a tendency to return would be observed among *fi.*s, as I thought it happened on their leaving the nest.

After positioning the tube, I saw that the ants on the trail, both those going to and out of the nest, as they reached the end of the tube, would pause for a while, turn from side to side, and crawl into the space between the tube and the junction of the backyard floor and the step. Some minutes later, I took some cotton wads and firmly wrapped and propped the ends of the tube, to ensure, as I hoped, that the ants could only reach and leave the nest by going through the tube. Generally, the *fn*.s, as they reached the tube, tended to return for a while, renew the attempt, turn from side to side, and then, lowering the front part of their bodies, crawled under the wad, where the scent track underlying the trail had been. Then, they returned, some 6-8 cm, went back to the wad, made a detour along the step and proceeded through the space between the tube and the junction. As they reached the wad at the other end, next to the nest, again they tried to crawl between it and the tube. This sort of progress became more frequent over time, and eventually, by going up the step, the ants would reach the half-blocked entrance to the nest. As for the *fi*.s, they went back along the short stretch between the entrance and the tube, and then again, until they finally established a route up the step and the cotton wad next to the nest. Only one ant entered the tube; it moved in circles for a while and then returned. Figure 69 illustrates the situation at the start of the observation.

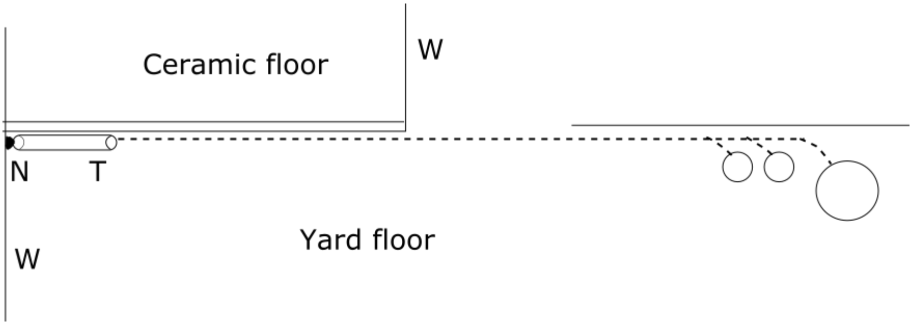

Figure 69: Illustration of the original situation in Observation 49.

Legend:
N: nest
Dotted line: trail
T: glass tube
W: wall
Circles: vases with plants visited by the ants

I adjusted the cotton wad round the end of the tube next to the nest. Now the ants could only go in and out through the tube. It was 2:10 p.m. I watched them for 20 minutes. During this time, a crowd of *fi*.s gradually gathered between the nest and the tube entrance, and another of *fn*.s, at their end of the tube and the nearest junction; they stood still, wavered, tried to crawl under the wad, half-climbed it, using two or four legs; and this while a number of them had already gone up the step towards the other end of the tube. After some time they would halt and return at longer distances – 10, 20, 50, 60 cm – and then come back, hesitate, and walk round the tube entrance.

At the other end, some *fi*.s entered the tube, went as far as 5 cm from the other end, and then returned. It was only when an *fn* went the whole way through the tube, that an *fi* did the same, and went outside towards the incentive (the plants in the vases). This was not repeated for many minutes. Some *fn*.s reached the tube carrying eggs and larvae. Could this be related to the fact that *fi*.s had been prevented from reaching the plants? From that point, they returned, partially at first, then definitely, to the vase from which they had come. Finally, one or other *fn* would enter the tube – sometimes only to hurry out again and run in circles. One or two ants eventually went all the way through the tube, and a hesitating path for *fi*.s was established on some stretches inside the tube, especially by the open end.

After some time, the following was observed: if, on reaching the tube, an *fn* came across an *fi* coming out of the tube, it halted, turned to left and right, then went into the tube until it reached the other end. When there was no *fi*, the *fn* could return for a while, enter the tube in a hurried, wavy march, or, in some cases, go all the way through the tube. I noticed groups of 5 or 6 *fn.s* round the nest, moving in circles on the floor of the roofed area and the backyard, as if searching for the nest.

Coming across the scent track seemed to reassure *fn*.s. However, I noticed that some of them, already inside the tube, would start running around. I saw some *fn*.s "sniffing" and cleaning their antennae when near the entrance of the tube, and *fi*.s doing the same inside it. In the first successful attempts to cover the path inside the tube, I noticed that *fn.s* proceeded with slight undulations and as if skidding. *Fi*.s meandered. At about 4 p.m., I interrupted the observation, but did not remove the glass tube.

On the following day, at 11 a.m., with a temperature of 18ºC and a light drizzle, I resumed the observation of the ants' behaviour inside the tube and while going in and out of it. The *fn.s* came from the vases and reached the tube by following the junction of the floor and the step leading to the sheltered area. First, they came across the cotton wad; in order to reach the tube, they had to turn a little to the left, since this was slightly away from the junction. Generally, they paused for a while before entering the tube, which seemed natural, since the surface was uneven, with the surface of the tube acting as a sort of step between different levels. Their progress was normal inside the tube. As for the *fi*.s, part of them went out of the tube in a normal fashion, and proceeded along the trail. Some of them, however, halted before entering the floor, briefly turned to left or right, moved in circles round the floor, and went back again. I thought this was normal too, since not all ants were foraging or focused on the trail. In fact, one *fi* coming out of the nest went into the tube carrying the remains of an insect, went on to the other end, then turned some 3 cm to the right along the floor, and then disposed of its burden. It was a rubbish collector, and, interestingly, its behaviour showed that the end of the tube was now their way out of the nest. Another ant went through the tube and towards the vases carrying an aphid; I do not know what it did to the animal. Many authors say that a number of ants deal with aphids and other sap-sucking animals as cattle, taking them inside their nests and relocating and herding them on some plants – as I have frequently observed. At 12:07 p.m., I finished the observation and removed the tube.

Four days later, the trail again followed the junction of the backyard floor and the low step leading to the roofed area. My intention was to see what would happen if the tube, once the path inside it had been re-established, had its ends reversed, from distal to proximal and vice-versa. I laid the tube in the same position and wrapped its ends with cotton, as I had done before. Now, however, I used a tiny piece of a wooden board to prop the end farthest from the nest.

Before changing the position of the tube, I saw that instances of reorientation and pauses only occurred near the piece of wood. Inside the tube, *fn*.s would preferably walk on the lower surface, and proceeded in a wavy march, now in wide, now in short bends, but never used the upper half, with their backs facing downwards. There was greater variation among *fi*.s, and the curves in their course were more frequent and narrow; they never used the upper half of the tube. It should be noticed that, differently from what had occurred some days before, directing the trail into the tube was easier than before. On that occasion, the ants had evinced a stronger and more persistent attachment to their previous path. I believe that their willingness to enter the tube now was due to their experience, preserved even after four days.

I reversed the tube and watched the trail for some minutes; nothing occurred that might be considered an effect of this alteration. The scent track underlying the trail certainly did not inform whether the ants moving through the tube were going towards the nest or the food incentive.

Seeing that reversing the ends of the tube had no effect on the trail, I decided to turn it on its axis and disconnect the points of entrance and exit and the points on the floor where the transition was made, next to the ends of the tube. So I rolled the tube in a half-circle round its axis, without altering its position. After this operation, the track inside the tube and the track on the floor were no longer contiguous, but on different levels. The path usually taken by the ants inside the tube was now on the upper part of it.

Changes in behaviour occurred at once. *Fn*.s gathered on the piece of wood next to the entrance; they halted, turned from left to right, "sniffed" (their antennae in a V position, moving up and down), and, moving their heads vigorously, they tried to move between the outer surface of the tube and the cotton, and then went back. When the odd ant happened to enter the tube, it proceeded quickly, its march interrupted by pauses, followed by brisk, energetic motions of the head, "sniffing", forelegs raised. Progress with sideway dislocation was common, with ants going up and down as they proceeded. One or other ant would cover some 5 cm inside the tube, turn back, and, taking the upper surface of the tube, head to the nest in an undulating course. *Fi*.s, on the other hand, also exhibited the same sort of progress, going up and down, now on the left, now on the right, but many of them covered the whole course inside the tube using the upper surface, with their backs facing downwards.

In a few minutes, oscillation gave way to more continuous paths. I rolled the tube back to its original position. Instances of crowding, reorientation, and “sniffing” at the entrance to the tube, as well as of waving courses inside, had clearly ceased. Again I rolled the tube, now at a 90° angle. Again, as in the first trail, there were signs of disturbance, followed by increasing normalisation in behaviour.

In short, disconnecting two stretches of a trail soon leads to major modifications in the ants’ behaviour; this was not the case when the directions on a given stretch were reversed. It should be pointed out that *fn.*s, more extensively observed than *fi.*s, seemed to base their orientation, to a slight extent, on their recognising the tube or its texture, etc.: they would hesitate at the entrance to the tube or on the piece of wood; however, once inside the tube, they tended to move on, even in the absence of a trail inside, but exhibiting the signs of disturbance mentioned above (pauses, reorientation, head movements, etc.).

I am concluding this series with a further observation with a transparent glass tube. The following morning, the cotton wad wrapping the end of the tube next to the nest was somewhat askew, while the wad at the other end was gone. Probably, since the previous night, the trail had resumed their previous course, along the junction of the floor and the step, and now marched under the outer surface of the glass tube. I replaced the cotton wads to ensure that the ants would have to enter the tube to come in and out of the nest. As an effect, soon there was a crowd of *fn.*s trying to crawl under the wad farthest away from the nest, as if they could feel the scent track underneath; which clearly seemed to be the case. The ants meandered back for a while and tried again to crawl under the wad. The trail took longer to go inside the tube – about thirty minutes – than it had the first time, and the process was partial and imperfect. I think this was because the outside of the tube and the part of its surface next to the soil had become orientation aids for the ants. Their apparent stupidity – their prolonged resistance to enter and explore the tube – stands in contrast with their greater ease in dealing with previous changes in the position of the tube. However, I do not think this is a sign of stupidity, but, rather, an expected and understandable response: the ants had marched with the tube to their side and above them; they persisted in this orientation, the more so because they could feel the scent track of the trail under the wad. It should be noticed that *fi.*s also took some time in looking for gaps in the cotton wad between the wall and the end of the tube next to the wall.

The conclusion to be drawn from these observations and experiments is quite clear; *Paratrechina fulva* develop a strong attachment to the scent track underlying their trail as an aid to orientation; this attachment is clearly visible in their efforts to find a lost scent track.

5.1 The ants' attachment to a trail as related to the orienting property of the underlying scent track, not to an automatic march-eliciting function of pheromones

It should be made clear at this point that the ants' attachment to a trail is not, as one might think, a consequence of their having their march automatically elicited by pheromones forming the chemical track underlying the trail. I think the function of this track, or its pheromones, is to provide orientation, not to prompt their march. That this is so can be seen in many facts presented in previous paragraphs as well as in some still to be reported. Among the latter, one should mention that the attachment to a trail and its underlying scent track is not exhibited by workers engaged in other tasks inside the nest, such as tending to the queen and immature individuals, extending and cleaning the nest, cases in which some of the activities involved are carried out outside the nest. In such a case – for instance, while carrying an immature individual to another location, such as a temporary or secondary nest, or carrying corpses or waste to be disposed of outside the trail, a worker may come and go through an active foraging trail and remain indifferent to all its operations. How, then, could one explain the attachment to the trail frequently observed outside the nest? I think it comes from the motivation prevailing among individual workers at a given moment. It seems that the ants outside are often engaged in foraging and provisioning the colony. It is known that the functions carried out by the workers in a nest, especially when they are monomorphic, change according to their ages, and that there is always a succession of activities to be performed by workers as they grow old. Foraging is generally carried out by older workers, which evince a special motivation to collect food and distribute it among their companions inside the nest. This motivation can be seen in their promptness, while on the trail, to regurgitate food to newly-arrived nest-mates, and in their repeated excursions to provide food for the ants inside the nest.

Other facts reveal that the function of the olfactory track underlying trails is to provide orientation, rather than trigger and preserve their march along the track, such as the tendency of these ants to establish a shorter or straighter route to the nest or the food source; this tendency leads them to temporarily leave the trail, as already pointed out. Sometimes just the opposite is observed – for instance, a trail crossing an open, smooth surface like a tiled wall, shows a tendency to leave this route for a path along the junction of the tiles and a wall; though longer than the original one, the new course is more efficient in terms of orientation.

5.2 AN ATTEMPT TO FIND OUT WHETHER THE ANTS ON A TRAIL, WHILE MARCHING TOWARDS THE NEST OR A FOOD SOURCE, RELY ON CUES THEY WOULD HAVE NORMALLY FOUND WHILE WALKING ON THE TRACK AND THE SURROUNDING AREA

It was seen in the observation above that reversing the ends of a glass tube on its plane, without rotating it round its axis, did not have any perceptible effect on the behaviour of the ants on the trail, whatever their direction. This is an indication, as already said, that the olfactory track underlying the trail has no element that can inform the ants whether they are going towards the nest or a food source. Would it not be possible, however, that these ants had a memory of their destination, based on such cues as the place they had come from – their nest or a food source – or those found on the way, such as the direction of light and winds, their having the junction of floor and step, or wall of outhouse, to left or right, or, still, of their coming across bloated or thin nest-mates on the way? The experiment in which I blew on single ants, generally at different points of their course along the trail, coming from any direction (Cf. Observation 37), pointed out that, as already shown, their cognition as to the location of the nest or the food source, and the direction to be followed, was admirable. I carried out the following experiment in order to ascertain, or at least to conceive some notion about it, whether the ants would use other cues, such as those mentioned above.

- *Observation 50 – Behaviour of some* Paratrechina fulva *ants transferred from a trail with a piece of cardboard and released at a different point of the same trail.*

The trail used in this observation was the same as in the previous one, that is, a trail connecting a nest (at the point where a wall joined the junction of a ceramic mosaic floor and a low step, and another wall) and a food source: honeydew produced by sap-sucking insects in vases of *Anthurium*, some 20 cm away from the junction and 3 m away from the nest entrance. Figure 70, Observation 50, is an approximate illustration of the situation.

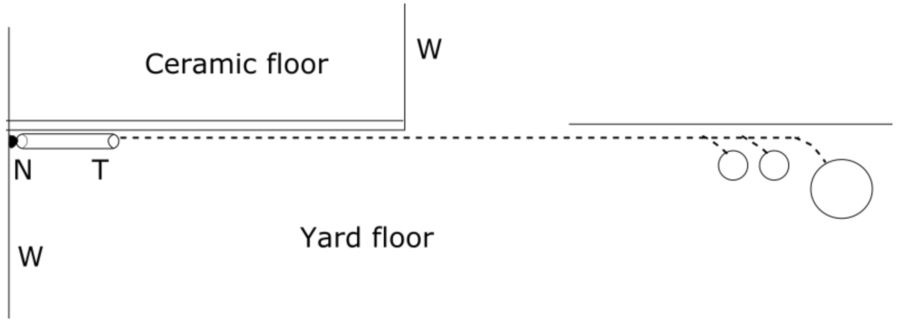

Figure 70: Illustration of the original situation in Observation 50.

Legend:
N: nest
Dashed line: trail
T: glass tube
W: wall
Circles: vases with plants visited by the ants

The observation concerns an experiment in which some ants were captured on a trail, one by one, with the aid of two cards, as already described. Once an ant was on the card it was moved to another point of the trail or the neighbouring area. The objective was to see how many *fi.*s (ants going towards the incentive) and *fn.*s (ants going towards the nest) would, after being captured and removed, stick to their course towards their original destination, and how many would head to the opposite destination. I thought the results could show whether these ants generally had a cognition as to the direction they had been following before being captured, even though unable, once on the card, to rely on a memory of space already covered; and also, as far as possible, to ascertain whether the ants, after being captured and removed, would rely on cues available in their new position on the trail – a harder task.

A problem with results was anticipated from the start. I expected part of the results to be biased, as in the experiment on the effects of blowing on an ant on a trail. *Fi*.s would tend to return to the nest, since this is the place they tend to seek after an experimental alteration on the trail. As for *fn*.s, the same factor would reinforce their orientation towards the nest. These trends would apparently suggest that the nest is a safety point to which they retreat more often than the incentive when a sudden alteration takes place on the trail, even though the incentive may share some of this quality because of cavities that may offer shelter and protection.

See, below, the results of the experiment, under the various conditions:

1) Ants captured and released on a stretch 70 cm-1.40 m from the nest:

Fi	***Fn***
Continued towards the incentive: 5 out of 7: (71%)	Continued towards the nest: 9 out of 9: (100%)
Returned to the nest: 2 out of 7: (29%)	Returned to the incentive: 0 out of 9: (0%)

2) Ants captured near one end of the trail and removed to the vicinity of the other end, towards which they had been going when captured:

Fi	***Fn***
Continued towards the incentive: 8 out of 11: (73%)	Continued towards the nest: 9 out of 11: (82%)
Returned to the nest: 3 out of 11: (27%)	Returned to the incentive: 2 out of 11: (18%)

3) Fi.s captured and released near the nest; *fn*.s captured and released near the incentive:

Fi	***Fn***
Continued towards the incentive: 2 out of 5: (40%)	Continued towards the nest: 6 out of 7: (86%)
Returned to the nest: 3 out of 5: (60%)	Returned to the incentive: 1 out of 7 (14%)

4) Captured near the incentive and released on the middle stretch the trail:

Fi	***Fn***
Continued to the incentive: 0 out of 7: (0%)	Continued to the nest: 2 out of 2: (100%)
Returned to the nest: 7 out of 7: (100%)	Returned to the incentive: 0 out of 2: (0%)

These results show that most *fi*.s tended to go on marching towards the incentive when captured and released halfway along the trail, and also when captured and released near the incentive, towards which they had been going. Under other conditions, most of them tended to return to the nest, which they had left to reach the incentive, especially when captured and released near the incentive, which is surprising. I suppose this was because they were the more disturbed by the alteration the more they had tried to reach a destination.

Then, collecting all the results, regardless of the place where each ant had been captured and released, I reached this situation:

Fi	***Fn***
Continued towards the incentive: 17 out of 28: (60.7%)	Continued towards the nest: 30 out of 34 (88.2%)
Returned to the nest: 11 out of 28 (39.3%)	Returned to the incentive: 4 out of 34 (11.8%)

The results under each condition and as a whole leave no doubt as to the tendency of *fn*.s to continue towards the nest, and of more than half the *fi*.s to return towards the nest, probably, I think because they associated it with shelter and safety.

It must be said that I always tried to handle the card with a captured ant in such a way as to ensure that it would leave the card in the opposite direction it had been going. However, I was not invariably successful. There was a remarkable case in which two *fn*.s, as I rotated the card to release them on the way to incentive, would make up for the rotation and remain, like compasses, oriented towards the nest.

One objective of the experiment was to ascertain whether the ants, after being captured and repositioned so as to reverse their direction, would stick to their original course; and, therefore, whether they had a cognition of their orientation in relatio y cannot be said to be general, since they were perceptible only in a few ants. One factor was that, after the experimental alteration, some ants would walk with raised gasters and leaning forward, as if paying closer attention to the olfactory track underlying the trail. Another factor was a tendency of some *fi.s near the nest,* to return to it on meeting head on with another *fi* or *fn* going toward the nest.

- *Observation 51 – Behaviour modifications in* P. fulva *upon being suddenly faced with a variously oriented, long, cylindrical object placed on their trail.*

A thin branch fallen on a trail of *P. fulva* makes them at first to hesitate and some of them even to return for a while; however, ants will soon go over the branch and follow the original course of the trail, and their behaviour will become normal again. A falling branch, leaf, flower, or any other part of a vegetable on the trail is probably a frequent alteration leading to behaviour changes in their environment, as it is perhaps shown by the relative ease with which they seem to handle it. But then how would they behave on being suddenly faced with an unknown object, resembling a small branch, on their trail? And what would be the effect of its being differently oriented in relation to the trail on the behaviour modifications to be observed? The observation below was carried out in order to answer these questions.

In this observation I used leads for propelling pencils of two different sizes: two 16mm-long x 1.5mm-thick leads, and two 20mm--long, 1.5mm-thick leads.

I initially rolled a smaller lead between my thumb and forefinger and laid it across a trail established along the junction of a floor and a wall. The lead was oriented in such a way as to leave more free space to the left both of *fis* and *fn*.s; one of the ends of the lead was 4 mm away from the junction.

What followed clearly evinced the influence of the junction on the orientation of the ants, as it might have been expected, given their tendency to form trails along junctions and use them as orientation aids. Both *fi*.s and *fn*.s, on reaching the lead, walked a little sideways, *fi.s* a little to the right, *fn.s* a little to the left, faced the object again, then went sideways again in the opposite direction until they attained the other side of the obstacle, the free space between it and the junction. Figure 71, below, illustrates the situation.

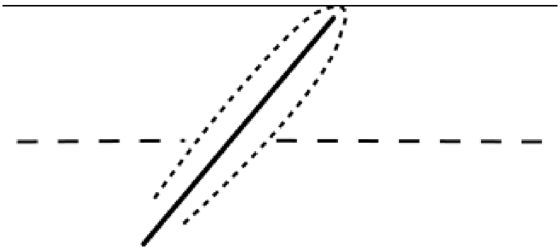

Figure 71: Orientation of ants faced with a 16 mm-long, 1.5 mm-thick lead on the trail, one of its ends being 4 mm away from the junction followed by the trail.

Legend:
Larger whole line: junction of wall and floor
Smaller whole line: lead
Longer dashed line: trail
Smaller dashed lines: courses taken by *fi*.s (ants coming from the nest, left of the trail) and by *fn*.s (ants coming from the food incentive, right of the trail)

At other moments in the observation I again checked the courses taken by the ants on coming across a variously oriented lead on the trail and near the junction. Since dealing with the effect of stimulation heterogeneities on the orientation of the ants, a subject already discussed in this chapter, is not the purpose of this observation, I will not discuss again the cases in which effects stemming from the presence of such a junction are seen. I will consider only those in which there are no other stimulation heterogeneities at work but a trail and a lead.

As a first observation of this kind, I laid a short lead on a trail established on a ceramic mosaic floor, its longitudinal axis slantwise to the trail, with more space available for the ants, both *fi.*s and *fn.*s, on the left than on the right, as shown in Figure 72, below.

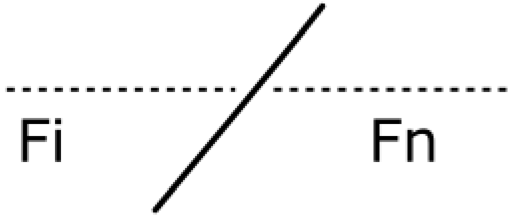

Figure 72: Positions in which a lead was laid on a trail.

Legend:
Whole line: lead
Dashed line: trail on a floor
Fi: ant marching towards the food incentive
Fn: ant marching towards the nest

At first both *fi.*s and *fn.*s, went forward into the area with more available space, moving slightly sideways to their left; the lead acted as a sort of watershed, leading the traffic from each direction to opposing ends of the trail. Figure 73, below, illustrates the situation.

After some time, *fi.*s were wavering before the lead, and going somewhat sideways, first to the left, then to the right, until facing the object again, when they would then turn right, apparently influenced by the track of the *fn.*s they seemed to be looking for. We might say that, on reaching the end nearest the lead, and not finding the track of the *fn.*s, they hesitated before going either left or right, until eventually going either way. If they continued by turning left, where there was no track of *fn.*s, their march would be frequently interrupted by brief pauses, until their reaching the trail again. Figure 73, drawing on the right, illustrates the tendencies then shown by *fi*.s.

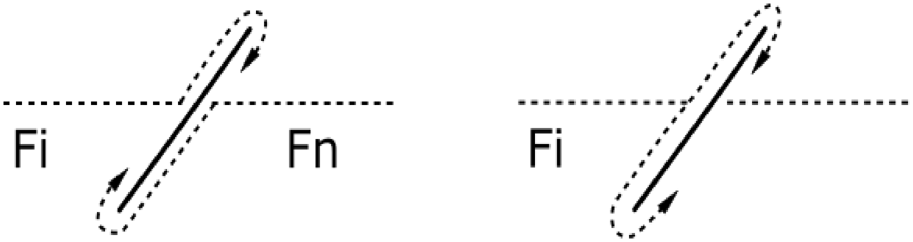

Figure 73: Tendencies in behaviour shown by ants coming from both directions (drawing on the left) and by fi.s, over time, apparently influenced by their search for a track of *fn*.s (drawing on the right).

Legend:
Whole line: a 16-mm long, 1.5-mm thick lead
Dashed horizontal line: trail
Dashed lines transversal to the trail: orientation of ants on facing the lead
Fi and *fn*: respectively, ants going towards the incentive and the nest

I then reversed the lead, that is, I left more free room on the right than on the left. There was a division in the traffic, with ants from both directions deflecting their march to the right, in order to find again the trail on the other side of the lead. *Fn*.s, however, could also, on being deflected to the right, go almost to the end of the lead, going somewhat sideways, and then return all the way back and past the other end. It seemed important for both alternatives the lengths of lead to either side of the ants. With the imperfect positioning, *fn*.s would reach the end more often than the middle of the lead; and there were two conflicting conditions to influence the choice: although there were fewer obstacles on the right, the distance to be covered in this direction was greater. As for the *fi*.s these two conditions coincided: there were fewer obstacles and a shorter course on the right. This difference in conditions apparently explains the differences in orientation of *fn*.s and *fi*.s on being faced with an obstruction. Figure 74, illustrates the orientations of *fi*.s (left), and *fn*.s (right).

Figure 74: Orientations of *fi*.s (left) and *fn*.s (right) before a lead across the trail, not in the middle of its length, but nearer one of its ends.

I then tried using a longer lead: 20 mm long and 1.5 mm thick. I laid it across the trail, oriented in the same way as the shorter lead in the preceding instance. As *fn*.s arrived, they turned right, and, a little sideways, deflected their course and went on; some also turned right, went almost halfway to the other end, went left for 1-1.5 cm, turned right again, always tending to go sideways, and deflected their course. Figure 75, below, illustrates the courses taken.

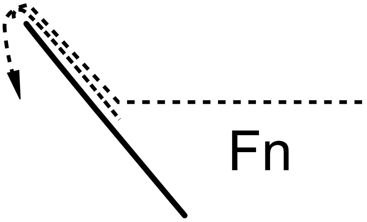

Figure 75: Illustration of courses taken by *fn*.s faced with a longer lead on the trail; the trail intersects the lead at a point near one of its ends and its middle.

Legend:
Whole line: lead
Dashed line: course of the trail before reaching the lead, and courses taken by the ants as they reached it.
Fn: ant marching towards the nest

The *fi*.s, on the other hand, turned right as they reached the lead, where they had a freer course, went on for about half its length, or a little more, went left, always tending sideways, deflected their course and went round the tip of the lead. Occasionally, *fi*.s would either go to the other side of the lead by turning right or by climbing it, after some oscillation from left to right and back. Figure 76, below, illustrates the former behaviour on the left, and the alternative behaviours of other *fi*.s on the right. As for ants going over the lead, this apparently occurs because, after some time facing the lead, they gradually adjust to its presence, until it ceases to be an alteration and becomes part of their habitual behaviour environment.

Figure 76: Courses *fi*.s were able to take after reorientation of the lead.

Legend:
Whole lines: 20 mm long, 1.5 mm thick lead
Dashed lines: course of the trail of *fi*.s before reaching the lead, and courses taken by them when next to it
Fi: ants coming from the nest towards the food incentive

It must be mentioned that I did not record separate individual behaviours because of their mutual influence and their development over time: each ant seemed to act also on the basis of deviant tracks left by other ants; therefore, it did not seem important to point out how many ants did this or that, since this was the cumulative result of unequal influences.

I end this experiment with a firm conviction that *fi*.s tend to follow a trail more thoroughly, or are more attached to its underlying olfactory track, than *fn*.s. I also conclude that in both groups of ants there are two tendencies, which, in this case, may work in opposition to or in conjunction with each other. One is the tendency to preserve the original direction of the body axis before an obstruction, since they often walked sideways beside it; the other is the tendency of not going too far from their original route. Consequently, when facing an obstacle, they chose the way with the shortest stretch to be covered away from the trail and the least change in direction.

Given the above on the tendencies in the orientation of the ants, it is clear why natural obstacles are not overcome in a persistent and steady way by taking the side of a branch with less available space; this occurs rather by taking the other side, with more available space, or even by going over the obstacle, which is more common, thus reconnecting the two stretches of the trail separated by the obstacle.

6 FUNCTIONS OF TRAILS IN THE LIVES OF ANTS

In an attempt to clarify the first and prime function of trails in the lives not only of *Paratrechina fulva*, but, certainly, of other ant species, I will report an observation, one of the first I carried out, which helped me to find my bearings on this question.

- *Observation 52 – On a trail established in an area of a floor in which the ants' scent track was not preserved; and the role of accidents in the environment in the orientation of the trail.*

This observation took place in the garden mentioned in some of the observations above, comprising two flower beds separated by a cement floor and bordered with a 5.5 cm wide and 1 cm high concrete ridge.

A few days before, some bits of sweets had been placed as food incentives on a tap and on a water meter cabinet in this garden. These incentives had gone dry and were no longer visited by the ants, until a light afternoon rain, lasting for some thirty minutes, soaked and softened them. As I went into the garden after the rain, I saw the largest number *P. fulva* ants I had seen so far; they were excited and formed a trail starting from their already mentioned nest, a hole in the same wall as the tap, and leading to the two incentives. Another trail, also very crowded, came from a second nest in the junction of the cement floor and another wall, opposite the first one, and proceeded along the floor and one of the ridges and then joined the other trail. It is this trail coming from the second nest that is really important in this observation. Figure 77, below, illustrates the situation.

The second trail marched on a strip of the cement floor leading to the entrance of our house for some 1-1.20 m until it reached one of the ridges bordering the flower bed and joined the trail coming from the first nest. It was a short route to the incentives, but not the shortest, which would be a straight line between the nest and one of the baits. It was not either the safest in terms of orientation, which might be provided by following the junction of the floor and this second wall, the house wall, and the first wall mentioned; however, the ridge bordering the flower bed supported their orientation and prevented them from going astray on their way to join the main trail coming from the first nest. A point to be stressed about this trail is that, while covering this 1m-1.20m stretch, devoid of elements that might support their orientation, the ants proceeded by fits and starts and zigzagged; the trail varied in width from 2 to 3 cm in this area, whereas it was linear when bordering the ridge. This was because, besides the lack of orientation aids provided by some heterogeneity in stimulation, the floor was wet and probably did not hold the olfactory track laid by the ants. Although prevented from following an olfactory track and relying on features of the terrain to reach the ridge, these ants, however, exhibited a sharp sense of direction and an admirable cognitive representation of the area. However it was, as compared with this stretch, the trail following the ridge of the garden bed was faster, more uniform, and much more efficient as a means of exchange with a valuable element in their environment. For this is, one might say, the first and foremost function of a trail or, rather, of the olfactory track on which it is established, and the probable reason for evolution to have endowed most, if not all, ant species with the tendency and ability to use it.

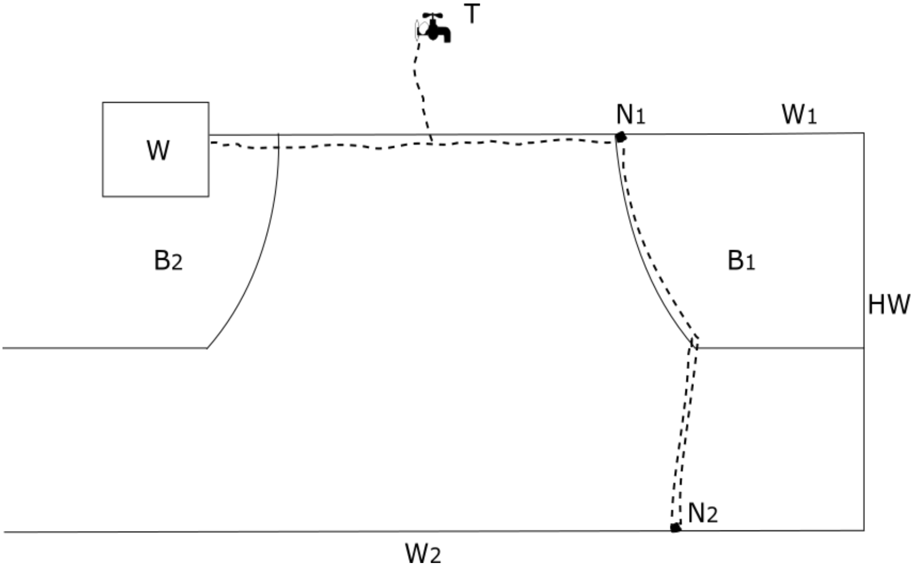

Figure 77: Approximate illustration of the situation in Observation 53.

Legend:
Dashed lines: trails coming from 2 shared nests
W_1 and W_2: walls separating the garden from neighbouring properties
N_1 and N_2: two nests occupied by the same colony of *P. fulva*
B_1 and B_2: flower beds separated from the cement floor by two concrete ridges
HW: wall of the house
T: tap with a piece of a sweet on top
W: water meter cabinet, also with a piece of a sweet on top.

This function, of providing orientation, speed, and efficiency to exchanges with the environment is the same that prompts humans to level and pave their routes to places of interest. As if emulating humans, some ant species not only rely on trails in activities of their interest, but also remove vegetables, straw, small lumps and pieces of rock to improve efficiency of traffic and transportation. This is seen, for instance, among ants that, like leafcutters, cultivate fungi as food in beds prepared with masticated leaves. As we see them carrying vegetable fragments often larger and heavier than them, we can understand why they have to keep their paths clean and unobstructed.

A second and very important function of a trail is that it works as a sort of probe, checking into the safety and normality of the environment in which the ants move. In fact, as thoroughly shown in this investigation, it is practically impossible to alter the environment of an established trail without prompting the ants into a state of alertness and inspection, then a readiness to interact with the alteration, positively or negatively, and even into avoidance and hurried flight. Especially in the latter cases, the trail is interrupted and it is re-established after prolonged or repeated exposure to the alteration, when it is made part of their mnemic record of the behaviour environment.

A possible third function seems to be that trails form a sort of natural extension of their nest, enabling the ants, especially when a trail has been established for a while, to move from a relatively stable and safe environment into a relatively unstable and changeable one, with breezes and winds, light and shade, unfamiliar objects, etc., with reasonable safety. This is suggested by a decreasing hesitancy to leave the nest and an increasing readiness to enter the trail. However, this may be but an outcome of the first function mentioned above: the trail itself becomes an orientation aid, a heterogeneity in the environment, which usually is seen as constant and unthreatening over time – and this, as already seen, makes the ants unprepared for a sudden and unusual alteration in the path.

7 SOME CASES IN WHICH A TRAIL EXCEPTIONALLY CONTRIBUTES TO NON-ADAPTIVE BEHAVIOUR

Trails, as we have seen, are generally an important adaptive resource for ants. However, there are cases in which they may not contribute to a non-adaptive behaviour. This is shown, I believe, in the two observations reported below, in which the ants seem to fall into a trap created by their own instincts, as T. C. Schneirla said in one of his works.

- *Observation 53 – On incessant trails without a clear objective in* Solenopsis saevissima Fremont Smith, 1885*, first in an artificial nest, then in a ceramic planter.*

Once I captured a colony of *Solenopsis saevissima* and kept it for a few days in an artificial nest, basically, a plastic bowl filled with soil and placed in a basin with water, a successful device to prevent them from escaping. I noticed that for some days a number of workers had established a practically endless trail along the wavy border of the bowl, in both directions, with apparently no other purpose but walking. No ant was seen on the outer surface of the bowl, but some would occasionally walk on the soil inside. One ant went round and round the inner surface of the bowl, a little above the soil.

I placed a piece of suet on the border of the bowl in an attempt to interrupt the trail and keep them from dying of exhaustion. Many of the ants, coming from boh directions, would raise their outstretched antennae, sometimes their heads, and even touch the suet with their antennal funiculi, but then they retreated. Many of them would make a detour and walk for a while on the surface of the bowl. Since the suet made them retreat, we might say it was not food they were after, for I had often seen individuals of this species on pieces of suet in the rubbish container in our yard. But they seemed to require something, for they formed the trail again. It is not unlikely that they did so because following a trail is an automatic action. However, I do not think so, because, as already said, ants disposing of waste or looking after immature individuals will not follow a trail going out of the nest. It could be the case, however, that foragers will join an established trail because they are used to the fact that trails in general lead to a required objective.

Some ten minutes later, one or other ant would climb the suet. Their attachment to the olfactory track was apparently ending, in part, for one or other ant would also come to the soil inside or attempt to do it, from different spots on the surface of the bowl. On the other hand, no ant walked on the outer surface of the bowl, and this seems to point to the experience that this would not lead them outside or to the soil inside. Fifteen minutes later a linear trail was formed connecting the nest in the soil and the suet, right under the incentive. Some of the ants on the trail marching on the rim of the bowl would stop before the bait and climb it, or wave their antennae at it, go round in a detour and join the trail further ahead.

One hour and fifteen minutes after the suet was positioned, the situation was the same: the ants paused before the incentive; some of them climbed it, while other, apparently obsessed with the trail, went round and joined the trail again further ahead. However, the number of ants on this trail was quite lower.

Five hours and ten minutes after the bait was laid, only one ant was marching on the rim, and only one was on the suet, whereas in the morning about 60-100 ants had been on the circular trail. They had, therefore, escaped the trap of a track without a destination. They had probably gone back to the soil, as there was no ant on the outer surface of the bowl.

On another occasion, I saw a trail of *Solenopsis saevissima*, similar to the one above, on a ceramic planter in which I had planted some bulbs. The ants, which I saw only the following morning, had come with the soil, taken from a bed fertilized with waste I had dug in. They marched on the upper edge of the planter, but I do not remember whether they went both ways or not.

I tried to interrupt the trail, and I partially did it by removing part of the soil covering the rim of the pot. Some ants, after hesitating or pausing, went on, while others went into holes in the soil, probably dug by themselves, next to the half-buried bulbs.

Later on, I saw a similar trail on the upper edge of the planter. I saw three dead ants which had probably fallen from the pot into the saucer under it. Perhaps a trail like this could spontaneously stop, but I did not go on with the observation. I removed the ants, one by one, and released them in the bed from which the soil had been taken.

The two endless trails this ant species had formed on the upper edges of the plastic bowl and the ceramic planter, not on their vertical surfaces, and I think this was because of some special conditions: these edges offered a continuous, circular track, and were also the only areas of the containers on which the ants could stand and walk on a horizontal plane, and on a surface narrow enough to resemble the linear scent track which ants apparently deposit on a floor as they move.

- *Observation 54 – On a clearly circular trail of* Labidus coecus *Latreille.*

In an autumn morning, as I and my family were about to leave our farm, our caretaker called me to see "an interesting thing". He opened the door of a wooden shed, with a dirt floor, on which, 30 cm away from the door, there was a perfectly circular trail, with a 10 cm-radius. In my estimate, there were at least some 200 ants of different sizes, including a black "soldier" twice as large as the average, which, as our naïve caretaker said, was "leading" the procession. Their march was perfectly synchronised and uniform, and, without exceptions, anticlockwise. Figure 78, below, is an approximate illustration of the trail.

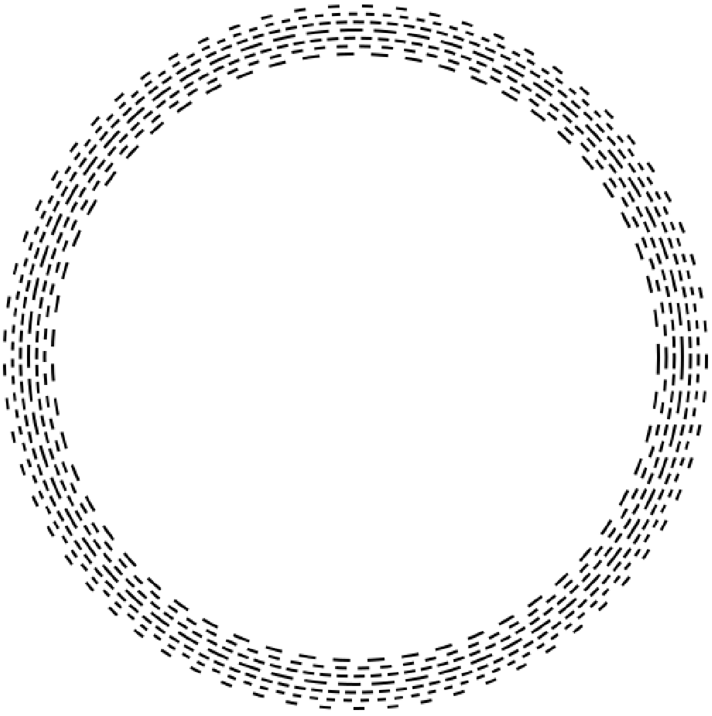

Figure 78: Approximate representation of a ring-shaped trail of *Labidus coecus.*

Legend:
Dots and dashes: marching ants

It was a redundant trail, without any objective, into which the ants had been led by their own instinct, or, more precisely, by their strong attachment to the olfactory track underlying trails. I think this group of ants had lost their way and were now isolated because the heavy rain of the previous night had washed away the olfactory track that might lead them back to the main trail formed by most of their colony. Some workers had, I suppose, walked in a circle, leaving an olfactory track that had been followed by others and attracted the ants isolated from the band. I could not understand how the main group's track had disappeared, since the floor inside the shed was not wet. However, I cannot discard the possibility that some rain had fallen near the door and lightly moistened the dirt floor, thus isolating the ants that had gone further into the shed.

The width of the trail varied from 1cm to 1.5cm, but the centre was stable, a sign that their march was oriented by a scent track, perhaps not exclusively, but in combination with the onward push of the mass of marching ants; hence, the variation in width. Speed was the same for all workers, and this imparted an impressive effect of stability to this moving object. Variations in the width of the trail were caused by changes in its outer rim. In an attempt to interrupt this vicious circle, I placed a piece of a corncob secant to the trail. Ants crowded the area and then traffic receded. Among the crowd, the "soldier" taken as the leader by the caretaker, turned left and right and then retraced its steps with no followers. In fact, many ants had independently reversed their courses, but covered only one third of the way before resuming their course after coming across ants going the other way.

I placed the corncob secant to the ring two more times, and in both cases the ants crowded the area, went back for a while, and then resumed their anticlockwise march. I also placed a pebble in the centre of the ring. For ten minutes there was not the slightest change in their march along the trail.

The circle they formed was perfect, at least along its inner edge. Once in a while, some ants would go 2-3 cm away from the ring and return. Within 1 m around the area, some isolated workers were seen aimlessly roaming about, probably remnants from the main migratory current. Their pace was lower than that of the ants on the trail. I captured two of these ants and placed them 2 or 3 cm away from the trail. They roamed about for a while, but soon joined the trail, and could no longer be distinguished by their speed.

The speed of the ants on the trail was generally uniform, as already said, and high and lively, as during a typical “raid”. This was an impressive show to my wife and my caretaker’s wife. The latter said it seemed as if the ants were playing chasey on a merry-go-round.

What I observed in this and the preceding trail made me fear for the ants and wonder what would happen as they became exhausted. However, neither I nor the caretaker could wait to see what would happen.

I believe this and the preceding observation show that trails may not always be beneficial to ants and, sometimes, though not frequently, may be even harmful.

CHAPTER V

MISCELLANNEOUS

1 CONTENTS OF THIS CHAPTER

In this chapter I report, among other topics, observations carried out on a variety of subjects, issues, or problems – not always related to *Paratrechina fulva* Mayr, 1862 – such as nest relocation, behaviour sensitisation, the existence or not of a cognitive motivation in the behaviour of ants, inefficient behaviours, behaviour biases, some uses of elevated mazes, the use of external referents and internal spatial representation in orientation, purpose induction, factors in experience determining fight and flight, as well as responses of other local ant species when faced with crushed nest-mates.

2 BEHAVIOUR OF *CAMPONOTUS CRASSUS* MAYR, 1862 DURING NEST RELOCATION

This species in the *Formicinae* subfamily is formed by small, stocky, dark grey ants, with workers varying in size from 3 mm to 1 cm; they live especially on the excretions of aphids, coccids, leafhoppers, etc., as well as on fruits. These ants are usually found in wooded areas, gardens, and orchards, and generally nidify in hollow branches and trunks and underground, but also, in urban areas, under tiles and in cracks in floors and walls. They are active during the day and their sight is good. I noticed, for instance, that individual ants can walk on wide, open floors without the aid of any external material signs, and also that their trails, which are usually persistent or even permanent, are established only towards the plants where the sap-feeding insects they tend are to be found, and this not so much because they need them for orientation, but because they are permanent. Their good sight can be easily perceived by moving a hand near or towards them as they walk on a branch or creeper: they generally halt, after going the other way, then bend their abdomens upwards between their legs and underneath their thoraxes, their antennae extended in a V-shape towards the intruder, in the typical posture they assume when squirting acid from the tip of their gasters at enemy ants. The observation below is an account of the behaviour exhibited by ants of this species while moving to another nest, which, by the way, resembles the behaviour exhibited by *P. fulva* in artificial nests.

- *Observation 55 – Behaviour of* Camponotus crassus *during a forced nest relocation.*

On a sunny afternoon, my neighbour lit a bonfire in his yard. It was made with branches and leaves of a peach tree and some old wood, near a discarded garage door, a corrugated metal sheet we used as a fence between our yards. The bonfire produced a lot of smoke. I suddenly noticed compact groups of *C. crassus* in our side of the fence. There were six of them, all of them on the troughs, none on the crests of the corrugated sheet. When there were a good number of them in a group – 15 in the largest one – the ants stood facing each other. When there were only two workers they would either do the same or stand side by side, sometimes totally still, sometimes moving their antennae. Many of them held larvae, pupae, or eggs. They dispersed and grouped again only when surrounded by a cloud of smoke.

In a range of some metres around the area, many ants walked aimlessly, or rushed about, sometimes turning from left to right and back. They would halt especially by orifices and cracks in the wall and in the cement blocks supporting the corrugated fence. Apparently, they were looking for a new site for the nest. Sometimes they stopped by some groups, touched the antennae of some of their nest-mates, cleaned their own antennae and legs, and then left; once in a while, they would try to snatch a larva from a motionless ant, but not vigorously; these ants resisted the attempt and did not let go of their burden.

The situation persisted. Groups dispersed when hit by smoke and gathered again in groups of 5 to 8 ants over an area of 40 x 40 cm on the corrugated metal. Then I noticed an ant coming out of a crevice next to the low wall supporting the fence; four other ants also walked in the area and occasionally went into the same crevice. Given its speed, the moving antennae, and the relatively few irregularities in its long course on the edge off the fence, this ant seemed quite resolute. I followed it, because it was clear that it had found a proper location for the new nest. It then went into the open surface of the fence in an oscillating march; it burst into the middle of a group of ants, grabbed a larva held by one of them, and dragged them both. The ant relinquished the larva. The snatcher hurried back to the edge of the fence and carried the larva into the crevice.

I saw it coming back towards a second group; again it grabbed a larva held by a nest-mate and pulled vigorously, but the ant held it firmly; the ant tried again and pulled another nest-mate for 0.5 cm towards the edge; then it grabbed a bunch of eggs from another ant; after some resistance, it succeeded and carried the eggs into the crevice. The action was repeated again and again. I noticed the workers would only release their larvae after a strong and determined pull.

As their burden was snatched away, the deprived ants would take any direction, clean their antennae, and approach other groups, in front of which they "jumped nervously" or "thrust their bodies forward" (jolts?), turned to no particular direction, walked in circles or went to the edge of the fence, then went down, I do not know whether in search of new wards, a new location for the nest, or the thief's track. I witnessed these actions a few times. The moving ants would not carry their nest-mates, at least not as long as there were still immature forms to be transported. Other workers, already free from their burdens, walked on and eventually reached a place where the snatchers had probably laid a more perceptible track, for they soon reached the site selected for the nest. Having reached the crevice, they might go out again, to snatch eggs, larvae, and pupae from other workers.

3 ON BEHAVIOURAL SENSITISATION

Under this topic I tried to ascertain whether a given substance, if associated with crushed ants on a trail, which, as we know, cause dramatic behaviour modifications in their nest-mates, would acquire, at least for a while, a stronger power in bringing about behaviour modifications – a phenomenon called "behavioural sensitisation" in psychology. I report below one observation carried out with this objective in mind.

- *Observation 56 – An observation on the possibility of sensitisation of the so-called alarm behaviour in* Paratrechina fulva.

I used in this observation a trail formed on a ceramic mosaic floor next to its junction with a wall. The trail was about 2 m long and connected the entrance of a nest of *P. fulva* in the floor to a cotton wad dipped in water and sugar. It comprised three successive phases: 1) crushing some ants at a certain point of the trail; then observe behaviour modifications caused by a cotton wad dipped in bleach (10% chlorine) placed a little earlier at another point, next to the trail; 2) placing a cotton wad with kerosene – a substance ants are averse to – and observe behaviour modifications exhibited by the ants coming from these two alterations as they passed by the wad dipped in chlorine; the objective of this second observation was to ascertain whether an alteration associated with crushed ants would on its own change the behaviour modifications caused by the wad dipped in bleach, an alteration of a different nature; and 3) finally, replacing the wad dipped in kerosene next to the dead ants with a cotton wad dipped in bleach; and observe again behaviour modifications caused by this association as the ants went past it.

1ST PHASE

One night, under electric light, I placed a cotton wad dipped in bleach halfway along the trail, that is, about 1 m from the nest entrance and 1 m from the lure. Figure 79, below, illustrates this phase of the observation. The wad was placed about 2 cm away from the junction of wall and floor, and about 1.5 cm away from the trail.

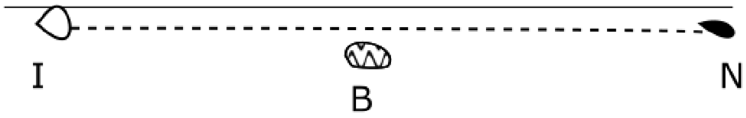

Figure 79: Approximate representation of the situation in Observation 56.

Legend:
N: nest
I: incentive
B: cotton wad dipped in bleach
Dashed line: Trail

I noticed some hesitancy and oscillation in the ants going towards the nest (*fn.s*) as they passed by the wad next to the junction of the floor and wall; this was less frequent among the ants coming the other way (*fi.s*). Some of these, on passing by the wad, would even pause, turn, and "sniff" it. Five minutes later, behaviour modifications were hardly discernible or, at least, less frequent and intense. I washed my hands with water and soap and then crushed three ants on the way to the incentive, some 30 cm away from the wad, and 2 cm from the trail. Returns, intense acceleration, undulating march, hesitancy – in short, the usual dramatic behaviour modifications – were seen in the vicinity. The number of ants decreased and sometimes the trail seemed about to disappear; soon, however, other ants were seen. I sat on the floor, some 50-70 cm away from the trail and started to record the behaviour of *fn.*s going past the wad with bleach. Eighteen minutes later the passage of both *fn.s* and *fi.s* by the dead ants caused far less disturbance than it had at the start of the observation. Record-taking took 25 minutes. Results are shown in column A, Table 14, below.

2ND PHASE

After these records, I placed a wad dipped in kerosene next to the crushed ants, on the same side as the wad dipped in bleach and the bait. The wad had a diameter of about 1 cm and was placed at first some 3 mm away from the group of dead ants. Figure 80, below, illustrates the situation. I then started to record behaviour modifications exhibited by *fn.*s as they reached the wad dipped in bleach, having gone past the set formed by the dead ants and the wad dipped in kerosene. Record-taking lasted for 25 minutes. Results are shown in column B, Table 14, below.

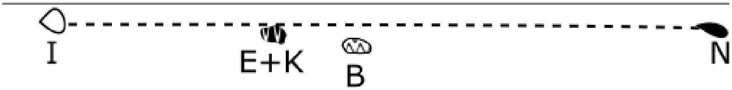

Figure 80: Approximate representation of the situation in the 2nd phase of Observation 56.
Legend:
N: nest
I: incentive
B: cotton wad dipped in bleach
E+K: Crushed ants and wad dipped in kerosene
Dashed line: Trail

3RD PHASE

I then removed the wad dipped in kerosene next to the dead ants. A tiny spot of kerosene was left but it gradually evaporated. There was absolutely no modification in the behaviour of the ants reaching the wad dipped in bleach after having gone past the dead ants, now alone, without the wad dipped in kerosene. After this, I placed a new cotton wad dipped in bleach in the same place where the wad with kerosene had been, and 3 mm away from the dead ants. Figure 81, below, illustrates the new situation. I then recorded the behaviour of *fn.*s going past the new set, the wad dipped in bleach and the dead ants, as they came across the new solitary wad dipped in bleach beyond. Record-taking went on for 17 minutes, when a *Solenopsis saevissima* ant was found on the trail by some *P. fulva*, and a crowd started to form. I interrupted record-taking to avoid influences of this event on the data.

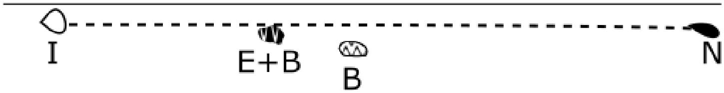

Figure 81: Approximate representation of the situation in the 3rd phase of Observation 56.
Legend:
N: nest
I: incentive
B: cotton wad dipped in bleach
E+B: Crushed ants beside a wad dipped in bleach
Dashed line: Trail

RESULTS AND DISCUSSION

The results, expressed in percentages of ants exhibiting a given behaviour category in the three phases, A, B, and C, of this observation are shown in Table 14, below.

- Phase A: going past the solitary wad dipped in bleach;
- Phase B: going past the wad in A after going past a wad dipped in kerosene next to three crushed members of the colony; and
- Phase C: going past the wad in A, after going past a wad dipped in bleach next to the three crushed ants mentioned above.

Behaviour categories	PHASE A Number of ants: 72	PHASE B Number of ants: 114	PHASE C Number of ants: 62
No modifications	42.7 %	53.5 %	27.4 %
Pause	2.7 %	6.1%	6.5
Acceleration	14.7 %	2.7 %	3.2 %
Hesitancy	26.7 %	29.8 %	43.5 %
Undulation	6.7 %	3.5 %	16.5 %
Jolt	8.0 %	4.4 %	3.2%

Table 14: Percentages of ants marching from the incentive to the nest exhibiting each of the recorded behaviour categories as they went past a solitary wad dipped in bleach during three successive phases.

DISCUSSION OF THE RESULTS IN THIS OBSERVATION

The percentage of ants exhibiting behaviour modifications is significantly higher in phase C than in phases A and B, and this indicates a significant behavioural sensitisation to the isolated wad dipped in bleach as the ants came across it after having gone past the alteration including crushed ants and bleach, as compared with coming across dead ants, either alone or in association with kerosene. This conclusion seems to be refuted only by two of the six behaviour categories recorded – acceleration and jolts. I believe this was due to the enormous increase in instances of hesitancy in phase C as compared with the two other phases. This is because hesitancy is not compatible with acceleration and also with jolts, which involve a sudden forward thrust and an abrupt backward motion.

Psychologists, according to Sato (1955), do not consider sensitisation as learning, given its short duration. In fact, if it were, it would be what has been conventionally called "one trial learning", a learning phenomenon that would be independent, if not from the law of effect or reinforcement, at least from the law of exercise or repetition. It does not involve the association of a stimulus with a given response, but of a stimulus with another stimulus. And, in this association, it does not seem to depend merely on the contiguity of the stimuli, but on something else: their simultaneous origination and similarity of aspects – in this case, the fact that the stimuli were suddenly experienced and were of an olfactory nature. In fact, it remains to be explained why the association was one of two stimuli or situations, not of the ants with the wall or the trail, which were also contiguous. I also think this might be an instance of sensitisation, something like when a quiet, habitually traversed street becomes a source of unpleasant connotations and fear after being the scene of a fatal accident we witnessed. And the fact that such feelings and fear last longer than is generally seen among animals seems to be due to our having a more long-lasting memory and being more socially solidary than them.

Sensitisation and habituation are generally considered as opposite phenomena. Habituation is generally considered as learning how to not respond to a stimulus or situation that does not bring any consequence or reinforcement to the agent. Opposing this opinion, I have shown that it does not involve refraining from responding to something, but responding to something in a different way: by adjusting to its presence as no longer a sudden alteration of a behaviour situation, but as a part of it, as shown by the fact that, if followed by a few repetitions, it can no longer occur without causing more behaviour modifications – a sign, I think, that a gradual mnemic record of its occurrence has been processed by the animals, enabling them to reintegrate and prepare for it when faced with the elements or circumstances that had preceded it. And although sensitisation, as I see it, involves an increase in the frequency of certain behaviours directed to a given stimulus or situation, I think it may possibly involve, in some way, the same primitive phenomenon of reintegration.

4 DOES AN ANT HAVE A COGNITIVE MOTIVATION?

I asked myself this question after the facts seen in the observation below.

- *Observation 57 – On the behaviours exhibited by a* P. fulva *worker as a lure was displaced.*

This observation, as many others I carried out, took place on a cement floor between two flower beds in one of the houses in which I have lived. A brick wall painted in yellow bordered one side of the floor. Near its junction with the floor, there was the entrance to a nest of *Paratrechina (Nylanderia) fulva* Mayr, a cavity in the plaster and bricks, next to one of two 5 cm-thick, 1 cm-high convex concrete ridges that separated the flower borders from the floor. There was a tap in the wall, some 60 cm from the floor, with some importance to our report.

I covered part of the floor with a rectangular cardboard sheet, one of its corners pointing to the wall and under the tap. I put two lures on the cardboard – two cotton wads dipped in a solution of water and sugar – some 15 cm away from the corner of the cardboard sheet closer to the wall, one on each side. The concentration of sugar in one of the wads was two times higher than in the other. Figure 82 illustrates the situation.

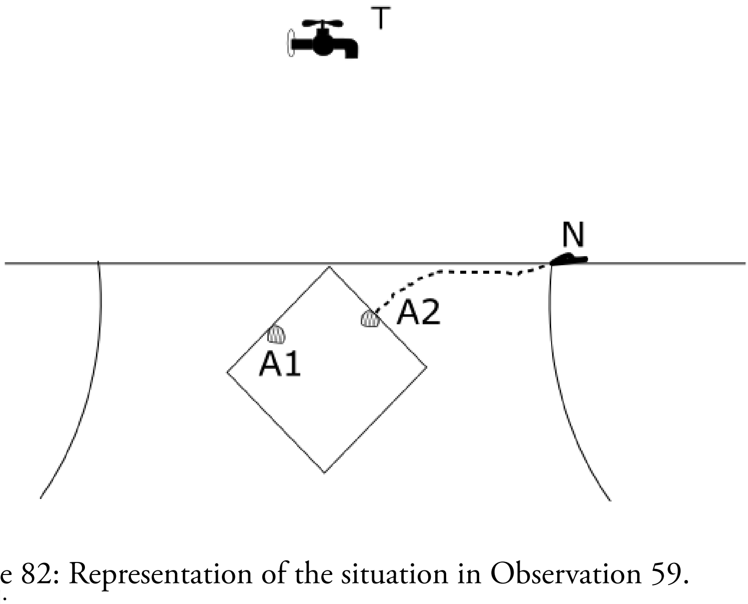

Figure 82: Representation of the situation in Observation 59.
Legend:
N: nest
A1 and A2: lures (cotton wads dipped in water and sugar), with single and double concentrations, respectively.
Dashed line: Path repeatedly taken by the ant that discovered the lure with a double concentration of sugar
T: Tap

I carried to the lures some ants I found roaming on the floor, and as they sucked the solution, I used a brush to mark them with white paint. I wanted to see whether, as Maeterlinck had claimed in one of his writings, the number of ants later visiting the wad with a double concentration of sugar would be twice as high as that of ants visiting the wad with the single concentration of sugar.

Soon a crowd started to form at the entrance of the nest. Half an hour later, I saw that one of the marked ants would repeatedly visit the lure with the double concentration of sugar. Each time it left the lure back to the nest, its gaster was visibly dilated. Some 35-45 seconds later, as it left the nest again, it was leaner, certainly because it had regurgitated the solution to its mates in the nest. On its way to the incentive it was sometimes closely followed by one or two ants, but only for a few centimetres. The behaviour of the pioneering ant was clear: it climbed the wad and stood still, sucking the solution, until its abdomen was bloated, when it would then return to the nest.

Then I did the following: before its return, I switched the positions of the wads, which were similar in all aspects but for the concentration of sugar. Now the place occupied by the wad with the double concentration was occupied by the wad with the single concentration.

The ant climbed the wad, but soon was walking on it, sometimes "sniffing" at the air. Then it sucked the solution and left. On its second visit, it climbed the wad again, walked on it, came down to the cardboard, and then went as far as 15 away from the lure, walking from side to side and "sniffing" at the air, as if "searching" for something.

I have a comment on the first part of the observation. First, the behaviours exhibited by this pioneering ant evoked the phenomenon called by Tolman (1932) "reward expectancy", the classical example of which was originally offered by Tinklepaugh on a study on chimpanzees. The author was investigating the animals' ability to carry out a "delayed reaction" – its ability to, as it were, refrain from an already initiated action, after being prevented from proceeding with it for some time. Delayed reaction was used by psychologists in the first decades of the 20th century as a way of studying memory and the existence of symbolic processes in animals. In his original observation, Tinklepaugh laid upside-down cups round a chimpanzee, and placed under one of them, visibly to the animal, some preferred fruit. After a delay of some seconds or minutes, depending on the trial, he released the animal to see whether it would choose the correct cup. In one of the trials, however, unobserved by the animal, he replaced the fruit with a lettuce leaf, which he knew was less appetising, and saw how the ape took the lettuce, lowered its arm, opened its hands, and let it drop, apparently disappointed.

Of course, the facts about the ant reported above do not imply that ants have the same intellective capacities of a chimpanzee, given the enormous difference in the complexity of their nervous systems. These facts probably do not even imply that ants have any intellective capacity. However, they suggest that this specific ant had been marked by the features of the incentive and, in some way, in each of its sorties, it anticipated them, or, at least, showed that it was pre-adjusted to them, so much so that it was apparently "baffled" by the changed incentive, and, at a certain point, seemed to reject it and to engage in what was apparently a search for the habitual incentive.

Second, it also seems noteworthy that the other ants that I carried to the incentives did not visit them again nor established any trail. But this is understandable: since they had not found the lures by themselves, it was no wonder they could not find them again. On the other hand, it seems harder to explain why some ants, despite their efforts, could not follow the pioneer on the cardboard. In fact, as already mentioned, I had frequently seen that ants in the vicinity of the nest, on being warned by some pioneering ant, would soon reach the new food source, either by going after the pioneer on its journey to the lure or by following its tracks. Could this difficulty be ascribed to their lack of experience with the cardboard, onto which they seemed reluctant to climb? Or could the cardboard absorb or disguise the scent track of the pioneer? On the other hand, why did the pioneer not deposit a stronger scent with the tip of its gaster, as I had often seen other pioneers do? Could it be because the incentive was relatively near the nest?

As the reader will see, my observations raise more questions that I cannot answer than otherwise, and this is due, to a great extent, to the very precariousness of any interpretation of the facts in these observations. Not to mention certain arbitrariness in the selection of facts to be reported, since other facts – the twitches and shortcuts of other ants, near or far from the nest, gestures exchanged during their encounters, halts and restarts, etc. – might certainly have been selected. Therefore, I would appreciate if readers would take into account the whole set of observations rather than individual observations before – needless to say – forming their own opinions in each case.

In the second part of the observation I put the wad with the double concentration of sugar on the tap. I waited for the marked ant, which continued to visit the wad with the single concentration, to climb it again. Then I removed the wad with the ant on it to the double concentration-wad on the tap. I wanted to see what the ant would do after leaving the lure.

After leaving the lure, the ant went up the wall and turned right; then it went down along the left side of the tap; it followed an oblique rather than a vertical course towards the first flower bed and away from the nest. As it reached the cement floor, it came across a nest-mate and stopped to regurgitate the solution amid mutual contact with their antennae. Then, already well thinner, it went up the wall again, with many wrong turns on the way, while the recipient of the regurgitated food returned to the nest. The feeder reached again the wad with the single concentration of sugar, now on top of the wad with the double concentration. After sucking for a while, it walked on the wall and went down to the floor. It came across four ants, left them apparently excited (they waved their antennae, probably asking for regurgitated food), but did not stop. It went towards the nest but, at the spot where it usually left the junction of floor and wall towards the lure on the cardboard, it repeated the action.

It walked on the cardboard towards the place where, before my intervention, it had regularly visited the single-concentration wad, which had replaced the double-concentration wad. The site could only be recognised by some moistness left by the wad. The ant walked aimlessly on the cardboard, going as far as 15 cm away from the spot, “sniffing” at the air, and then returned to the site where the wad had been. It then went to the wall and up the rough surface of the mortar, where some nest-mates were already walking, and then to the single-concentration wad, on top of the double-concentration wad, which the ant failed to locate on the tap.

It walked on the single-concentration wad and a little way up, but did not ingest any solution, and then went down, back to the nest. It seems rather strange, but, given the relatively simple nervous system of ants as compared with those of mammals, it would not be unreasonable to ask: could the behaviours exhibited be indications of a cognitive motivation?

5 SOME EXAMPLES OF UTTERLY INEFFICIENT BEHAVIOURS IN *PARATRECHINA FULVA*

After the preceding topic, which apparently suggests the possibility of some cognitive complexity in certain behaviours of *P. fulva* workers, it seems fair to present some actions which, in contrast, suggest some stupidity or, at least, lack of plasticity in these ants. I report below three observations about these actions.

- *Observation 58 – On the apparently endless transportation of remnants of a cockroach by a worker.*

One morning I found a trail with tens of *P. fulva* ants coming out of a crevice between two tiles on a wall, beside a kitchen sink, and going towards a young and plump, still wingless cockroach which they were predating on the floor, 1.5 m below. I had never noticed ants going out of that crevice, but, as ants frequently move along sheltered paths, I would not be surprised if these ants, those in the bathroom, or those in a door post were part of the same colony. Other ants went down along the sink cabinet, coming from the same tiled wall, but from the opposite corner.

The fact to be reported is that I saw a worker carrying a dark, almost totally black piece of the cockroach, a sphere with 2-2.5 mm in diameter. I found the ant already coming down to the bait instead of the nest. When it was some 8cm away from the cockroach, and still on the wall, it turned back. It went to the crevice, the entrance to the nest, and did the following: the bait held by the mandibles, but above its head, the ant pushed its load against the narrow crevice. With its middle and front legs on the edge of the straight horizontal crevice, it vainly tried to force its way. Sometimes ants inside the crevice outstretched their antennae into a V-position and moved them up and down. However, none of the ants inside grabbed the cockroach piece. The carrier forced its way here and there along the crevice, both left and right, sometimes for a long while; it walked to the right, where there was a contiguous, but blocked crevice, and also tried to force its way; it returned to the nest entrance and tried again, but to no avail, since the height of the ant and the ball did not fit the entrance. Many ants came out of the crevice in a rich flow towards the bait, sometimes almost pushing the carrier out of the way.

An interesting fact was that this ant, after reorienting its body, stood next to the trail, turned towards the bait, and covered all the way down the wall, generally walking parallel to the trail, at a distance of 1mm from it; tens of ants followed the track, but they did not change in any way their behaviour while going past the carrier. The ant went as far as 0.5 cm from the bait and then returned to the nest, and again persisted in prolonged manoeuvres to enter; it went upward for 5 cm, then round the area, and down again for 5 cm, in the vicinity of the entrance. During a more prolonged excursion, this ant tried a few times to force the ball with its legs into a very different, wider crevice.

The ant came down again and went as far as 9 cm from the bait, then up again, and repeating the manoeuvres to enter the nest; it then roamed around the area and went down again. It then went under the cockroach, walked as much as 5cm behind it, and then went up the wall. The occasions in which different behaviours were seen occurred either near the bait or the nest; when on the trail, the ant simply carried on with its burden, and its behaviour differed in no way from those of its nest-mates. I saw the ant repeat all these motions more than ten times. Once, it briefly laid the ball 1 cm behind the bait, but soon grabbed it again. I then left it to attend to other things.

- *Observation 59 – Joint transportation of a load by* P. fulva *ants.*

After the episode above, I saw two ants going up the wall with a circular brown piece of the cockroach. It seemed to be a clypeus and looked greasy and shiny when seen under a magnifying glass (a 10x magnification thread counter) and a torch. When they grabbed the piece from opposite sides, the ant at the back hindered their progress and was pushed by the ant at the fore. The piece being small, I could clearly see that *Paratrechina fulva* ants did not do as *Pheidole oxyops* ants, which orient themselves well when walking backwards and, therefore, pull their burden to the nest very efficiently in this way. *Paratrechina fulva* ants go forward and reorient their bodies whenever they are not frontal to the nest, with the load in their mandibles up above their heads. I noticed that one or other ant on the trail would open its mandibles, the glossa half-way up its height, and “bite” and push its burden in such a way as to enable it to have its front facing the nest. This made their nest-mates to passively gyrate, and the outcome was that all of them and their burden were pushed out of the route and further away from the nest, sometimes as far as 10 cm or more along the wall.

When there were only two ants holding the burden with their mandibles, one on each side, I touched the ant with its back to the nest with the thread counter; it retreated; the other ant, now alone with the burden, went towards the nest, but its course was uncertain; the burden was too large and the ant could not extend its antennae forward and along both sides of the load as ants usually do; hence its course was full of mistakes as compared with that in the collective route. I repeated the operation a few times: when the ant going backwards was driven away, the impasse was solved and progress towards the nest continued, whereas driving away the ant at the front led to erring circles and to the burden being carried further away from the nest.

Why should this piece of the cockroach prompt other ants to “help”? Was it because of its size or some other feature? Why did the small sphere in the preceding observation not attract the same “help”? However it is, in *P. fulva*, food is transported to the nest almost exclusively in the form of liquids or solutions inside the crop or collective stomach, to be later regurgitated to their nest-mates. Given this specialisation, one would say the ants in this species are not prepared for transporting solid food, especially if this involves mutual effort.

I used a stick to carry the cockroach’s clypeus to a spot some 4 mm away from the nest entrance; it stuck to the surface. For about one hour, several ants tried to carry it to the nest, but then I had to attend to other things and did not see the outcome; however, it was clear that the clypeus did not fit the entrance. This “help” frequently led the load 1 cm or more away from the nest; I do not how long this went on, because I set out to observe another episode, described below.

- *Observation 60 – Transportation of a fellow worker by its antenna as if it were an inanimate burden.*

I could not understand this scene: I saw a *P. fulva* dragging another by one of its antennae. It grabbed the other ant by the junction of its funiculus and scape. Both ants had their legs on the tiled wall, but the one pulling was more firmly planted on the track leading to the nest. The ant being pulled resisted by holding firmly to the surface; it was positioned slantwise to the trail. One of the ants passing by touched the captor, and it loosened its grip for a while, and a very strong grip it was: it stretched the other ant's antenna so much that I was afraid it might pull it out.

The other ant took the opportunity and walked away to the nest, 20 cm above, in a normal gait; there were other ants by the entrance, but they did not seem disturbed by the new arrival. It was certainly a nest-mate. I think the captor, while among the ants on the cockroach had mistakenly grabbed its nest-mate's antenna and then pulled it towards the nest as if it were part of the prey. This possibility suggested that *P. fulva* workers could be very stupid in their responses: whatever ended up in their mandibles was a load that had to be carried to the nest, independently of how it behaved. The odours of the captured ant were certainly available to the captor, but this was not enough to fix the mistake.

The subsequent behaviour of the captor was the same behaviour usually seen when an ant with a load is deprived of it: it went upwards for 10 cm, downward for 10 cm, then to either side, but always keeping the spot where its burden had been taken away as central. During a longer walk it reached the nest entrance and then returned; I spent half an hour watching the ant going up and down for 15-20 cm from this point. Was it possible that an ant, after being captured, whatever its properties, had to be treated as a load because ants only pay attention to the properties of a load before it is captured, and then are no longer affected by its stimuli?

6 SOME BEHAVIOUR BIASES IN ANTS AS SHOWN BY THEIR ACTION IN ELEVATED MAZES

6.1 BIAS TO KEEP A GENERAL OR PREVAILING DIRECTION WHEN DISTANCING THEMSELVES IN A COURSE OUTSIDE THE NEST

An objection to a hypothesis proposed by T. C. Schneirla in a text discussing and comparing maze learning by ants and laboratory rats prompted me to carry out some observations regarding the behaviour of ants in elevated mazes. The objective of these observations, some of them presented below, was to reveal certain behaviour biases in ants which, although if find it difficult to determine whether they are innate or acquired, have some importance as instruments in turning this behaviour into an adaptive one.

- *Observation 61 – On an alternative interpretation to T. C. Schneirla's on the existence of an acquired dynamic postural factor that might be important to determine maze learning by ants.*

T. C. Schneirla says in one of his articles (Cf. Schneirla, 1960) that the first exits in a maze enable the development of a response trend that will simplify the process of learning to deal with dead ends and enhance performance in the maze. According to him, a sequence of two or three turns to the right or left would lead ants – and rats too, according to a study by Witkin – to acquire a mechanical disposition through which they could, when faced with two alternatives, left or right, either go out of, or continue along a centrifugal curve, rather than take a route closing or completing the circuit. This disposition or tendency, which he calls centrifugal swing, would be a dynamic postural scheme originating in their marching along several paths and influencing the direction to be taken by them at a subsequent bifurcation. Then, through the sequence of motions performed, this would gradually simplify decision-making at turning points and entrances to dead ends.

Observing the maze employed by Schneirla in his study and the two alternatives the ants were offered to move along after having covered a semi-circuitous route, I noticed that the alternative providing a centrifugal route to this course coincided with the one leading them to keep the general course they had taken, away from the nest. In my opinion, the latter condition, rather than the factor proposed by Schneirla, would determine the choice of a path.

I think it does not make any sense that an ant coming from the nest, in order to reach a food source, should retreat for a while towards the nest from which it was distancing itself; it would be equally nonsensical that it should distance itself from the nest as a means of reaching it. I believe that natural selection, over millions of years, has endowed ants with a tendency to follow a more general direction when moving away, both when they leave the nest to forage and when they return with provisions. I thought that a decision as to which interpretation was correct, Schneirla's or mine, could be reached by using a maze in which the two alternatives offered after a semicircular course were not coincidental, but opposed. I then devised and built a maze, depicted in Figure 83, below, with cardboard strips elevated with pins and needles.

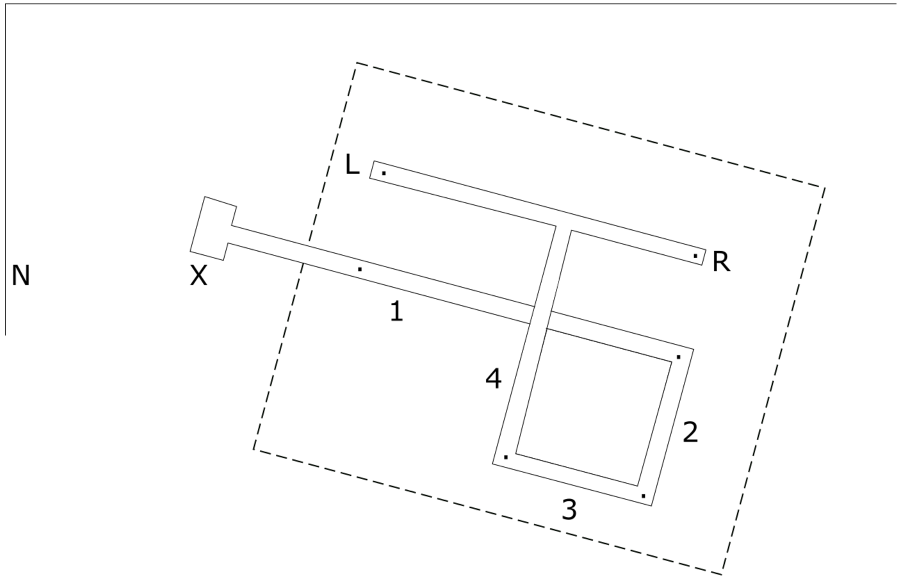

Figure 83: Approximate reproduction of an elevated maze providing, after a circular route, two exits leading to two baits (cotton wads dipped in a solution of water and sugar): one on the left, that corresponds to the centrifugal swing proposed by Schneirla, one on the right, that corresponds to a factor preserving the general direction for distancing prevailing in the maze.

Legend:
Dashed line: wooden board to which the maze was attached with pins and needles
L and R: arms of a T at the ends of which baits (cotton wads dipped in sugary water) were placed
X: Entrance to the maze, adhesive tape attached to the ground and the maze
1, 2, 3, and 4: Maze segments. Note that segment 1 goes under segment 4
Dots: pins and needles supporting the maze
N: nest of *Paratrechina fulva*

The maze was built on a 29 cm x 17 cm wooden board with 1 cm-wide strips of cardboard; the segments had the following lengths: (1), 22 cm, (2) and (3), 8 cm, (4), 10.5 cm. A strip of adhesive tape was used to connect the kitchen floor and the entrance to the maze and provide access to the ants from a *P. fulva* nest near the device. The device had its LR arm a few centimetres away from the junction of the floor and a wall on which the ants from this nest used to walk, but not on the day of the experiment. Two similar baits were placed at the ends of LR, two halves of a cotton wad dipped in a solution of water and sugar.

Segments (3) and (4) were 2.3 cm above the board. Segments (4) and LR formed a one-piece T, in which L extended towards the nest centrifugally, whereas R extended to the opposite direction, centripetally. The ends of RL were 3.5 cm above the board, supported by needles, in such a way that the T stem extended over the tape providing access to the maze (1). The height was adjusted more than once during the experiment to prevent the ants from jumping from (4) to (1). The needles stood in aluminium baking cups half-filled with water at the start of the observation. The other supporting pins were only immersed in water when the odd ant, near the end of the observation, went down the pin. Records were taken for 6 hours and 24 minutes, starting at 11:24 p.m. on a particularly cold night – which certainly curbed the ants' liveliness.

As for the procedure to be adopted, the ideal would be that an ant from the nest would spontaneously enter the maze and, on finding one of the baits, go to the nest and return to the bait followed by other workers, thus inducing the establishment of a trail. To avoid the bias produced by olfactory tracks the ideal procedure would be to use other cardboard strips to cover these tracks after an ant completed its trips. This was clearly laborious and forbidding. Besides, no ant in the vicinity spontaneously climbed the maze, and, after some time, it was clear that none would.

As things stood, I decided not to worry with the accumulation of scent in the maze. However, to prevent conditions from favouring my hypothesis, I at first carried most of the ants, one by one, to bait L, so that the track would be more vivid in this area. My intention was to induce the formation of a trail, but it did not happen. Since trails form in a few minutes under normal conditions, this event showed how difficult it is for these ants to go through mazes like this, which reminded me of a remark by Lubbock (1898) on the aversion they show towards needlessly long routes – more precisely, their aversion to retreating in order to attain an objective – and this lends some further support to my interpretation as compared to Schneirla's.

Initially, I placed 15 ants on bait L and 10 on bait R, one by one. The greater accumulation of scent tracks on L was reinforced by the fact that all ants placed on R, on leaving the bait went to the end L and tended, as other ants coming from bait L, to go down the supporting needle in an attempt to leave the maze, which sometimes they did by swimming or walking on the surface of the water – something we may ascribe to a cognition of the direction to the nest. After a frustrated attempt of going down the needle, some ants would return and repeatedly walk back and forth along the T bar, sometimes reaching the entrance to segment (3), which they would either not enter or enter to remain only for a while. Ants that happened to reach the start of segment (4) would annoyingly not go on. It was clear they resisted returning to the bait or taking a course leading them further away from the nest or in the opposite direction. It is evident that learning a maze is especially difficult for ants since it sometimes implies retreating before going ahead; this is also the case for many other animals, such as rats, in whose performance Schneirla saw the action of an acquired centrifugal swing factor.

After the initial phase, in which the ants were individually transported on a card to one of the two baits on the LR bar, I spent hours on end putting ants, sometimes in groups of two or three, at some point on segment (1), and trying to prevent them from going back before proceeding to the end of the maze.

Collecting the results of this observation was difficult, and sometimes conditions in the maze had to be modified, as described below.

The first ant to surprisingly reach the final bar of the maze went to bait R; it took 1 hour and 15 minutes to do so. I lowered the entrance tape (1) a little in order to prevent ants from jumping from the stem (4) to the entrance, which they sometimes did. During this phase another ant reached the end of the maze, going towards R; it took 1 hour and 30 minutes.

I lowered strip (1) so that its end now touched the surface of the board and made for easier access, and placed pieces of cotton round the pins and the main needle to prevent the ants from using them either to enter or leave. After this, 2 ants reached bait L, and 5 bait R; this took them 1 hour and 18 minutes.

Then I placed the needle supporting tip R of LR in a small aluminium baking cup filled with water. Twenty-six minutes later, 1 ant had reached bait L, and 3 bait R. One hour and 2 minutes later, 4 other ants had reached bait L, and 12 bait R. Forty minutes later, 23 ants had reached bait L, and 46 bait R. Ants coming from the nest were now more numerous in the area and entered the maze through segment (1).

I then covered segment LR with a 7 cm x 1 cm strip of cardboard, leaving 3.5 cm for each half of the bar in T. Five minutes later, 1 ant had reached bait L, and 3 bait R. I interrupted the observation and noticed that 5 ants had drowned in the baking cup under L; this probably happened because the cup was only half-full and its inner surface too smooth, causing the ants to slip into the water.

The results of this record were 31 ants that chose L as against 71 that chose R. The chi square for the difference between these frequencies was of 15.68, which is statistically significant beyond 0.05%, confirming therefore, my claim that taking a direction after a semi-circuitous route is the consequence of a tendency in ants to keep a general distancing direction in the maze rather than of an acquired tendency to a centrifugal swing, as claimed by Schneirla.

If ants, at a certain point in a course outside, show a tendency to maintain a general distancing direction, it is possible to observe this tendency using simpler mazes than the one above. The observation below was carried out considering this possibility.

- *Observation 62 – On the existence or not of a bias in ants to maintain a general distancing direction.*

A simpler device than the one used in the preceding observation could be a T-shaped elevated maze with the aligned arms forming two angles with the T stem, not straight in relation to it, but one regressive, the other progressive, the sum of which is 180º. I report below one observation with elevated mazes of this kind, carried out by a group of 16 students as an assignment for one subject under my care in a Psychology course. I gave each student one of 16 mazes made with grey 1 cm wide cardboard strips, the hands of which formed with the stem, to right and left, pairs of angles measuring 90-90, 95-85, 100-80, 105-75, 110-70, 115-65, 120-60, 125-55, 130-50, 135-45, 140-40, 155-35, 160-20, 165-15 and 170-10 degrees.

The use of a maze with arms forming straight angles with the stem was considered as a control. Unfortunately, the maze with 130-50 angles was not used, since the student in charge left before the start. In each maze the base of the stem was supported by an upright nail inside a small baking cup filled with water, while the other end joined the arms, the ends of which were supported by equal wooden blocks under their ends.

The observation was carried out with *Solenopsis saevissima* Fremont-Smith, 1885 ants captured from the same colony and kept in a clay pot with soil taken from the vicinity of their nest. The students had different abilities and therefore the number of ants tested varied from 4 to 16, totalling 151 ants, with an average of 10.07 per student. The students were previously warned that they might be stung and instructed to use a strip of cardboard to carry the ants one by one to the stem of the maze.

The results were 101 ants that entered the strips forming progressive arms from the stem and 50 ants that entered the strips forming regressive arms. The Fisher's t for this difference was statistically significant beyond he confidence level of 1%.

Two aspects in these results seem to require some comments. First, in this T maze, with arms forming right angles with the stem, 5 ants chose to enter one of the arms while 2 ants chose the other one; we expected the numbers to be the same or almost the same. I think this was so because the favoured arm was more shaded. Lighting conditions in the arms were not controlled. However, I do not think this factor might be invoked when considering the main results because, during the observation, the students took their places round a long table we used for seminars, except for two students who sat in front of each other at a small table in the adjoining room. It should also be mentioned that progressive routes were preferred only when they were larger than regressive ones in at least 30 degrees. This seems to indicate that keeping the general distancing direction became apparent as a factor only when one of the alternative routes was clearly seen as an extension of the stem, not merely as a detour.

6.2 USE OF A SIMPLE MAZE TO DETECT PREFERENCES OR BIASES IN THE BEHAVIOUR OF ANTS

It might be supposed that, in a T maze with arms forming right angles with the stem, a reasonable number of ants compelled to walk on it to its end would tend to enter each arm in approximately equal numbers. Therefore, these mazes can be used to test the preference of ants when faced with two different properties, each of them presented in one of the arms.

As an example of this, I am going to consider the hypothesis in the previous observation, that the difference in the number of ants entering the control maze might be due to different lighting conditions in each arm. To test the hypothesis, I carried out an observation using an elevated T maze, as reported below.

- *Observation 63 – On the preference of* P. fulva *ants for a shady arm to one in full light in an elevated T-shaped maze.*

I used a T-shaped maze made with two 15 cm x ½ cm strips of cardboard. One of the ends of the strips used for the stem stood 8 cm high on a plastic lid with a nail in the centre surrounded by a mixture of water and creolin in a glass bowl with a diameter of 11.5 cm. Water was used to limit their movements in the maze and force them to choose one of the arms, one of them lighted, the other in the shade. The new choice of container for the liquid as well as of its nature was motivated by the fact that, in mazes like the one used before, the ants placed at the entrance to the stem tended to leave using the nail that raised it and the water in the small aluminium cup that held it. The change successfully prevented this. From the free end to the end resting on the single strip forming the arms, there was a decrease in height, from 8 to 6 cm. The two arms formed straight angles with the stem and their ends were supported by two wooden blocks with the same size. The two arms were different in that one of them was under the full light of a 100-watt light bulb on the ceiling, and the other in the shade or partial shade produced by a notebook interposed between the lamp and the arm. During half of the tests the stem was in full light, during the other half in half-shade. In the latter case, an open notebook was used to project the shade. The ants were taken from a clay pot with soil to which they had been transferred before and placed individually on the plastic lid at the beginning of the stem. Each strip of the arms was changed whenever an ant walked on it. On the other hand, the strip forming the stem was changed only when 10 ants had been tested, and not because the scent track was interfering with the choice of the arm, but because, after some tests, the ants would hesitate or even turn back for a while along the stem as they reached the junction with the arms, probably because the scent track was interrupted at this point. I noticed that when there were not scent tracks on the stem the ants walked more efficiently. Some ants, on reaching the junction of the stem and arms, "sniffed" at both sides before making a choice.

Twenty-two ants were tested in the maze. Twenty of them chose the shady arm and two the lighted arm, a difference statistically significant beyond the confidence level of 0.01. This result reveals a bias, in *P. fulva* workers faced with a choice between a shady and a lighted course, to choose, conditions being the same, the shady path. On the other hand, their having been exposed to light or shade while on the stem had no effect on their choice of an arm.

While testing for biases or preferences of ants for arms with different features or properties – smell, nature, thickness, smoothness, gravity, the physical state of a given food item found on them, etc. – it is important that conditions not being considered are the same. Therefore, it is important that both arms in the device can be similarly treaded on and have the same degree of smoothness, inclination in relation to gravity, lighting conditions, etc.; scent tracks left by the ants should be prevented from interfering with their choice of an arm to be followed. However, it is difficult to meet these recommendations. A maze can be made with different materials – wood, cardboard, wire, plastic or glass tubes, etc. – as long as they are appropriate to the conditions to be tested. Personally, I do not see this as especially important. In my opinion, it is more relevant trying to find out whether there is a factor in previous experience that may induce or originate a behaviour bias. The observations below were guided by this concern.

6.3 ATTEMPTS TO FIND OUT SOME PREVIOUS EXPERIENCE FACTOR IN THE SHAPING OF A BEHAVIOUR BIAS OR TENDENCY

A first attempt in this work to ascertain whether a given previous experience might lead to a behaviour bias had its origin in a hypothesis I developed, namely, that the ants, on being suddenly faced with a choice between two stimuli or situations, would prefer to orient their behaviour towards the most familiar one. In order to test this conjecture, I carried out the observation below.

- *Observation 64 – Ascertaining whether* P. fulva *ants previously exposed to one of two different scents, on being released to walk on an elevated platform made with two strips of cardboard, each of them bearing one of the scents, would evince a preference for the odour to which they had been exposed.*

I employed three bottles with soil in this Observation, A, B, and C; A was scented with genipap, B with mandarin juice, and C, used as a control, received no scent at all. Before starting the observation, I kept several *Paratrechina fulva* workers from the same colony inside the bottles for half an hour, and certainly longer before the end, as the bottles were temporarily opened for ants to be used. My intention at first was to leave them longer in the bottles before the start, but I found out that, after being held captive for one hour in a previous attempt, all the ants in a bottle scented with orange juice were dead, as well as most of the ants in a bottle scented with mandarin juice. When preparing new bottles I replaced the scent of orange juice with that of genipap so as to avoid the repetition of a citric scent. The ants had certainly never been exposed to genipap, a fruit that did not occur in the area, a present from a visitor from a distant place.

The procedure was to place these ants, one by one, on one of two raised cardboard strips, namely, strip A, rubbed with genipap, and strip B, with mandarin peel juice. The strips, 24 cm long and 1 cm large, were juxtaposed and their ends were supported by two wooden blocks. Each ant was caught with the aid of a cotton wad and alternately released at one of the ends of a strip, A or B, in the middle of its width. Records were taken for the time each of them remained on each of the strips before reaching the other end.

Ten ants fell off the strips before reaching the end and were disregarded in the records, as well as two other ants with anomalous times on the strips, probably because of injuries inflicted during their manipulation. In the end, 62 ants were observed, 20 from bottle (A), 19 from bottle (B), and 23 from bottle (C). The scents were renewed six times during the observation.

RESULTS OF THIS OBSERVATION

Time of permanence of the ants on each of two juxtaposed strips are shown in Table 15, below.

Time of permanence (seconds) on strips A and B of ants from group (G) placed on strip A: On strip A: 93.00; on strip B: 48.73. Fisher's t for difference between averages: 2.43*.
Time of permanence (seconds) on strips A and B of ants from group (G) placed on strip B: On strip A: 27.77; on strip B: 46.22; Fisher's t for difference between averages: 1.01.
Time of permanence (seconds) on strips A and B of ants from group (M) placed on strip A: On strip A: 53; on strip B: 36.7. Fisher's t for difference between averages: 1.33.
Time of permanence (seconds) on strips A and B of ants from group (M) placed on strip B: On strip A: 34.89; on strip B: 52.22; Fisher's t for difference between averages: 1.95.
Time of permanence (seconds) on strips A and B of ants from group (C) placed on strip A: On strip A: 53.92; on strip B: 19.25. Fisher's t for difference between averages: 7.60**.
Time of permanence (seconds) on strips A and B of ants from group (C) placed on strip B: On strip A: 32.64; on strip B: 65.90. Fisher's t for difference between averages: 2.30*.

Table 15: Average time of permanence of ants from three groups, namely, group (G), previously exposed to the scent of genipap, group (M), previously exposed to the scent of mandarin, and group (C), deliberately not exposed to any scent at all, on two juxtaposed elevated cardboard strips, A, scented with genipap, and B, scented with mandarin, in two different situations: when released on strip A, and when released on strip B. Also Fisher's t for the differences between average times of permanence on each strip of the three groups of ants tested.

* *Statistically significant at the confidence level of 0.05.*

** *Statistically significant at the confidence level of 0.01.*

This table shows an unexpected result: the ants from the three groups exhibited a clear bias: to remain most of the time and, therefore, to prefer, out of the two juxtaposed elevated strips, the one on which they had been first placed. It was as if the path to be followed were established by the initial sensorial situation. It is true that only in 50 % of the cases the difference in their preference for remaining on the strip on which they were released was statistically significant, but in all six cases this bias was suggested. Apparently, the preference for walking on the strip on which they had been placed was not greater because once in a while an ant, on being released on the strip, faced the other strip and entered it; then it tended to remain there most of the time. If not for this, the bias to remain on the strip on which they had been placed would certainly be higher.

Now, I am going to consider the objective of my observation: to find out whether the ants previously exposed to a given scent would evince a bias to spend most of their course on the strip, out of two, bearing the scent to which they had been previously exposed. If it were true, the ants exposed to scent G would remain longer on strip A in their course towards the other end than the ants in the control group, which had not been exposed to the scent. And, *mutatis mutandi*, the ants previously exposed to scent M would remain longer on strip B on their way than the ants in the control group, which had not been exposed to it. In order to test this possibility I relied on the calculation of the Fisher´s t for the differences in corresponding averages, that is, between the average time of permanence of the ants in groups G and C on strip A, and between the average time of permanence of the ants in groups M and C on strip B. Table 16, below, shows the results of the test.

Average time of permanence of ants previously exposed to the scent of genipap on an elevated strip with the same scent: 93 seconds. Average time of permanence of the ants in the control group on the same strip: 53.92. Fisher's t for the difference between averages: 1.45 – not statistically significant.
Average time of permanence of ants previously exposed to the scent of mandarin on an elevated strip with the same scent: 34.89 seconds. Average time of permanence of the ants in the control group on the same strip: 32.64. Fisher´s t for the difference between averages: 1.09 – not statistically significant.

Table 16: Average time of permanence of ants previously exposed to a given scent and of ants in the control group (not previously exposed to it) on the strips bearing the corresponding scent, and Fisher's t for the difference between these averages.

The results in the table above do not show any evidence that ants previously exposed to the scents of genipap or mandarin juice developed a tendency to walk longer on strips with these scents than ants not previously exposed to them.

A last point to be considered is whether the ants in the three groups, on their journeys on the elevated strips scented either with genipap or mandarin juice, showed any preference for walking longer on any of them. The average time of permanence of the ants from the three groups was 46.29 seconds on strip A and 43.61 seconds on strip B. The Fisher's t for the difference between the averages was 0.154 – not statistically significant. There was not, therefore, any significant preference of the ants for either of the scented strips.

A new attempt to ascertain whether a given previous experience could lead to a behaviour bias originated in a fact seen in the preceding observation: on being captured with a cotton wad, ants apparently tangled in the cotton fibres seemed to leave the wad and enter the elevated path more readily than the ants that could freely walk on the wad. This realisation led to the observation reported below.

- *Observation 65 – On the induction of an escape intent in P. fulva.*

Bearing in mind the fact mentioned in the preceding paragraph, I formed the hypothesis that ants left unrestrained on the cotton wad require more time and reorientation of the wad to keep them facing the outside strip they are supposed to enter than ants restrained on the wad by being lightly pressed against it. To test the hypothesis, I used a cotton wad with a diameter of 3 cm and a cardboard strip 1 cm wide with its ends resting on two 7.5 cm high wooden blocks. The ants were individually taken from a glass container with soil and transferred to the wad with the aid of a small spoon; once on the wad, each ant was either left unrestrained or lightly pressed against it. Ten seconds later, the wad was turned until the ant faced the cardboard strip; then, with a stop-watch, I recorded how much time each ant would spend to leave the wad for the strip and the number of times the wad would have to be turned to orient the ant towards the exit before it left for the strip. The cardboard strip was scented with orange juice in an attempt to make it more noticeable to the ants.

RESULTS

Thirty-six ants – alternating restrained and unrestrained ants – were tested. The 18 unrestrained ants spent an average of 5.17 seconds to leave the cotton wad for the cardboard strip. Two of them, however, were anomalous as regards the time spent to enter the strip – 24s and 22s, respectively – and therefore were disregarded, thus changing the average to 4.19 seconds. As for the number of turns of the wad required before the ants entered the cardboard strip, I did not think it was necessary to disregard them; therefore, the average number of turns was 5.17 for 38 ants.

It should be pointed out for this conclusion that some of the ants restrained among the fibres sometimes seemed a little stiff on being released while others seemed more intent on biting their way out than on escaping through the cardboard strip. The average time in leaving the wad for the cardboard was 2.72 seconds, and the average number of turns needed for them to leave was 0.72. The Fisher's t for the difference between the averages in time spent in leaving for the cardboard strip was 4.19, and for the number of turns of the wad was 2.68 – both statistically significant beyond the confidence level of 0.01. These results show that restraining ants on a cotton wad induces escape intent more definitely than leaving them unrestrained on the wad, even though, in the latter case, the ants evince the same motivation in their actions, though to a lesser degree.

7 ON THE USE OF EXTERNAL REFERENTS FOR ORIENTATION BY ANTS

V. Cornetz (1914) claimed that, after a journey outside, ants would return to the nest by reversing their course and covering the same length in a straight line; he did not take into account the occasional turns (which he called *tournoiements de Turner*) exhibited by ants from time to time round an area or spot. These turns would be instrumental in finding new food sources or other elements of interest at the time, such as a new location for the nest. On covering the same distance on its way back, an ant would carry out similar turns in its search for familiar aspects of the environment on which it would rely to find its nest. The first part in its orientation would be the outcome of a central mechanism, an automatism not depending on the environment, while the final part would be an investigation dependent on previous individual experience and, therefore, on memory.

In Observation 38, in which I dealt with the effects of blowing on individual ants at specific points of a trail, I claimed that the ants, because of their continued experience of a trail, rather than a central automatism, could have records enabling them to establish, for each point of a now familiar path, a relatively precise memory or assessment of the direction to follow and their distances from each end of the trail, that is, the food source and the nest. And, in Observation 51, in which the ants were passively moved from a point of the trail to another, and therefore could not rely on this cognition for their return, I argued that they probably used for this purpose certain external referents, such as the direction of light or wind, or even their perception of recurrent or relatively constant aspects of the environment, such as the appearance of certain volumes, or the left or right side of a familiar junction of two surfaces – floor and wall, for instance.

What would happen, however, if instead of being moved from a point of the trail to another the ants were moved to a partially or totally unknown site, as I have often seen, when strong winds carry them quite a long way from their nests? I suppose that, given the relative frequency of such events and the clear advantage an ant colony derives from the greatest possible collaboration of its members in common tasks, there must have been a selective pressure towards enabling stray ants to find their way back to the nest. In order to do so not merely by chance, they would have to rely on external referents, such as the direction of light or winds, patterns of light and shade in the sky, large objects, etc. There are some excellent studies on the navigation of ants and their use of external referents, but summarising and commenting on them is outside the scope of this work. My objective here is only to present the simple and perhaps untried method on which I relied in my search for clues that stray ants might use to find their nest. This was the purpose of the observations below.

- *Observation 66 – Some data on the orientation of ants removed with a lure to another location.*

The data referred to were collected in a variety of situations, listed and presented below.

1. The orientation of ants moved with a food incentive to a nearby place, in the same general situation, but outside the trail

The observation took place in the evening, on a cement floor between two flower beds, a setting already described elsewhere in this work. A piece of a sweet, used to induce a trail starting at a nest of *P. fulva* some 40 cm away, was removed, with several ants on it, from a low concrete ridge separating a flower bed from the floor, to a spot on the floor about 50 cm away from the nest. This was the main nest in the area, located in a crevice in the wall, at the point where it joined the ridge. The result was that all ants fled in many different directions on their way to the wall; none went straight towards it; after a while they were zigzagging, but progressing towards the wall, where they joined a thinner trail from a secondary nest and finally reached the main nest. Figure 84, below, illustrates the situation.

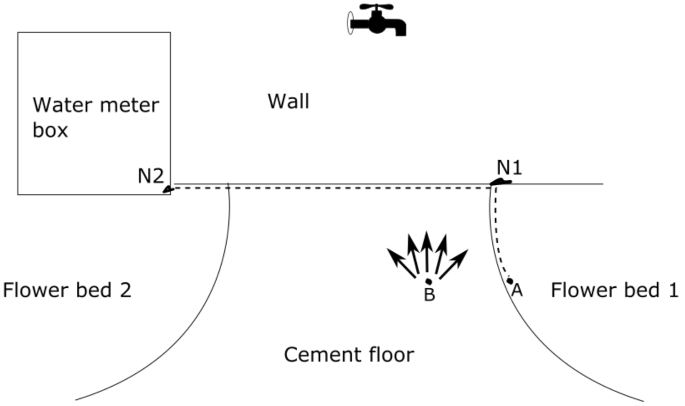

Figure 84: Approximate representation of the situation in Observation 66.

Legend:
Dashed line: trail connecting nest 1 to the incentive in its initial position
Dotted line: thinner trail connecting nests 1 and 2
A: incentive in its initial position
B: incentive after being moved to the cement floor
Arrows: courses followed by the ants when the bait was put in another location

I believe that the behaviour of these ants was caused by their relying on the direction of the light in the environment for orientation;

this came from a light bulb 5 m away, at the entrance of the house, and another on a lamp post further away. It might also have been caused by the sight of the nearby wall.

Another observation of the same kind was carried out soon after the end of a lengthy observation, in which I blew on the ants at seven different points on a 3.20 m long trail, established on a kitchen floor, along some of its junctions with two walls, connecting a nest on a third wall and a bait, a cotton wad dipped in water and sugar (See Figure 48, above). At the end of the observation, I took the bait and moved it parallel to the wall closer to the nest, 40 cm further into the kitchen. Most of the ants set out towards the wall where the trail was closer to the nest, while the others went to the side walls. None went towards the other end of the kitchen, with no walls nearby.

It seems that, being used to walking on the kitchen floor, beside its junction with the walls, and the environment being the same, the ants had no difficulties in orienting themselves towards them. They could probably see them.

2. Orientation of ants moved with a food incentive to a different environment and substrate

On another occasion, in the same setting represented in Figure 84 above, and with the same lighting conditions, the bait was a piece of a sweet on the top of a garden tap, next to the wall. A thick trail of *P. fulva* went towards it, practically on a vertical course up the wall, coming from the main nest and following the wall and floor junction. I took the bait into the house, with the lights on, and placed it on a granilite step 1 m away from the entrance, the door of which was kept open. It was full of ants, and they immediately hurried away in all directions; sometimes they went back to the bait, but left it again. I think that, since they could not find the scent track underlying the trail and being prepared to go down a vertical surface but unable to do it in the new location, they went away aimlessly. It is also possible that a change of substrate, from a brick wall to a granilite floor, and a change of planes, from vertical to horizontal, also influenced this behaviour.

3. The orientation of ants moved with a food incentive from a horizontal plane to a vertical one, and vice-versa.

In this observation, I first picked up a bait (a cotton wad dipped in water and sugar) with some *P. fulva* ants from a cement floor and held it out towards a brick wall. The ants ran away through my fingers, probably because my hand was extended with its longitudinal axis perpendicular to the wall, with back and palm forming roughly horizontal surfaces.

I put the bait back on the floor. I took it again a little later and put it on a piece of cardboard and held it at a 30-degree angle in relation to the floor. The ants left it aimlessly, walking in circles. The change in the inclination of the base probably caused this behaviour. But what about its different nature? Did it have a part in this result? If it did, why did it not in the preceding observation? Was it because it was inclined in relation to the horizontal plane? Unfortunately, I did not attempt to reduce the inclination.

Second observation: a trail of *Solenopsis saevissima* came on a straight course from its nest, next to an avocado tree in the yard, towards a bait (a cotton wad dipped in a solution of water and sugar) placed on a shopping cart wheel and pressed against the wall of a dumping room some 20 cm above the floor. I then placed it on the same wall, a little above and to the left of its original location. Most of the ants left downwards. It seemed reasonable: they went up to reach the bait, down towards the nest; there was no change either in the verticality or the nature of the substrate.

The bait was placed in its original position on the wall. Again, I placed it on the cement floor in the room, a little to the left of its original location. They did not leave aimlessly, but in a broad strip parallel to the trail between the bait and the nest by the avocado tree. Therefore, it seems that in this case, the change from a vertical to a horizontal plane did not have any influence on the orientation of these ants. The location was familiar, they had already walked along the floor towards the wall, and the light coming through the door was the same as that of the trail.

Third Observation: On a certain evening, with the light bulb in the yard on, I placed a 20 cm x 20 cm wooden board on a floor where, along its junction with the wall, there was a trail of *P. fulva* visiting a bin with kitchen scraps. The board stood upright with an incentive attached to its top (a cotton wad dipped in water and sugar); I placed four ants on it. After a while, I noticed that a great number of ants were going up to the bait and back. I laid a large dictionary close to the upright board in a horizontal position; I quickly removed the bait and placed it centrally on its cover. Some fifteen ants immediately left the bait, moving in circles in all directions. After a short stretch they started roaming round the book. I set the book in an upright position. Six remaining ants, hidden under the bait, left, one by one, towards the floor, as the ants had done when on the board. Therefore, it seems clear that, since the plane on which they stood was preserved, they oriented themselves as they had previously done, even though they were on a substrate of a different nature. When the substrate is unknown and bears no tracks, and when its plane has been modified, ants leave aimlessly and then walk in circles.

I moved the cotton wad back to the upright board. Some ten minutes later, after recording the event, I resumed the observation, with the dictionary still on a horizontal plane, but now with the back cover up. About 20 or more ants left it, a slightly larger number of them in a course that led them away from the nest, apparently ignoring the direction of the light. They left in all directions and were soon roaming around.

I moved the bait back to the board and went away for a while. When I returned, I put an upright notebook beside the board and the bait in the middle of it. The ants hesitated before heading for the notebook, but when they did, they went in all directions, but invariably heading for the half of the notebook facing the floor. There were about fifteen ants. Therefore, they preserved their orientation towards the nest when the substrate on which they had been placed remained, as the board did, upright.

4. Orientation of *Solenopsis saevissima* ants moved on a bait from a wall to another part of their trail which, as usual, ran along the junction of a low step and a ceramic floor.

There was a bait (a cotton wad dipped in a solution of water and sugar) covered with ants by the entrance of an inactive piping elbow in a brick wall. I moved it to a spot of their trail which, as usual, came from a nest by an avocado tree and followed the junction of the floor and a low step. They did not leave the bait in circles; all of them left slowly and gradually towards the tree. So, they were removed from a vertical substrate to a horizontal one and were not disoriented. I think that recognising the trail and its surroundings was definitely an aid to their orientation. The fact of their leaving the bait slowly suggests that they recognised the place to which they had been removed, and, therefore, were not in a hurry to leave.

5. Orientation of ants in the tribe Attini when moved from a spot on a trail to another location.

Once, in a cemetery, I saw several leafcutter workers (*Acromyrmex sp.,* and *Atta sexdens rubropilosa* Forel, 1908) walking on a tomb, collecting rose petals and leaves and going past each other without any conflict. I captured some workers by holding their vegetable burden, and then moved them to another point of the trail or other area; they would stand still for 5-10 seconds, still holding their burden, then resume their previous orientation and proceed. I witnessed this sort of behaviour on other occasions. I think they could resume their previous orientation based on the light in the environment.

6. Orientation of *P. fulva* ants moved from one environment to a similar one.

There was an ant trail between a rubbish bin in a kitchen porch and a nest in the junction of a low step and a wall. This porch looked out on a yard with another porch opposite, adjoining an office; this was similar to the kitchen porch in all aspects: painting, side walls, a small step leading to the yard, a mosaic ceramic floor, and light coming from the yard. The objective of this observation was to see what orientation the ants in the bin would take as it was removed from the kitchen to the office porch and turned on its axis in 180 degrees. Figure 85 illustrates the situation and the results. In its new position, the bin occupied the same relative position in relation to the step as in its original location. Both positions were similar within the two symmetrical porches. The arrow in position 2 in the illustration indicates the approximate direction from which the ants would leave if the previous exit point were used. The adjoining dotted area stands for the position on the floor from which they left. They left aimlessly, and sometimes returned to the bin, walking in circles. It is instructive that they would not go down the step. They hesitated for a while on the brink, reoriented themselves, covered part of its length, and roamed around on the floor. This was seen in all ants approaching the border of the porch. This border, or interruption of the horizontal plane, guided the ants on their return to the nest in their original situation, and their behaviour, after being transported to a similar environment, showed signs that they had a mnemic record of this use. More: in the new situation, on reaching the wall through the junction of the floor and the step, the ants tried for quite a while to enter a cavity which I had blocked with cotton in the previous observation and which resembled the entrance to the nest in the original situation. It was only later, as they increased their range round the bin, that the ants started to go down for a while and to climb the low step; eventually they joined a thin trail along the junction of the step and the yard floor – an event that, like others, showed how easily one or even more colonies can split up into interconnected communities.

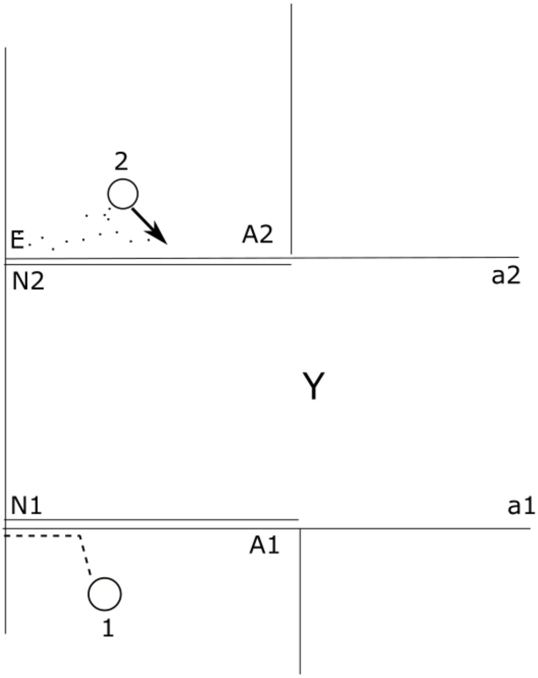

Figure 85: Situation as a rubbish bin was moved from the floor of a kitchen porch to a similar one, symmetrical with the former, adjoining an office on the other side of the yard, and results.
Legend:
Dashed line: trail
N_1 and N_2: nests
1 and 2: rubbish bin in its original and new locations in two symmetrical porches
Dotted line: ants coming out of the bin in position 2
A_1 and A_2: low steps leading to the yard floor
Arrow: position at which the ants should leave in the new position, with the bin turned in 180 degrees.
E: hole beside a third, blocked nest
Y: yard
a_1 and a_2: junctions of floor and walls

8 THE RELATIONSHIP OF EXTERNAL REFERENTS AND INTERNAL REPRESENTATION IN THE ORIENTATION OF ANTS

On a certain occasion, I suggested to a Psychology student, Helena Kihome Kuhme[32], interested in the orientation of ants and in some claims by Cornetz (1914) on the subject, that she should carry out an experiment with a leafcutter species, *Atta sexdens rubropilosa* Forel 1908, in my laboratory. She should use lighting in this totally dark room – it had been deliberately built without windows – first from one side, then from the other, of one of our *in vitro* leafcutter nests. She used candles to light the environment and carry out the experiment; the results seemed to fit a discussion on the relationship I believe there is between external referents and their mnemic representation by ants, and this is why I will discuss it under this topic.

- *Observation 67 – An experiment on the orientation of a colony of leafcutters,* Atta sexdens rubropilosa *Forel, 1908, exposed to two lighting conditions.*

The colony used in the experiment was, like other new colonies in the laboratory, in a transparent glass cylinder set on an acrylic sheet inside an aluminium tray. It was placed on a 60 cm wide and 1 m long Formica table with its edges smeared with grease to prevent the ants from escaping. The *in vitro* colony was placed at one end of the table, while at the other end there were leaves, and, on one of the sides, a row of lighted candles. A lighted candle was placed beside the leaves to make them and the ants visible in that area. Figure 86 represents the situation and the results in the first phase of the experiment.

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[32] I am indebted for her precious help.

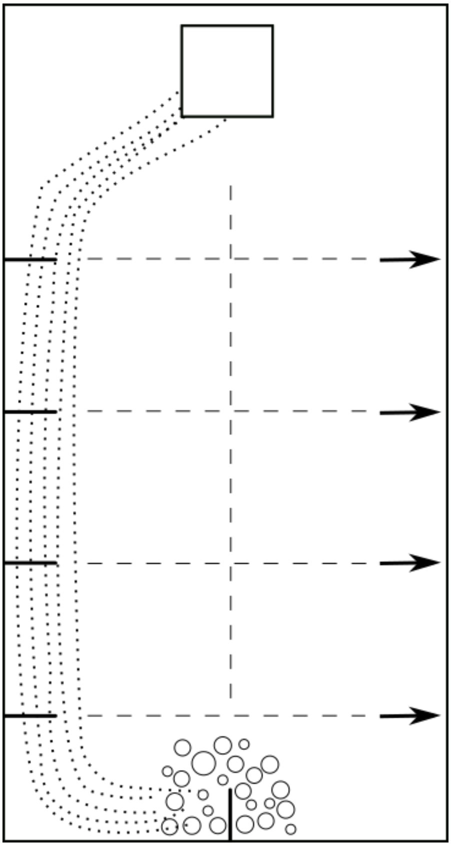

Figure 86: Approximate representation of the initial situation in Observation 67.

Legend:
Small rectangle: glass cylinder at one end of the table, holding a colony of *Atta sexdens rubropilosa* Forel, 1908
Small circles: leaves at the other end of the table
Straight bars: lighted candles on one side of the table, except for one at the other end, among the leaves
Arrows on the right: places on the other side of the table to which the candles would be moved in the second phase of the experiment
Dotted lines: paths followed by ants going to the leaves and returning without any after the candles were lighted
Dashed line: course taken by a few ants which returned to the nest carrying vegetable fragments

The result in the first part of the experiment was that most ants moved along a strip bordering the row of candles between the nest and the leaves and then back. The strip was broader next to the nest and the leaves. Some of the ants walked on and among the leaves; some of them apparently tried to raise one or other, while others cut fragments out of the leaves. Most of them, however, seemed only to explore the portion of the table occupied by the strip and the leaves. Twelve ants carried fragments following a straight course from the leaves to the nest.

In my opinion, the results above show that the ants were attracted by light in their orientation due to a positive taxis, seen also in *Paratrechina fulva*, as shown in Figure 16, and their tendency to use external referents in their orientation. As for the surprising use of a straighter course to the nest by ants bearing leaf fragments in the absence of scent tracks left by other ants, it suggests that these ants relied on a representation or map formed as they connected in their memories the expansion of their routes towards these objects. So far, I had thought that this ability, of following a straighter course to the nest than to the provisions, was due to the fact that nests have fixed positions and are more constant than provisions, which are generally found in a wider variety of locations in the environment. However, the data collected by my student show that it is not like this, since the locations of both the nest and the provision source were new in the situation. However, it was only when going towards the nest that the ants showed a tendency to shorten their course, and, therefore, certain independence from external referents and a greater reliance on a representation of the spatial distribution of the elements in the situation, that is, a cognitive map of the situation. These findings suggest that ants 1) only carry fragments when they have mastered the general, mnemonic direction of the nest; as we have seen, only a few did it; in a study on the transportation of vegetables by these leafcutters in my laboratory, Otília Caresia (1977) found out that, frequently, the ants that cut the vegetables do not carry them; and, that 2) the ants that carry the fragments establish a cognitive map to the nest (a prime object) more easily than to the provisions, or that, regardless of their previous experiences with nests or provisions, they tend to orient themselves differently according to their destination: orientation towards the source of provisions would depend more on external referents (more environmentally-based) than orientation towards the nest, based on representation and memory. This tendency to carry vegetables could be either innate or acquired – it would be important to find it out. Data collected in my laboratory by Ana Maria A. Carvalho (1973), to be used in a doctoral paper, show that carriers are among the oldest members in their colonies, suggesting that they probably have more experience, something that has been confirmed by several students in other ant species.

In the second phase of the experiment, when the candles were moved to the other side of the table, most of the ants going towards the leaves or vice-versa, after some hesitancy and confusion, established their course within a strip in the central part of the table, connecting more directly the nest and leaves; the strip broadened at both ends. Figure 87, below, illustrates the new situation and results.

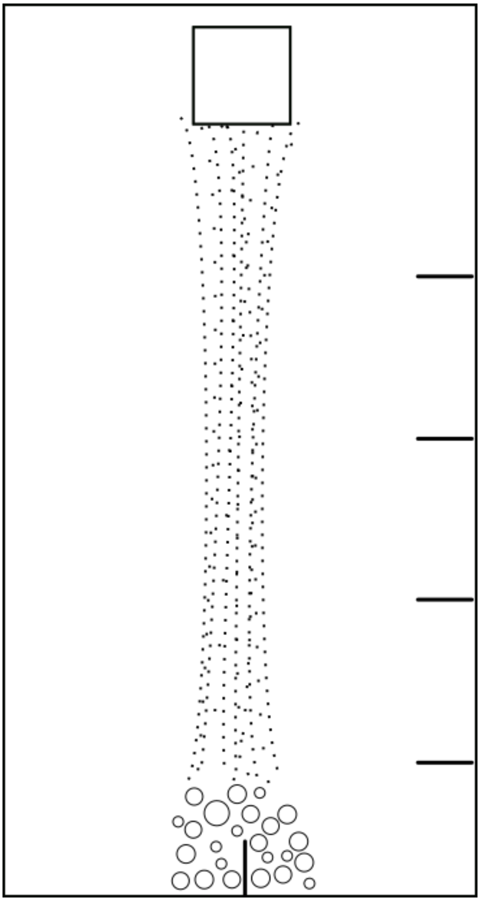

Figure 87: situation and results in the second phase of the experiment carried out by Helena K. Kuhme, when the lighted candles were moved to the other side of the table.

Legend:
Small rectangle: colony of *Atta sexdens rubropilosa* Forel, 1908, in a glass container with an acrylic base
Straight bars: lighted candles
Small circles: leaves
Dotted lines: paths taken by the ants

Their moving to the centre of the table seems to suggest that the ants were attracted by the lighted candles in their new positions, but only up to a point. The outcome of this reliance on light for orientation, if complete, should have moved the strip from its original course to the right, next to the candles in their new location. Since this did not happen, it seems clear that the ants, even those without a burden, do not rely only on external referents for their orientation, but also on a cognitive map containing the main elements in the field. There seems to have been a compromise between the use of representational factors and external referents in the orientation, or between being attracted to light – the result of a positive phototaxis – and following the track left by ants carrying vegetable fragments. Now, if this is the case, why did they not stick to the tracks persistently and intensively deposited along the first route? Was it because their attraction to light prevented it? If so, why did this attraction not have the same effect regarding the certainly slighter tracks left by the ants with burdens? However it was, another result was that the number of ants among the leaves gradually decreased after the candles were moved, as shown by counting them at five-minute intervals, a sign that the change was a source of disturbance.

As for the ants carrying burdens, the change also caused modifications in their behaviour. All of them, six in the new phase, now meandered in their march, apparently tending to the side where the candles had been, and, except for two ants, were not able to carry their loads to the nest in fifteen minutes. Two of them let go of their burdens halfway along the course, a sign that they had lost their sense of orientation. These facts show that the ants with burdens did take into account external referents in their orientation, and that, because they did no longer follow them strictly, the impression was that they now disregarded them. Mastering the general direction to the nest, therefore, is not something that works in any situation: it is something to be set against the data presented to the senses. Better still, the cognitive map guiding the ants is not a map enabling them to set out in a sort of blind flight: it enables them to spatially relate with referents in the situation in a proper way. Then, it seems that neither factor in the orientation occurs independently: the use of external referents and the use of a spatial representation of the elements in the situation. The ants following the candles do not do it automatically or inevitably – they do not reach the flames – but use them instead as a clue to something represented, so much so that they can modify this use when the candles are moved.

The author of the experiment started from the claim: “According to Cornetz (1914), a scout might keep a general spatial direction as a purely internal document, independent from the external environment – by combining visual, tactile, olfactory, and auditory perceptions.” She supposes that “documenting” would involve memorising. Would this memorising be purely subjective or depend on being activated by external referents, on their relationships with them? Helena Kuhme concluded that her data went against Cornetz’s hypothesis that “the scout keeps an internal mnemonic record of the course to be taken, independently of external referents”. “For Cornetz, this memorising would include the angle or detour taken by a scout during its outward journey, its successively relating its individual attitudes to a general one, and its memorising of it, as well as the distance covered.” She says that if the ants had such forms of memorising, they would not be upset by the candles being moved. Also: “For it is somewhat illogical to speak of a purely subjective memory, independent from the outside.” She concludes that “subjective abilities”, the factors mentioned by Cornetz, are not precluded in the experiment, but could not dispense with the external environment to be used.

I agree with the author and am glad about the notion that teachers do not only teach, but also learn with their students, sometimes a lot. And I add a comment: the memory of ants would be established by contact with the external environment. It being absent, however, how could it properly guide an ant? I think this confusion started because Cornetz noticed that ants acted in agreement or disagreement with elements in the environment, but he would not go as far as supposing that ants cognitively represented the environment, and that, on the basis of these representations, the aspects in the environment would take on the function of specific referents in orientation.

9 ON SOME FACTORS IN INDIVIDUAL EXPERIENCE THAT DETERMINE A TENDENCY TO FIGHT OR FLIGHT IN INDIVIDUALS OF DIFFERENT SPECIES

Zoologists generally assume that territoriality is innate in many animals. In the case of ants, I believe that the tendency to territoriality may be so. However, I ask: would it not be possible that fight and flight in individuals of a group or a species, when faced with a different group or species, are influenced by factors in individual experience, as well as, of course, factors in temper, liveliness, mobility, constitution, etc.? Dealing with ants in their natural behaviour, an impression gradually formed that the permanence of individuals of a given species in a given location would determine or promote attack against individuals of other species later entering the area; and that, in the same way, if individuals of both species arrived at the same time they would not attack, but rather avoid each other; and if the individuals of a species outnumbered those of the other, they would tend to attack, and, should the opposite be the case, to flee. Both preceding others in an area, and being there in greater numbers would create, as it were, due to the mnemic record of animals in a given species, an impression that the location did not belong to others arriving later or in inferior numbers.

I decided to test these hypotheses with a simple procedure: by introducing ants of a few species living in my area into 10 cm^3 transparent glass containers with plastic stoppers, simultaneously and at different times, in equal and unequal numbers, and record the ensuing events. Before this I would keep some individuals of different species, captured in their nests, in a number of different containers. Observation 68, reported below, describes the procedure and the results.

- *Observation 68 – On the testing of some hypotheses on the prompting of fight or flight in individuals of different species by some conditions in their individual experiences.*

First procedure – I kept three *Solenopsis saevissima* workers, one of them larger and with a bigger head – a “soldier” – inside a glass container for 1 hour 15 minutes. Then I introduced a *Paratrechina fulva* worker, captured with a cotton wad. It started running, whereas the others simply walked. It clearly avoided contact with the others, which, however, did not seem interested in attacking it. Whenever it happened to come across a *S. saevissima*, it shivered, sped up, and followed a wavy course, all of it hurriedly. It seemed clearly to avoid the other ants. Some minutes later, as it happened to be between two of them, it was suddenly attacked by both; it ran jerkily away. One of the rivals started walking with its abdomen raised and jaws abducted. More than one minute later, a small *S. saevissima* attacked and gripped the *P. fulva*. The two other ants passed by the grappling ants but showed no interest and kept walking.

The *S. saevissima* holding the *P. fulva* moved its gaster towards its head, stung it, and let it go. The prey went limp, almost totally still. The other two ants would sometimes pass by it and even touch it, but leave it alone. It lay there, almost on its side, and barely moved. Three minutes later, its body was clearly contracted. The others seemed livelier as they approached the ant, but did not touch it. Two minutes later, the large *S. saevissima* soldier went over to the *P. fulva* and again pointed its gaster to its head; the prey moved even less than before.

Second procedure – I took a *Solenopsis saevissima* worker from one of the glass containers in which I had stored a number of them; I did it with a card, which was bitten by the ant. I put it inside another container, where I had kept 3 *P. fulva* ants for 45 minutes. All the ants were upset, but it was the *P. fulva* ants that fled on coming across the *S. saevissima.* The latter would not turn aside; the others avoided it. Once it seemed about to attack one of them, but it escaped to one side.

Four minutes later, the *S. saevissima* attacked two *P. fulva* ants, and they ran away. The *S. saevissima* started to tremble and clean its antennae. Three minutes later, I put a cotton wad dipped in water and sugar on the bottom of the container. Some minutes later, the only ant that had visited the bait and increased in size was the *S. saevissima.* The three *P. fulva* ants gathered together on the plastic cap, where the other ant would not go.

I moved the container and the three *P. fulva* ants were still upset and avoiding contact with the *S. saevissima*. I shook the bait: they went closer to the stranger and then retreated in a wavy course. In their meetings, it was the *S. saevissima* that determined changes in direction. In this case, the fact that an ant species outnumbered the other did not lead to their being dominant, but this seemed to be so because of their specific temperament. *Paratrechina fulva* ants proved to be timid, using their great mobility to avoid contact with their rival, which, on the other hand, seemed unafraid.

Third procedure – The *P. fulva* placed inside the bottle with the three *Solenopsis saevissima* ants was dead; it rolled from side to side as I shook the container. I then placed a *Camponotus crassus* worker inside it. It did not attack the *S. saevissima* ants, but avoided them. They did not go after it, but whenever they met face to face, they threatened it, with abducted jaws and raised, trembling abdomens; the *C. crassus* fled. After some minutes, I saw the *C. crassus* walking with a *S. saevissima* clinging to one of its legs; it was apparently dead, I do not know how. Perhaps the other ant had defended itself. The other ants were also walking, but paid no attention to the *C. crassus*, which seemed very agitated and always turned aside upon meeting a rival. In this case the dissuading effect of being outnumbered was clear.

Fourth procedure – I placed three *Camponotus crassus* ants in a third container. Once there, they started to lick the tip of their gasters, something which is also occasionally observed in *S. saevissima*. Ten minutes later, I put a small *S. saevissima* inside the container. It avoided contact with the *C. crassus* ants, well bigger, but was not in a hurry; it walked to and fro and sometimes even under one of them. The latter seemed annoyed: with a jolt it pointed its jaws to the *S. saevissima*, which then ran away with its abdomen raised. The *C. crassus* did not go after the intruder, but seemed to be interested in capturing it. Four minutes after being placed in the container, the *S. saevissima* went too near a *C. crassus*, was captured and had its abdomen severed with a bite. It is interesting that the *C. crassus* did not go after the intruder, but tried to catch it whenever it was within reach.

In this case, precedence and being in greater numbers were evidently factors stimulating fight.

Fifth procedure – I placed six *Paratrechina fulva* workers inside a glass container. Thirty minutes later, I also introduced a *Solenopsis saevissima* worker, slightly larger than any of the *P. fulva* ants. The *S. saevissima* did not attack any of them; it only tried to flee. As I opened the lid to introduce it, there was confusion among the ants, which would sometimes rush at the intruder and then run away. The *S. saevissima* ran away, but whenever they met head on, it confronted its rival. It raised its body, gyrated, and jolted. The *P. fulva* ants seemed very curious: they went near the *S. saevissima*, smelled and touched it, and then ran away. Sometimes they seemed to do it intentionally, but in most occurrences it seemed just a chance encounter. The *S. saevissima* had a wavier gait and was more agitated than the others. Once, a *P. fulva* ant briefly attacked the intruder, which ran away and started running around. One or other *P. fulva* would sometimes flee from the intruder, but generally this was not the case. I saw one of them turning its abdomen towards it and go after it, though somewhat cautiously. Further ahead the *S. saevissima* came across a *P. fulva* from behind; it turned back and then came across another one, but now face to face; it was attacked, but the confrontation did not last: it fled instead of confronting the other. Ten minutes after being placed inside the container, its movements seemed a little impaired. Typically, the *P. fulva* ants gathered on the upper part of the container.

When attacked, the *S. saevissima* defended itself. A little later I saw it on the bottom of the container, its body contracted. The others had probably killed it with squirts of acid in the few encounters they had had. They started to come near it and were apparently curious.

In this observation, precedence in the container and greater numbers apparently led even the timid *P. fulva* ants to fight.

Sixth procedure – A *Camponotus melanoticus* and a *P. fulva* workers were separately captured with a cotton wad. Both were placed inside a glass container, the *C. melanoticus* 30 seconds before the *P. fulva.* They avoided each other during their encounters. Perhaps 30 seconds had not been enough for the *C. melanoticus* to better adapt to the location, though I had already noticed that this ant species generally has a mild temperament. The *P. fulva* seemed more upset than the other and exhibited jolts as it hurried away in a wavy course after these encounters. But the *C. melanoticus* also avoided the *P. fulva.* It did not try to catch it in their encounters: it turned back with a jolt instead. It was also slower than the other.

In this observation I tend to think that the precedence of the *C. melanoticus* inside the container was not enough to make it more assertive towards the other ant. It was as if they had been simultaneously introduced in the container.

I then introduced a *Camponotus crassus* worker in the container. The three ants avoided each other, especially the *C. crassus*. The *C. melanoticus* seemed uninterested in it, and the *P. fulva* would not flee, but raise a little its abdomen when facing it. The *C. crassus* seemed lightly injured.

Seventh procedure – I placed a bait (a cotton wad dipped in water and sugar) with about 20 *Solenopsis saevissima* ants inside the container used in procedure 4, with three *Camponotus crassus* workers and a dead *Solenopsis saevissima* already inside. I wanted to see the weight of previous exposure as compared with greater numbers. As the *S. saevissima* ants left the bait, two *C. crassus* ants started to run, while one remained, attacking the intruders and being occasionally attacked by them. Another *C. crassus* lost its patience and started biting them. Apparently, the *C. crassus* did not intentionally looked for them, but chance encounters resulted in attack, especially by the *C. crassus*. The *S. saevissima* ants apparently did not want to attack, but defended themselves. They were easily cut, however, and the others would catch with their mandibles all that came their way. A *C. crassus* walked with a *S. saevissima* attached to one of its legs. The *C. crassus* only attacked moving ants, clearly getting hold of their petioles to cut them in two. Only active living ants were attacked, whereas those slightly moving were left alone.

Seventeen minutes after being introduced, only four *S. saevissima* workers were still active. They would not take the initiative of attacking but to defend themselves. Three minutes later there were only two living ants: one that stood as still as possible under the mangled bodies or under the bait, showing no interest in attacking, while the other clung to the leg of a *C. crassus*; the others had all been killed. Apparently precedence prevailed over greater numbers; however, I do not know whether the fact that the *C. crassus* had killed a *S. saevissima* before had any influence in the results.

Eighth procedure – I put a large *Solenopsis saevissima* worker and a larger, mid-sized *Camponotus crassus* inside a glass container at the same time. They avoided each other as they went on and on round the container. The *C. crassus* seemed more upset and intent on avoiding the other. It also ran faster.

Some minutes later, they would sometimes come across each other without any attack. Apparently, there was neither mutual interest nor avoidance. When face to face, the *S. saevissima* would half raise its abdomen, but there was no attack. After some 10 minutes, I accidentally hurt the *C. crassus* while opening and closing the container; I decided to take it out and end the session. Simultaneously introduced in the container, therefore, these two workers of different species did not attack and avoided each other instead.

Ninth procedure – In the container used in the fourth procedure there were now only two living ants out of the original three *Camponotus crassus* workers. The third had died, I do not know how, and lay on the bottom of the container. Perhaps it had been hurt by some *S. saevissima.* The other two did not walk as much as they had done before, perhaps because they were tired. I introduced a *Camponotus fuchsae* worker in the container. I had long kept an artificial nest with this ant species, which seemed to be one of the most irritable and aggressive. Whenever the large glass arena in which the colony had been placed was manipulated, workers would come out, with trembling abdomens and open jaws, in search of invaders, and ended up fiercely attacking the corpses of nest-mates or any other residue or object they found in their way. Considering this, I expected that, once inside the container, it would attack the *C. crassus* ants.

Contrary to what I had expected, the *C. fuchsae* hurried away whenever it came across the other ants. The smaller *C. crassus* did not seem hostile. The larger one, on the other hand, curved its abdomen between the legs and underneath the thorax and apparently squirted acid at the intruder. The action was repeated many times, and the intruder seemed very disturbed. The *C. crassus* abducted its mandibles, went after the *C. fuchsae*, and, at a certain distance, aimed its abdomen at it. Eight minutes after being introduced, the *C. fuchsae* lay dying on the bottom. It barely moved a leg.

In this episode, the outcome may be ascribed to precedence in the container and greater numbers.

Tenth procedure – Eight *P. fulva* ants were left inside a glass container for three hours and a half. I then introduced a *Camponotus fuchsae* worker in the container. The *P. fulva* ants were upset and avoided it. The *C. fuchsae* started to clean its antennae, but also avoided the other ants, which gathered on the upper part, on the cap. I turned the container upside down. One of them attacked and ran away. The intruder was upset and fled. I turned the container again. One or other *P. fulva* ant would quickly bite the intruder's legs and run. Disturbed, the *C. fuchsae* ran away.

The *P. fulva* ants went up again to the cap, where the *C. fuchsae* would not go. I turned the container again. Interestingly, the *P. fulva* ants only ran around and only attacked from behind and then fled. Once in a while, one of them would come down, walk around, attack, and run. During some two minutes, two or three *P. fulva* ants jointly attacked and ran. They no longer fled, but the intruder did. In fact, the *P. fulva* ants would come, retreat, come again, and then gather on the cap. Whenever I turned the container and the intruder fell on them, they rushed and attacked, usually for only a while, and then retreated again. One or other would come down only when the intruder was too agitated: apparently, they attacked only when some threat was sensed. The ants attacked from behind and ran away when the other ant turned. I had to strike the container for them to go down and attack. Otherwise, they went up to the cap and showed no interest in the intruder. Sometimes it found itself face to face with a *P. fulva*, but did not attack. It fled.

Eleventh procedure – I introduced a large *Camponotus fuchsae* worker in a container in which fifty *Solenopsis saevissima* workers had been for some 5 hours. They did not attack nor fled. It so happened that, while walking to and fro, only one of them caught one of its legs and did not let go until it was bitten. When the *C. fuchsae* accidentally fell on other ants, another ant gripped one of its legs and aimed its raised abdomen at it. It escaped and touched the bitten area with its mandibles. One or other ant would bite it when it moved, walked over them or came too near them. They would rarely come from a distance to attack.

Apparently, even in larger numbers, the *S. saevissima* ants would not attack unless the *C. fuchsae* was in front of them. The latter, being outnumbered, seemed intent only on escaping.

Twelfth procedure – I put three *Camponotus melanoticus* workers, one of them a soldier, inside a glass container. After 1 hour and 20 minutes I introduced three *Solenopsis saevissima* workers in the container. Inside, there was a cotton wad, a shelter for the new arrivals, which were well smaller than the other ants. The *C. melanoticus* soldier crushed a *S. saevissima w*ith its mandibles. The other two *C. melanoticus* ants seemed peaceful, whereas the soldier would try to capture any intruder that came too near. It went to the ant it had killed, caught it and crushed it again. Its two nest-mates tolerated the intruders as they passed between their legs and seemed not to be interested in them.

Seventeen minutes after the start of the procedure I introduced a *Camponotus fuchsae* worker in the container. The soldier seemed interested in catching it, but not much. The *C. melanoticus* workers, however, were sweet: they let the *S. saevissima* remain under and on their gasters. As for the *C. fuchsae*, it seemed interested only in fleeing the others.

Thirteenth procedure – I simultaneously placed four *P. fulva* and four *S. saevissima* ants I had just captured into a glass container without a cap. They showed no interest in fighting, only in escaping from the container, which they readily did, and I finished the observation. Certainly, not having stayed long enough in the unknown place to which they had been moved, their only concern was to escape.

Fourteenth procedure – I have not found this observation in my protocols – perhaps I did not record it – but I clearly remember it. I put a *P. fulva* and a *C. melanoticus* inside a glass container at the same time. They avoided each other and did not seem inclined to attack. I had to be away for perhaps two hours and, on coming back, to my surprise, I saw them, notwithstanding the enormous difference in size, engaged in mutual regurgitation. I could not, however, determine which of them was regurgitating and which was receiving the regurgitated food. This observation confirmed my impression about the timid and unaggressive temperament of these two species.

After these observations, I think I may say that, generally speaking, they confirm my hypotheses regarding some factors in the individual experience of ants of different species which may determine, in their encounters, a tendency either to fight or flight, or to mutual tolerance. A graduate student later reproduced these observations in a more detailed and controlled fashion for her Master degree research (Cf. N. L. S. Wakahara, 1981) and generally achieved the same results, but focusing at length on differences in the temperament and fighting tactics exhibited by different species.

10 ON THE REACIONS OF SOME OTHER REGIONAL ANT SPECIES WHEN FACING CRUSHED NEST-MATES

Under this topic I am going to report some brief observations concerning the reaction of some local ant species upon finding crushed nest-mates on a trail. The objective of these observations was not to study in detail their reactions, but to test the generality or otherwise of behaviour modifications caused by this form of alteration and briefly compare them with those seen in *Paratrechina fulva*. In the account below, only observations carried out with identified ants, at least for genus, are reported.[33] Useful information about most of the species considered here can be found in Luederwaldt (1926).

PONERINAE

- *Termitopone marginata* (Roger, 1861)

This was the only Ponerinae species studied in this connection. It is a glossy black ant, relatively large (a little more than 1 cm long), with a long sting. Differently from most Ponerinae, it lives in relatively populous colonies (at least several hundreds of individuals). According to Lemko (personal communication), they are popularly known in Brazil as “fox-ants” or “skunk-ants” and specialise in predating termites.

A first observation with the species was carried out with a trail with tens of ants along a stretch of ground without vegetation, extending from a pile of rubble and broken bricks to some scattered orifices 5 m

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[33] One species of Pheidole and one of Acromyrmex considered in this account were identified by Friar Walter Kempf, but, unfortunately, both identifications and samples were lost. Besides Friar Kempf, I am also indebted to Karol Lemko and Carlos R. Brandão for identifying the species.

beyond, from which they skilfully extracted termites. Since Termitopone marginata has an exceptionally resistant chitinous tegument and seems always ready to sting, which it does exceptionally well, I prudently decided not to crush the ants with my fingers. I used a stone to crush one of the workers on a small half-buried rock, on which the trail was clearly visible. On reaching this alteration point their reactions were generally as follows. Ants carrying termites, when about 5 cm from the dead ant, turned back in a wavy course – at least wavier than when they were in more distant areas – in a clearly accelerated march, with brisk zigzag moves, sometimes all along their course to the vicinity of the orifices. Some of them, however, halted when about 5 or 3 cm from the alteration point, and started going from side to side in a hesitating detour; they bypassed the dead ant and went as far as 10 cm or 15 cm from the trail and joined it again further ahead; then they went on in a somewhat wavy course, faster than before. As for the ants going towards the termites, a number of them turned back, some of them following an undulating course part of the way, others until their destination. Other ants went as far as 0.5 cm from the dead ant in a brisk zigzag course, their antennae moving a lot ("sniffing"), and then circled the alteration point in a slightly wavy course. Once in a while, some ants, with or without a burden, as soon as they started on their way back, turned their gasters once or twice to left or right; it was as if they were about to sting, but they did not exhibit their stings. This happened especially when an ant touched another from behind; on these occasions, besides the movements mentioned above, the ant also quickly turned towards the other ant. Along the trail, their relatively quick march was suddenly interrupted by a brief pause every 10 cm or 15 cm. Twenty minutes later, there was almost no return: only detours, acceleration, and slight undulation. None was seen leaving their burdens, but all of them exhibited some alteration in behaviour in the vicinity of the alteration point. There was no decrease, if any, in flow intensity. No jolts were observed.

A second observation with this species in the absence of a trail, carried out on another occasion, yielded very different results. Once I saw a group of *T. marginata* slowly wandering by the side of a road; I prudently crushed one of them with the tip of my shoe. Many ants passed by at a distance of 1 cm or less from the dead ant and exhibited no discernible behaviour modification, except for some brief "sniffing" and a light detour, and even these were doubtful; however, detours apparently did occur, since it was highly unlikely that in their meandering on the terrain some of the ants would not come across the alteration point unless by making a detour. Anyway, the absence of returns, undulation, acceleration, wide detours, and thrusting motions of the gaster was in sharp contrast with the phenomena observed in other instances, when an ant was crushed on the trail.

DORYLINAE

- *Labidus coecus* (Latreille)

I considered this species of army ant in Observation 42, dealing with a trail represented in Figure 60, and reported many aspects of its behaviour and of other Dorylinae. I also reported some of their reactions when faced with crushed nest-mates. There is not much of relevance to be said in this context. When I crushed some *L. coecus* workers at two points of the trail or column, their displacement became a little faster and wavier near the alteration points; some ants also tended to roam around, turning their heads from side to side and vigorously moving their antennae. Some reared their bodies and stood on their hind legs, with open mandibles and rhythmic motions of their cephalothoraxes, as if pouncing. Some ants would exceptionally turn back. Others climbed the crushed body. Therefore, traffic was jammed in the altered areas. Behaviour modifications were restricted to the altered area and not especially dramatic: they were not different, for instance, from the modifications observed when one blows on them or when an ant of another species is crushed on their trail.

On another occasion I observed another trail of *Labidus coecus*, with fewer individuals. The trail marched on a cement floor, close to its junction with a wall, between a rainwater drain and a box with rubbish. Inside the drain one could see a bunch of interlocked ants. Inside the box, the ants visited a can with remnants of butter and picked up cooked rice grains, lettuce bits, and lemon seeds, perhaps because they were smeared with vegetable oil. I crushed a few workers, one at a time, at some spots of the trail. The result was similar to the one in the previous observation: a small crowd of ants climbing and pulling at the body, some of them pausing, walking to and fro when 3 cm or 4 cm from the body, going round with undulating motions – which, it should be mentioned, is always seen in their ordinary march and makes them look very agitated – reorientations and returns. However, I could observe, more clearly than before, that the twitches exhibited by the ants, such as pouncing at the air on getting near the alteration point, looked like a chaotic cluster of jolts, sniffing motions, and an aggressive posture: extending their antennae upward or forward, standing on their hind legs, quickly thrusting forward their cephalothoraxes like the shuttle of a sewing machine, while bending their abdomens under their thoraxes and opening their mandibles. I noticed, however, that sometimes the same movements could be seen in other ants, at other points of the trail, with no apparent reason; they only became more noticeable and generalised near a crushed nest-mate or when an alien ant suddenly crossed the trail, or when one blew on them.

For comparison purposes, I employed a variety of objects on the trail as experimental alterations in both observations. Before my forefinger, with or without the scent of crushed ants, or a sweet, they did not exhibit any modifications in behaviour, except for livelier motions of their antennae, and a detour of 0.5 to 1 cm. Before invalid ants (some *Solenopsis saevissima* and a *Camponotus crassus*), they made a 3 mm detour for a while, until some small and middle-sized ants started pulling them, raised on their hind legs, their bent abdomens repeatedly thrust towards them between their legs and thoraxes. I noticed that they performed the same stinging motions at a food item, but this was perhaps just an accompaniment to the effort of their mandibles to rip it apart. Before alien and mobile ants, *S. saevissima* and *Pheidole sp.* tended to move like a shuttle, pinch bodies with their mandibles and bend their abdomens against them in a livelier fashion, something which, strangely enough, was repeated when in the face of a vegetable fibre fallen on the trail. Generally speaking, it seems that a crushed nest-mate stood out among other alterations on the trail because it prompted more traffic jams, returns, and did not elicit bending motions of the abdomen as ants do when about to sting.

Labidus praedator

The crushing of some individuals of these black ants in a migratory column 3-4 cm wide as they walked through some branches and grass tufts by a wood at dusk caused some jamming, increased undulation in their march, and some roaming around of workers. It is possible that the pressure of a great number of ants and the width of the column (and, therefore, the absence of a clearly linear trail) were responsible for the mild behaviour modifications observed.

In these observations regarding behaviour modifications of Dorylinae jolts were not seen (at least as a separate form of motion), returns were few, acceleration was low, undulation was merely an accentuation of what was normally seen in an unaltered trail; also there was practically no reduction in flow intensity resulting from an experimental alteration.

MYRMICINAE

- *Solenopsis saevissima* (Fr. Smith, 1855)

One observation of behaviour modifications in this species dealt with a trail, mentioned in Observation 45, a slightly modified illustration of which is shown below as Figure 88. It was a short trail about 20 cm long, most of which running next to the edge of a batten and connecting an orifice in a cement floor, the entrance to the nest, to a bait (a cotton wad dipped in sugared water). After two ants were crushed halfway along the trail, their nest-mates, which had been marching at a slow pace, adopted an undulating march, their abdomens raised and trembling, their speed lightly increased, exhibiting aimless turns on the terrain. In about 2 minutes the trail had become a 20 cm wide column. Figure 89, below, illustrates the change. However, journeys to the bait continued and, within some minutes, the trail recovered its original aspect, except at the alteration point, where individual courses were unpredictably reoriented.

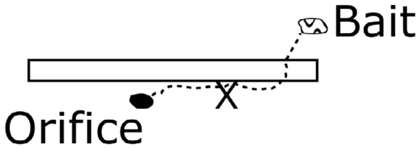

Figure 88: A trail of *Solenopsis saevissima* workers on a cement floor, following the length of a batten.

Legend:
Dotted line: trail under a batten, along one of its edges
Whole lines: batten edges
X: alteration point
Black point: nest entrance.

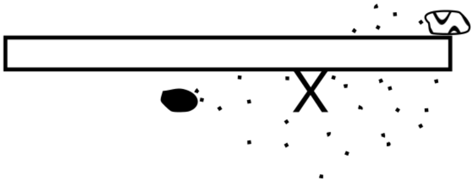

Figure 89: Distribution of *Solenopsis saevissima* ants after two of them were crushed on the trail represented in the previous picture.

Legend:
Black circle: entrance to the nest
White circle: bait
X: alteration point
Scattered dots: ants after the alteration

In other observations with trails a few metres long, running along the junction of floors and walls, crushed nest-mates found on the way caused in ants on both sides of the trail a number of somewhat slow, undulating returns (*S. saevissima* rarely runs), with abdomens conspicuously raised and slight shivers. On these occasions, their mandibles were greatly abducted. Jolts were not seen in this species.

- *Genus Pheidole*

Although I have often seen *Pheidole oxyops* nests, with their semicircular openings in the soil, generally in areas devoid of vegetation, I have only once recorded their reactions when faced with crushed nest-

-mates. It was an apparently new colony, established in an area without vegetation measuring some 40 cm in diameter. A number of slim small workers came in and out of the nest, and sometimes the relatively large head of a soldier could be seen sticking out of the entrance.

I crushed two workers on a relatively irregular and short stretch of the trail, near the low vegetation surrounding the nest[34]. Many ants, when 10 cm from the alteration point, would pause briefly and start running in an undulating course, with lively motions of their antennae, following a route away from the trail. Many of them, after roaming round the dead ants, returned in an accelerated march to the nest or the edge of vegetation from which they had come. Five minutes later, the trail had vanished, as if by magic, as well as the ants by the entrance of the nest.

On another occasion, I crushed a worker 4 cm away from a hole in the wall; it was the entrance to a nest, and a number of workers of an unidentified *Pheidole* species could be seen carrying the bodies of woodlice, gnats, and other ant species. A worker with a burden, on approaching the body, roamed round more than under normal conditions and seemed disoriented. Among the ants coming out of the hole and those coming back the most common reaction was "sniffing" at close quarters, preceded by the bending of their thoraxes and abdomens. Many of the ants coming out meandered for a while with bent abdomens and returned to the nest; others, however, would go on, apparently resuming their normal foraging activities. Five minutes after the ant was crushed, and when these behaviour modifications were still clearly discernible, a worker carried the dead ant to the nest; other ants came out of the nest, but did not exhibit any perceptible behaviour modification, not even when walking on the alteration point. I believe it was an ant species with relatively good eyesight, since the workers followed independent courses and did not seem inclined to follow such markers as walls and fences.

A new observation was carried out with another *Pheidole* species, with workers of variable sizes, but generally larger than the previous species and with glossier black bodies. The "soldiers", about 0.5 cm long, had red heads, thoraxes varying from reddish-brown to black, while their jaws and the

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[34] This species, as far as I could see, hardly ever forms trails.

rest of their bodies were black. I crushed one of the workers 5 cm ahead of an earthworm that the ants were dragging to the nest. The ants that turned to the dead ant left aimlessly in a wavy course and at a brisk pace; the others abandoned the burden in a hurry. Later, I threw a crushed worker near the entrance to the nest, where many of its nest-mates could be seen: the body was grabbed and dragged along an uncertain course, while the others ran round the area in a wavy course; a "soldier" came out and did the same. A finger positioned 2 cm away from the entrance caused no perceptible modifications in the lively moving circle of ants, but a finger used to crush another ant, under the same circumstances, prompted them into an undulating rush round the area, followed by withdrawal into the nest; soon, no ant was to be seen in the vicinity.

- *Cremastogastrini*

I kept for some time two colonies of different unidentified *Cremastogaster* species in two artificial nests. They were small, monomorphic black ants, with the typical heart-shaped abdomen, and their size ranged from approximately 2mm in one case and 3.5 mm in the other. I faced the ants in these colonies, as they walked on the glass plates covering their nests, either with a crushed nest-mate or its remnants on the tip of my finger. They did not respond by running, but generally by raising their trembling abdomens, a milky-looking drop of poison showing on the tip.

Later on, in the countryside, I saw some ants strongly resembling the bigger species I kept in the artificial nests. They walked along a 40 cm stretch on an L-shaped branch some 2 cm above the soil, keeping a wide space between each other. I placed the crushed body of an ant on the soil, next to the base of the branch. The ants on the branch halted when about 5 cm or 8 cm from the body and returned to the foliage at a slightly increased pace, and with their abdomens raised, almost touching their heads. One ant coming down the branch also raised its abdomen and turned back upon coming across one of the returning ants. As for the ants coming from the ground, they went as far as 3 cm from the body, then rushed away in a undulating course, with their abdomens raised; other ants, after all this, stopped 3 cm away from the body, their heads turned towards it, the tips of their abdomens vigorously trembling in the air.

- *Attini*

I observed the reaction to crushed nest-mates and, for comparison purposes, to other kinds of stimuli, among a few species of leaf-cutting, fungus-growing ants in the genera *Atta* and *Acromyrmex*. I report below the conditions under which the observations were carried out and their results.

- *Atta laevigata*

I once saw these particularly large-headed, glossy ants, popularly called "glass-heads" walking in great numbers (about 120 per minute, according to my count) on a "road"[35] about 10 cm wide, many of them carrying fragments of grass. I crushed some workers using my shoes instead of my hand in order to have a good number of dead ants. Behaviour modifications caused by this alteration in the approaching ants were immediate. Many of them halted, roamed round the area, exchanged touches with their antennae, dragged the dead; others left the "road" with abducted mandibles, while others, on hurrying by with their burdens, seemed to skid and fall on their sides at the spot where the ants had been crushed. Around the area, for about 1 m, the trail became a 30-40 cm wide column. I captured tens of these ants and put them inside a glass container; later, I introduced some crushed ants. There was a great confusion in the container and soon they were grappling with and mangling each other.

- *Atta sexdens rubropilosa* (Forel, 1908)

I placed a mid-sized worker on a 2 cm-wide "road", a few centimetres away from an orifice in the soil, the entrance of an underground tunnel. There were not many workers in the column, and most of them were either mid- or small-sized. The latter gathered round the dead ant, touched it with their antennae, and started roaming round the area, extending the width of the column at this point to 6-10 cm. A mid-sized worker ran towards the body with open mandibles, grabbed it and then let it go; it apparently threatened its smaller nest-mates (it made a move towards them with open mandibles, but did not grab them) and "bit" a piece of straw. A big "soldier", 20 cm away, after coming across some returning ants, went

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[35] A stretch on the terrain stripped of vegetation and detritus by *Attini* ants and regularly used by them for foraging and transportation of vegetable fragments.

towards the dead ant; it proceeded at an accelerated speed, following a widely wavy course, its head well raised, lowering and raising its body as it went. Another "soldier" walked past its dead nest-mate at a distance of 1 cm, coming at a high speed from the nest entrance (30 cm away) in a sinuous march, its legs wide apart, and then halted; while doing so it raised its head higher up and exhibited three jolting motions at 1-2 second intervals: each jolt was an energetic thrust of its body with legs planted on the soil, as if in aborted attacks which almost lifted it off the ground.

Raising the front part of their bodies and cleaning the antennae with their forelegs were common occurrences near the altered area; on other occasions, assuming the same posture, some ants would "sniff" at the air. Those bearing leaves hesitated for a while (turned left and right) and went on, a little away from the trail (1cm), but sometimes going as far as 4 or 5 cm out of their route, returning to it later on; two or three let their burden fall and went hurriedly back, lowering their generally raised heads towards the ground at intervals; a few fell on their sides, burden and all, while passing beside the disturbed area, by now "clogged" with small workers. It was very interesting how an undulating motion was propagated right after the experimental alteration to as far as 20 or 30 cm on both sides of the "road".

Results were similar with other columns. Blowing on them after crushing a nest-mate produced almost no modifications; however, when this was done before the ant was crushed, it definitely prompted, though for a shorter time, wavier courses and a wider spreading out of the column than the crushing event itself. One would say that the first alteration introduced was relatively more effective in causing behaviour modifications.

Later, I found ants of the same species going up and down the whole surface of two tree trunks, forming no definite trail. In one case, crushing an ant caused the ants coming towards the altered area in a bloc to go past it following a dislocated course, very accelerated and undulating, resembling a series of fast, repeated bounds, with mandibles hitting the trunk at intervals. In other case, besides events like these, many ants also fell off and abandoned their burdens during the first minute. Later on, blowing on them caused almost no modifications.

In my laboratory, where I kept a large artificial nest of this ant species, I sometimes collected a few workers and put them in a glass container, and later, a crushed nest-mate. This increased the agitation of the swarming ants and the intensity of their stridulations, but I did not see them fighting on these occasions. In the first few weeks following the settlement of the colony, blowing on the brass screens of the nest, as well as the oscillations or vibrations caused by shocks or heavy vehicles in the neighbourhood greatly upset the workers and even led them to remove larvae from their fungus gardens. Later, they would become relatively indifferent to these alterations.

- *Atta sp., probably Atta bisphaerica*

I crushed an individual of this 2-5 mm long, grass-cutting species on a sparse trail, marching on a 2 cm wide “road”. A small worker repeatedly ran around the dead ant, in a circle with 5 cm of diameter; another ant, bearing a grass leaf, when a few centimetres from the altered area, slowly made a detour and rejoined the trail 10 cm ahead; from this point on, it started running in fits and starts, its march interrupted by brief pauses; it then rolled on the ground while still holding the burden, and, when 50 cm away from the altered area, abandoned its route again. A mid-sized worker approached the dead ant, touched it with its mandibles, and then briskly pulled its body back with a jolt. Ants without leaves approached and engaged in a sort of undulating dance round the body, turning towards each other and exchanging touches with their antennae. Those bearing grass leaves would typically stop at varying distances (ranging from 2 cm to 20 cm) from the alteration, suddenly leaving their route, often falling on their sides, and joining the “road” again further ahead, at a faster pace and stumbling over each other. A somewhat smallish ant stood on its hind legs and raised its body and, when near the dead ant, repeatedly thrust the front part of its body back and forth in a series of jolts.

- *Atta sp*

Once, while walking on a tiled floor between two flower beds, I found a very active and thick trail of small (about 3 mm long) leafcutters, many of them bearing small fragments of rose leaves. Gusts of wind hit the trail perpendicularly, and the trail seemed to persist only because it followed a relatively deep groove between two rows of tiles. Figure 90, below, illustrates the situation.

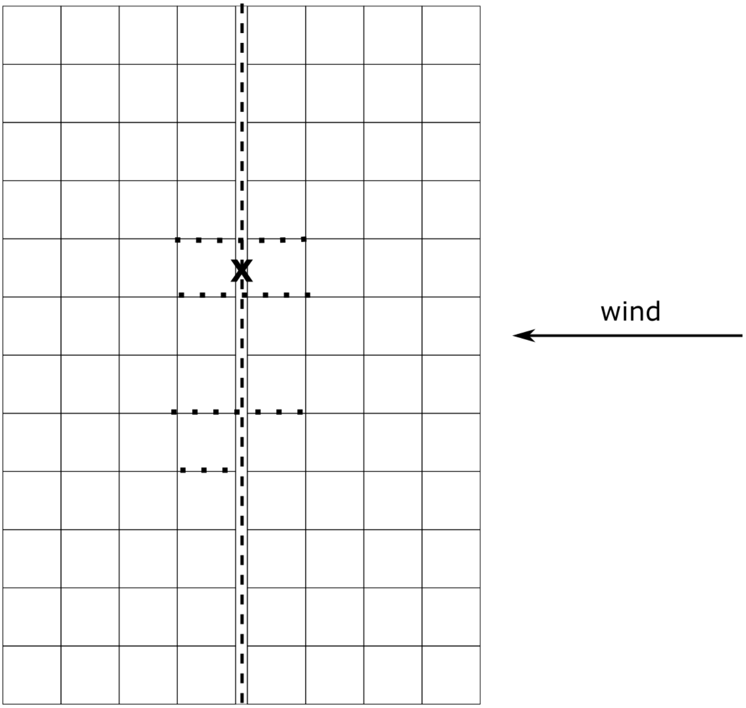

Figure 90: Part of a trail formed by small ants from a colony of an unidentified *Atta* species.
Legend:
Whole lines: grooves between tiles
Dashed line: trail
Dotted lines: attempted detours
X: Alteration point (crushed ants)

Crushing a worker generally caused the following behaviour modifications in the ants in the area: many of those marching towards the rose bush turned back when a few centimetres from the alteration point; some attempted a detour, always using some groove perpendicular to the trail; none completed the detour: some were swept away by the wind – since the grooves were not deep enough to shelter them – while others returned to the trail, forming a moving obstacle in the altered area. As for the ants going the other way, they would not abandon their burdens, but wavered for a while (turning from side to side before the dead ant); sometimes they went past it in a wavy course, very often falling on their sides with their burdens; sometimes, while returning or taking a lateral groove, they were blown away by the wind. Considering these behaviour modifications as a whole, especially the fact that the attempted detours occurred only along the lateral grooves, I had the impression that the ants were simultaneously avoiding the dead ants and the winds.

- *Acromyrmex sp*

The following observations took place in a building near the seashore, where I found a trail formed by monomorphic workers, their colour something between black and greyish brown, running along one of the upper edges of a brick wall and then downwards to the cement floor, where they collected crumbs and bits of grape skins. The trail persisted with the same layout for two nights in a row, occasions in which it was observed under torchlight. Figure 91, below, illustrates the stretch of the trail on which alterations were carried out.

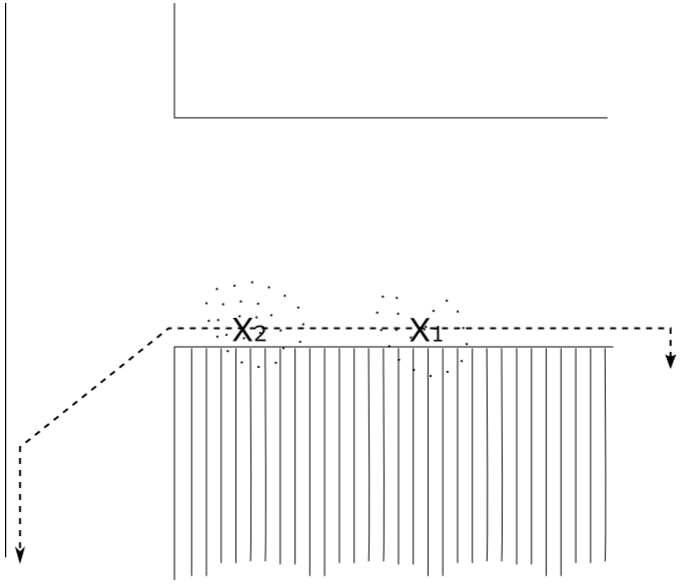

Figure 91: Approximate representation of a trail of *Acromyrmex sp.* on the upper surface of a brick wall.

Legend:
X_1 and X_2: alteration points in two successive nights
Dashed line: original course of the trail
Dotted line: detours after experimental alterations

On the first night I crushed a worker on the trail, 40 cm away from its point of reorientation on the wall. Ants turned back and ran around on both sides. Most of the ants, however, halted when 1 cm or 0.5 cm from the dead ant, one or other exhibiting a jolt, suddenly thrusting its body upwards with its legs planted on the ground, while others "sniffed" at the alteration point. A number of ants with burdens would halt and stand still for quite a few seconds, while others redirected their course to the vertical surface of the wall; some of them would very often fall off the wall. Traffic near the alteration point was somewhat confused, and considerably spread out as compared with the original course of the trail.

On the second night, after I had scattered some bread slices on the floor, some scouts appeared and, after a while, a trail was formed, similar to the one seen on the preceding night. I then crushed a worker 3 cm away from the turning point of the trail on the wall. There was a great confusion: ants turned hurriedly aside in slightly wavy courses, some fell off the wall, or went rapidly back and forth; some halted when 1 cm or 2 cm away, exhibited a series of two or three jolts, their heads raised and antennae vigorously moving. Among those coming from the nest, a number of them marched on in a wavy course when at a distance of 15 cm to 10 cm from the alteration point, and seemed to seek contact with the returning ants (they went slightly away from their course to touch them with their antennae); many went past the body in an undulating detour; many of them slowly approached and repeatedly "sniffed" it; then, walking sideways, they went round the dead ant with their heads pointed towards it; among those carrying bread crumbs, two turned back, abandoning their burdens, which were picked up by others; the others halted, raised their heads when at 1 cm from the alteration point, turned from side to side, and went on in a detour. On both sides of the alteration, the trail became a column about 4 cm wide; there was much coming and going, and sometimes ants approached the body and touched it with their mandibles; then they ran at a quicker pace in an undulating course in any direction. Sometimes, when there was a sudden breeze, the ants around the body ran windingly away in any direction. When I blew on the crowd, a big mass of ants returned to the nest in a wavy, accelerated course, leaving a wide gap on the trail, near the alteration point, for one minute or more. I do not know why behaviour modifications were a little more dramatic on the second night.

DOLICHODERINAE

Tapinoma melanocephalum (Fabricius, 1793)

This was the only Dolichoderinae species I observed; it is popularly known as the ghost ant because of the somewhat transparent, milky colour of its appendages and gaster. It has a visible dark patch and its body can apparently be greatly distended. Its head and thorax are dark brown, and its petiole has only one node, not visible when it is observed dorsally. It is a stingless ant that defends itself very efficiently by squirting a sticky secretion from its anal glands that is very irritant and fatal to its enemies. It is a monomorphic species, with tiny workers (about 1 to 1.5 mm) that walk slowly when on a trail, but can run very fast when on its own, occasions in which it seems to glide aimlessly. It is cosmopolitan and widely distributed in tropical and subtropical latitudes; its origin is as yet unknown. Colonies have several queens, move frequently and seem tolerant of each other. It is an opportunistic species as to nest location: grass tufts, waste, wardrobes and appliances, books, greenhouses; a limiting factor is lack of water. They feed on the honeydew of aphids and other insects, as well as small dead animals (they can kill a cricket with their sticky secretions), sweets, raw meat, bananas, apples, dog and cat food, etc. They have lived in my house for some years, and I think that they do not move because they can find plenty of food and easy access to humidity in areas such as the kitchen, laundry, and bathrooms.

On a certain occasion, late at night, I found a trail of these tiny ants on a tiled wall next to a kitchen sink. It was a 75 cm long U-shaped trail, connecting two orifices in a groove between two tile rows. Figure 92 illustrates the situation.

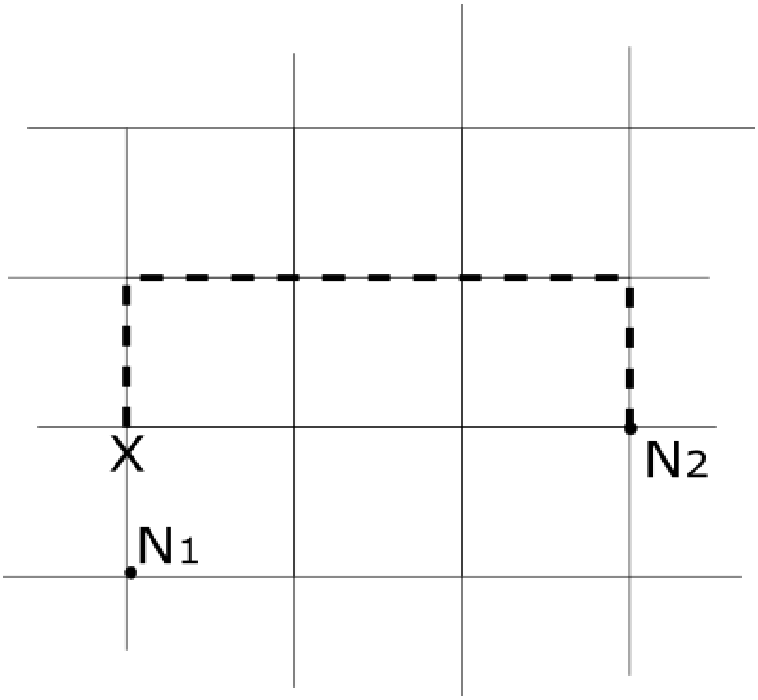

Figure 92: Approximate representation of a trail of *Tapinoma melanocephalum* on the tiled wall of a kitchen.

Legend:
N_1 and N_2: Orifices serving as entrances to secondary stations or nests
Dashed line: trail
X: alteration point

I crushed two ants on the trail; however, only one of the bodies remained on it, together with a stain left by the other crushed ant, a little lower down the wall, right on the rough white cemented groove between the tiles. The body was next to the upper edge of the groove, on the route of the trail, which ran parallel to it. Traffic was quite heavy in both directions of the trail, and the space between individuals was very small.

The ants were greatly upset by the event. When 1 to 0.5 cm from their crushed nest-mate, coming from 1 to 2 mm up the cemented groove, they would start running at a great speed around the dead ant in erratic courses. An impressive fact was that a good number of ants went as far as 1 or 2 mm from the dead ant, above the groove, and moved as if they were skating fast, without, or barely proceeding, backwards, forwards, or sideways. Some even touched the crushed body. A good part of the trail disappeared, but a great number remained, going round the dead body randomly, and coming and going repeatedly. Many of them returned and entered the orifices again; the number of ants coming out of them decreased, many of them walking only for a few centimetres, while others went on until the next orifice. At night, under artificial lighting, it was difficult to see details such as movements of the antennae, or even the antennae themselves. The circling motion of the ants was sinuous and clearly wavy. The behaviour modifications in this case did not seem less dramatic than those observed in *P. fulva.* Half an hour later, they were still running.

FORMICINAE

- *Camponotus crassus* (Mayr, 1862)

I described this ant species, measuring from 3 mm to 1 cm and with excellent eyesight, under the first topic in this chapter. Once I saw a thick trail with hundreds of these ants coming from a hole in a wooden post and along a cement floor and into an orifice in a rainwater pipe in the opposite wall. The most remarkable fact about this trail was the large number of "soldiers" as compared with those of mid-sized and small workers.

I crushed some workers at various points of the trail on the cement floor. Their nest-mates hurried up, walking in circles round the alteration point; some turned back or made a detour or touched the crushed bodies and then walked in circles again, generally with their abdomens bent underneath the thorax and between the legs, apparently vibrating.

On other occasions I crushed one *C. crassus* worker on trails formed along the junction of two walls, with less remarkable effects. Generally, the ants tended to pause briefly when 5 or 6 cm from the alteration point, their abdomens bent, as described above, but not as vigorously, and then went on at a quicker march, in a detour 3-5 cm away from the dead ant. When the ant was crushed in an open space, freely traversed by these ants and devoid of trails, its nest-mates would form a highly mobile crowd round the dead body; they touched it, ran round the vicinity, returned to the body and hurried away, generally with abdomens bent between their legs and thoraxes.

I saw no instances of jolts among these ants when faced with a dead nest-mate; I saw them, however, in artificial nests as a reaction to one breathing on them or to mechanical shocks, when they would suddenly thrust their bodies forward, their legs forming an arch but firmly planted on the ground.

- *Camponotus rufipes* (Fabricius, 1775)

The individuals of this species observed by me were relatively large (from 4 mm to a little more than 1 cm). They are brownish black in colour, with reddish legs, and their bodies are covered with short hairs, which give them a light gold, velvety appearance. They often feed on the excretions of scale insects and aphids, which they apparently protect from intruders on the trees.[36]

I saw a few of them on a fence, walking along the narrow edge of a wooden board, towards a grapevine. They were thin, but fat on their way back, with bloated, transparent gasters. There were not many: one ant walked on the board every 1 minute and a half.

I crushed a worker midway along the trail, on the narrow surface of the board. Reactions were very dramatic. The first ant to arrive when on its way to the grapevine exhibited a violent jolt when 15 cm from the altered area, walked at a quicker pace and in an undulating course, and then crawled under a strip of wood across the board. It stayed there, some 35 cm from the alteration point, apparently hiding. Another ant, exceptionally close to the first one (about 5 cm) halted when it came across the returning ant, and quickly followed the other in an undulating course to the same hiding place. They touched each other for a while and then resumed their way towards the dead ant, frequently stepping onto the wider surface of the board, their abdomens raised, following a wavy course (in fact, they walked as if their legs had suddenly gone stiff , zigzagging all over the way);

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[36] Karol Lemko, personal communication.

then, their antennae vigorously moving, they "sniffed" the body, climbed it, one by one, and then went back, without having reached the grapevine.

Other ants exhibited similar behaviour modifications, usually when 10-15 cm from the alteration point. Most of the ants going to the grapevine halted, after returning for a while, "sniffing", sometimes circling, whereas the fat ants coming from the grapevine never retraced their steps for too long; however, their course was undulating and they exhibited energetic jolts; they returned for a while after a detour, as if to "examine" the altered area, roamed around and resumed their march, using the broader, vertical surface of the board instead of the narrow one. One or other ant even crossed the altered area, at a high speed and in an undulating course.

I could clearly observe one of the jolts in the species, in an individual going to the grapevine: it shook its head all of a sudden and with violence; its abdomen was raised, and its antennae burst into movement, together or independently.

After some time, the entire trail had moved to the broader surface of the board; I noticed behaviour modifications at the points of this dislocated trail where I had used a handkerchief to collect some specimens for identification.

- *Camponotus cupiens*

According to Friar Walter Kempf[37], *C. cupiens* and *C. fuchsae*, considered below, were classified as varieties of *Camponotus abdominalis* (Fabricius, 1804), but a taxonomic revision redefined them as separate species.

C. cupiens workers, as far as I can see, vary in size (from 4 mm to a little more than 1 cm long). They are yellow and have black heads. According to Karol Lemko[38], they are carnivorous, but also enjoy sweet substances, and, when attacking other animals, such as humans, they open a gash with their mandibles and, with the tip of their gasters, squirt formic acid at it. I have found nests of this ant species in rotten trunks (a habitat

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[37] Personal communication.

[38] Personal communication.

favoured by many *Camponotus* species, earning them the name of "carpenter ants") and, once, in a large wooden case in a pantry. I see these ants following independent routes, almost always at night, often carrying dead cockroaches and moths, either whole or in bits.

Exceptionally, I saw them forming a trail next to the junction of a wall and a cement floor; it was a very active trail, but not clearly defined, as many workers sometimes followed independent courses full of quick circling moves. I crushed one of them on the trail, and its nest-mates started running around following wavy courses, approaching and running from the dead ants, sometimes in what looked like "somersaults", difficult to discern under the poor lighting. The trail was greatly reduced over time and their route was dislocated.

On another occasion – an exceptionally cold winter night – I found some 20 or 30 ants of this species walking on a wall towards a chicken bone. It was not a clearly defined trail, since there was much roaming around the bait and somewhat independent individual courses. I crushed a worker next to the wall, 1.7 m away from the bone, thus prompting these behaviour modifications: when 30 cm from the alteration point, a number of ants (among them some "soldiers" with their powerful jaws) generally reversed their course, and their gait, on either way, seemed arrested, as if their legs had been glued to the floor and a great effort was needed to move them; some of them, strangely enough, literally rolled on the ground, in a succession of jolts that each time pushed them 1 to 3 cm to the side; some of them went up the wall without any definite course, while others went past the dead ant with no apparent behaviour modifications. It was as if, since instances of return to the bait occurred, each approach or touch by an ant followed by modifications would induce in others the phenomena of arrested march, slight raising of the abdomen, and violent jolts or rolling motions, as if the ants had been suddenly poisoned with petrol fumes or as if they were engaged in a fictitious fight. Raising the head and "sniffing" at the altered area (from which the wind blew) was frequent. Soon there was no ant on the terrain which did not exhibit some behaviour modification, even though visiting the bait occasionally. Facing the ants with a finger used to crush a worker 2 cm ahead made them "sniff", hurry away, and then to repeated jolts, especially when the finger touched the soil.

On another occasion, under better lighting conditions, I could observe the movements involved in the strange jolts of *C. cupiens.* Once, while smoking, I went into a small room, turned on the light, and noticed three *C. cupiens* workers on a dead cockroach. After a few seconds, perhaps because of the light or other stimuli my presence had produced, they exhibited a succession of jolts, went to the wall, roamed around, and returned to the dead cockroach. At intervals, sometimes even when they paused while cutting up the cockroach, new jolts could be seen. These comprised a sudden upward movement of the head, with antennae barely moving (sometimes totally still) and stretched upward and ahead; simultaneously to these movements of the head, a sudden backward thrust ran along their bodies, while their legs in the meantime stood still. Exceptionally, this backward thrust was strong enough to detach their legs from the soil in a sort of low jump.

- *Camponotus fuchsae*

As already said, this is a glossy black ant, generally larger than *C. cupiens*, with big-jawed “soldiers”, ready to attack any intruder. I have found nests of this ant species under rocks and in excavations.

My observations of this generally nocturnal ant and its reactions to dead nest-mates were limited to a colony in an artificial nest, a large wooden case with a glass lid hanging over a tub with water. Whenever I threw a crushed nest-mate on the lid when there were ants walking on it, some of them hurried into the nest, while others attacked it, released it, ran around in wavy courses, “bit” an older corpse, a piece of straw, a bit of bee’s wax (used to seal part of the lid) or even a drop of water. Once in a while there were jolts, sudden forward movements of the body, with legs still; when these occurred inside the nest, the impact of their heads against the walls produced a peculiar sound. Some ants, especially smaller ones, simply ran around in disorderly wavy courses. These same phenomena could be seen, though mitigated, when one blew on them, or when an object was thrown inside the structure (food items could be fiercely attacked before being consumed), or when there was a mechanical impact. Unfortunately, I still have not found a trail of this species for other tests.

- *Camponotus melanoticus*

These are long black ants, with yellowish legs, very agile and not aggressive. My observations were limited to their reactions on being faced with a crushed nest-mate on the tip of my finger. Under these circumstances, they started running around in wavy courses, with their abdomens slightly raised. When faced with another finger, free from stimuli caused by the crushing of another nest-mate, the ants, generally speaking, would not avoid it, except when it was suddenly moved; instead, they would generally raise their heads, "sniff" it, and even climb it. I have not been able to observe a trail of this ant species, either.

It is clear that the data presented above, on behaviour modifications exhibited by other ant species besides *Paratrechina fulva* on being faced with crushed nest-mates, are greatly impaired for comparative purposes, since they were not collected under uniform conditions; among other things that ought to have been considered are the nature of the trails, when they were used, whether there were markers in the situation and how familiar the ants were with the terrain. Notwithstanding these shortcomings, I believe these data may serve as the start of a comparison, albeit a rough one, or suggest directions for a comparative study; therefore, I will briefly examine them.

First, it must be pointed out that the observations above leave no doubt as to the fact that behaviour modifications exhibited by ants when faced with crushed nest-mates, in spite of peculiarities of each species, seem to be general enough. If one adds the claim set forth by Wheeler (1910) – who worked with a good number of ant species, especially from the Northern hemisphere – that ants of any species will abandon a place where nest-mates have been killed or injured, the impression becomes even stronger. And more: in all species considered, even though they were not many, the crushed body of a nest-mate acted – considering how they returned, took detours, or simply left the altered area – especially with the apparent character of a "modifying or repelling obstacle". It is true that in some cases, besides avoidance and flight, the experimental alteration also prompted reactions with the apparent character of inspection (for instance, "sniffing" and a tendency to gather round the dead body) or aggression or defence (such as abducting the mandibles and bending the abdomen, frequent in their agonistic behaviour, and, also, biting and stinging surrounding objects, as if blaming them; however, flight and avoidance seemed to prevail over other modifications.

Second, it should be mentioned that, among the species observed, only a few – *T. melanocephalum, C. rufipes, C. cupiens*, and, to a lesser extent, *Crematogaster sp., S. saevissima*, and some *Pheidole* species – exhibited modifications as dramatic (that is, a disorganised behaviour as compared with that prevailing so far) as those of *P. fulva* when faced with a similar experimental alteration; all these species, it should be noticed, are part of the Formicinae, Dolichoderinae, and Myrmicinae subfamilies. On the other hand, it should also be pointed out that behaviour modifications were relatively less pronounced in the two *Labidus* species, which are Dorylinae, and *Termitopone marginata*, which is a Ponerinae. Are these differences in the severity of behaviour modifications between these subfamilies merely occasional or do they signal other factors stemming from their taxonomy?

Although these 5 subfamilies are scarcely represented as regards the number of species considered in these observations, and though these observations have yielded data which are far from satisfactory or sufficient – especially because of the conditions in which they were undertaken – for a very relevant discussion, the question posed above is important enough to deserve some detailed consideration.

Among the five subspecies considered, Dorylinae, especially, with their carnivorous habits, like Ponerinae, and, to a certain extent, Myrmicinae, are considered, phylogenetically, and – this must be stressed – socially, as on a lower level than Dolichoderinae, and, most specially, Formicinae.

Therefore, in short, one might in a general way, order the five subfamilies described in these observations into the following sequence, from upper to lower degrees of social development attained in the course of evolution: Formicinae, Dolichoderinae, Myrmicinae, Dorylinae, and Ponerinae. One might say then that the difference between the three upper and the two lower subspecies, as regards the severity of behaviour modifications before a crushed nest-mate, supports, *grosso modo*, the hypothesis above, that there is a correspondence between the severity of behaviour modifications, on the one hand, and the level of social development, on the other hand. The fact that Dolichoderinae and Formicinae were more "disturbed" (as shown in stronger disruption of a previous behaviour) than Myrmicinae, which, in their turn, were more disturbed than Dorylinae and Ponerinae in these observations, also supports the hypothesis. However, the same hypothesis is countered by the fact that *Termitopone marginata*, in the Ponerinae subfamily, exhibited severer behaviour modifications on their trails than the two *Labidus* species, which are Dorylinae, when the opposite was to be expected, considering their taxonomic position.

It might be possible then, by acquiring fresh and better data, and extending the research to more genera and species in each subfamily, to find the correspondence suggested in the hypothesis, or at least a trend towards it. However, I would like to suggest another possibility: that this hypothesis were rephrased, in such a way that a straightforward correspondence between severity of behaviour modifications before dead nest-mates in a given species and the level of social development they have attained were replaced, instead, with a correspondence between this severity and certain discrete characteristics in the social activity of a given species. In this way it would be theoretically possible, for instance, that a given ant species might exhibit, if compared to others, a more complex social organization without being, however, on an upper level as regards the closeness of interactions among members, or the character of reciprocal attraction exhibited by them.

It seems convenient to remember in this connection a suggestion already presented under one of the topics in this research: that the greater effectiveness of a crushed nest-mate's head, as compared with other body parts in the same condition, in mediating or prompting behaviour modifications with the character of flight in *P. fulva,* might perhaps be due to the prominence of the cephalic area in the social activities of this ant, especially under the form of reciprocal regurgitation. One would say that regurgitation implies not only an extreme psychological availability for individual interactions, evolutionarily conditioned, but also a great opportunity in the course of ontogenesis – involving, as it happens to involve, close and prolonged body contact – for familiarisation and, more important perhaps, attraction towards stimuli originating from a nest-mate's body. Now, it is precisely in this aspect – reciprocal regurgitation – that Ponerinae seem to surpass Dorylinae (Cf. Morley, 1954, p. 110), even though, on their turn, they are clearly surpassed by all the other subfamilies considered here.

Some considerations on the phylogenetic and ontogenetic development of ants, especially regarding their habits of reciprocal regurgitation, seem to be pertinent here. Primitive Ponerinae – some genera of which still exist in Australia, such as *Myrmecia* – are admittedly similar, both in habits and morphology, to solitary wasps, from which they presumably descend; they live in small groups (a few tens of individuals) in roughly excavated holes; individuals hunt and collect nectar on their own, and, except when defending the nest – in reaction, apparently, to the stridulation of a nest-mate – or in the concerted action of some species when hunting termites, they practically do not cooperate. Their castes barely differ in morphology and habits; they generally eat their food where they find it, except when there are larvae in the nest. When this is the case, they bring insects, either whole or in parts, and throw them to the larvae – which, if compared to other subfamilies, are relatively very mobile and independent – or let them successively hang over different larvae. According to Forel (1923, volume V, ch. 70), however, certain termite-eating Ponerinae species transport each other, though rarely, and clean each other, as in the case of the genus *Diacamma,* which is a good start in social instincts in these ants, notwithstanding the lack of regurgitation.

Morley (1954) shows how extraordinary were the changes in morphology and typical habits that primitive Ponerinae had to go through before the emergence of the more complex societies observed in higher ant subfamilies became possible. Apparently, almost all these changes have evolved under a selective pressure towards increased populations in colonies. Females became progressively specialized in reproduction, with a consequent morphological and instinctive change that eventually led to their confinement within the nest; males, on their turn, underwent changes in size and interests, which were finally restricted to "chasing after queens". For the colony, these events meant a reduced workforce, and, at the same time, an increase in population, with the implied need of more work to extend chambers, look after the brood, clean the nest, and provide the colony with food. The solution to this economic problem in the course of evolution was attained by modifying the worker caste, to which all tasks finally devolved. They had to undergo anatomic and psychological changes in order to become more cooperative and plastic and face the modified conditions of a new society. The course of these changes, as shown by Morley, was somewhat diverse in the evolutionary history of many ants. Many of them, however, are of lesser interest here. A very efficient and widespread adaptation, and of special interest in this connection, regarding the problem of supplying food to a colony, was the development of a "crop", or social stomach – or, at least, the modification of a body part allowing for its use as a sort of "food basket" in conjunction with a change in the form of their food, which became almost exclusively liquid, and an improved capacity for regurgitation.

It is true that other ants have evolved other solutions for the specific problem of supplying food. Morley, for instance, says that army ants (Dorylinae) have never evolved a regurgitation mechanism, but, on the other hand, never build permanent nests nor have any need of searching for food day after day in the same area. Then, Morley (1954) mentions the granivorous and fungus-growing ants among the Myrmicinae, which, though having evolved the capacity of regurgitation, also developed other partial solutions that prevented this mechanism from becoming fully developed in their societies: the transformation of starch from seeds into sugar, among the former, and the consumption of fungi grown in beds made of chewed leaves among the latter.[39] These solutions, however, are relatively exceptional if compared with the first solution mentioned above, the importance of which in the society of higher ants is expressed by Morley (*Opus cit.)* when he says that the crop is the fundamental organ in the social life of ants, and regurgitation the essence of their lives, the core of their existence.

On the basis of what has been shown, it seems reasonable to accept the degree of reciprocal regurgitation among members of a colony as an indication, if not of a higher level in social development – since other mechanisms may express this higher position – at least of the extent

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[39] Cf. also about these issues, Wheeler, 1910; Forel, 1923, volume V; Michener and Michener, 1951; Goetsch, 1957; Autuori,1942 and 1947; and Hölldobler and Wilson, 1990.

to which ants are inclined to interact on a properly individual level, and of the extent to which they see the body of another ant as the immediate object of their action, and thus, apparently, of the extent to which they can include this body in their experience and assess it in a positive way. Given these capacities, one might correspondingly expect relatively more dramatic behaviour modifications before the deformed body of a nest-mate on the part of ants with a higher development of regurgitation. I will now explain how this expectation is reasonably confirmed by the observations described in this work.

First, it should be mentioned that the phenomenon of reciprocal regurgitation does not occur among Dorylinae, that it apparently occurs, but on a lower level, among Ponerinae, and, on higher levels among Myrmicinae, Dolichoderinae, and, especially, Formicinae. Although no measurements have been taken for the occurrence of regurgitation in this work, it seems at least suggestive that the sequence of regurgitations observed in the subfamilies considered corresponds with precision to the sequence of levels of severity in their behaviour modifications when faced with a crushed nest-mate. It seems also very significant that this hypothesis can even account for the difference in levels of severity in behaviour modifications exhibited by different species within a single subfamily.

Let us consider, for instance, the Myrmicinae observed in this research. The most dramatic instance of disorganized behaviour before a crushed nest-mate was seen in a *Cremastogaster* species; in their natural habitat, ants in this genus frequently live, exclusively or almost exclusively, on the honeydew of aphids and scale insects; this kind of food must be transported in liquid or viscous form, and their transference to colony members inside the nest must be made through oral trophallaxis (the exchange of liquids regurgitated from the crop). Another species closely observed for the severity of its reactions, at least in some cases, was *Solenopsis saevissima*, which also relies, though not as exclusively, on the herding of plant parasites. After them in the sequence comes the *Pheidole* species, which generally feed on insects and seeds[40]; for this reason – because they transfer solid food to their nest-mates – they apparently rely less often on regurgitation in their ordinary lives than the preceding genera. Finally, on

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[40] (Cf. Holldöbler and Wilson, 1999; Wheeler, 1910; Michener and Michener, 1951; Luederwaldt, 1926).

the lowest rung among Myrmicinae as regards dramatic flight reactions, we apparently have the *Atta* and *Acromyrmex* species; as already mentioned, in many aspects, blowing on them first as an experimental alteration was as effective, or more, in prompting behaviour modifications than facing them with a crushed nest-mate. Part of these results may be explained – if the behaviour modifications seen in these ants occur for the same reasons as those in *P. fulva* – to the fact that, since they march on relatively wide strips along the terrain ("roads"), their choice of diverging routes to avoid the small area occupied by the alteration was little limited. Other results, however, might be correlated with factors associated with the low development of their regurgitation habits, pointed out by Morley (1954).

Let us consider, finally, *Tapinoma melanocephalum*, Dorylinae, and the Formicinae, the behaviour modifications of which have been considered in this research. These species, included in the two taxonomically highest ant subfamilies and with the highest social development, exhibited the most dramatic behaviour modifications on being faced with a crushed nest-mate. Among them, *Paratrechina fulva* was the species with the most dramatic and long-lasting reactions. Could this not be explained in the light of the fact that, among all ants observed here, this species is the one that clearly attains, given the great capacity of extending its social stomach, the condition of a "temporary replete",[41] a living reservoir of food, always ready to share it with its nest-mates? Using artificial nests, I could confirm the great frequency with which these ants engage in reciprocal regurgitation, instances of which can be seen even while they are tending to their "cattle", sap-sucking insects, or when they set off towards a food item, occasions in which, one might say, regurgitation is superfluous. On the other hand, considering the other Formicinae species we have observed, all of them in the genus *Camponotus,* I believe there is not much ground in these observations allowing for a comparison based on the severity of behaviour modifications exhibited. Among these species, *C. crassus* certainly seemed to respond in a not very dramatic way when faced with crushed nest-

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[41] It should be noticed that Morley (1954) considers the replete condition, as found in Australian honey-pot ants (genus *Melophorus*) and the honey-ants from the Garden of the Gods (genus *Myrmecocystus,* from Colorado) – in which some workers act as "living honey reservoirs", hanging from the ceiling of their nests and available to their companions – as a *hypertrophy of regurgitation functions* evolved as an adaptation to areas subject to prolonged droughts (Cf. also Wheeler, 1910, ch. XX; Forel, 1923, v. III; Michener andMichener, 1951, ch. 18; Hölldobler and Wilson, 1990, *passim*).

-mates. Could this be accounted for by the relatively good eyesight of this species, and the ensuing wider choices of paths they have when facing an experimental alteration? Anyway, it should be remembered that practically all other *Camponotus* species considered in detail – which, as Formicinae, must engage in oral trophallaxy more often than most Myrmicinae – generally surpassed all ants observed as regards severity of behaviour modifications, excepting *P. fulva* and, apparently, *Tapinoma melanocephalum* and *Crematogaster sp.* These results seem relevant for the hypothesis, and, therefore, notwithstanding the generally superficial character of the observations reported here, deserve more study.

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APPENDICES

I: AN INVITATION/JUSTIFICATION FOR THE NATURALISTIC STUDY OF ANIMAL BEHAVIOUR[42]

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SUMMARY

The principal reasons why it seems nowadays scientifically useful and even indispensable to observe behaviour as it occurs in the field centre around the need to correct and to complete the picture of animal behaviour that the psychological laboratory has been offering. Having abandoned the ecological orientation which was so promising till the beginning of the present century, psychologists concentrated themselves for approximately three decades almost exclusively on the study of reflexes, considered to be the basic units out of which all behaviour is built; their researches have generally been conducted with virtuosity and abstractness, and have not tended to promote real insight into animal processes as biological phenomena; many of them have become for this reason literally scientifically boring.

Contrastingly, comparative ethology has taken up the ecological approach that psychologists have abandoned, and has become the true modern comparative science of animal behaviour; through its achievements, it has been revealing how psychologists have restricted their observational bases, how they have ignored the behavioural problems rela-

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[42] Originally published in Jornal Brasileiro de Psicologia, v. 1, n. 2, p. 37-57, 1965.

ting to the biological cycle of animals, and how they have neglected true comparisons: those which are necessary to help in determining the course behavioural evolution must have taken. According to this criticism, the relations that the two methods, naturalistic and experimental, should have as supplementary approaches to the comparative study of behaviour were indicated, and a criticism was finally made of those psychologists who tend to proceed as if theoretical insight and the pleasure that accompanies it have no place in science construction.

1 Aim

This article intends to provide some reasons as to why the scientific study of animal behaviour as it occurs in nature is, at any given time, but especially now, as well as extremely pleasant, useful, and even indispensable. These will lead to the examination of some developments in psychology that took place early in this century, and then of the way the present impact of the so-called comparative ethology on psychology has been eliciting and seems likely to elicit a renewed interest in and a promising rebirth of this field of study.

2 The nature lover's reason

Why an invitation for the study of animal behaviour as it occurs in nature?

If a complex answer is not required, we might say, quite simply and without any qualms, that it is because we love animals and delight in their manifestations, which we call behaviour, especially those that are spontaneous, free from any artificial limitation, which are undoubtedly the most interesting.

We might perhaps admit that our fascination with the natural behaviour of an animal simply corresponds – as Tinbergen thinks to be a possibility in his own case (Cf. 1, p. 301) – to the operation of the hunting instinct, fixed or interrupted in the appetitive phase of watching and stalking the prey; or, like Lorenz (2, *passim*: 3, 286 and 288) often implies, that it results from the natural curiosity of men, who are also animals, as to the ancestral origins of their own activities, and from an inarticulate longing for a time of closer communion with nature.

3 The earnest man's argument

This reason might be said to be enough justification for the naturalistic study of animal behaviour. However, it would seem hardly capable of imparting dignity to the endeavour in a world extremely concerned with effectiveness and material progress. Thus, for instance, it is possible that, for the earnest investigator, for whom science stands above individual pleasure and is carried out thanks to perseverance, patience, even suffering – as he emaciates in the artificial environment of a laboratory, trying to develop more accurate analysis techniques, notwithstanding the frequently boring nature of this task – this reason might look merely as an excuse for laziness in the Chinese way: a loose justification an individual would give in order to be able, at peace with his own conscience, to lie on the grass on a spring day and delight in the popular songs of birds or the classical pieces of crickets, and tremble to the sensual caress of the wind.

4 Refuting the "earnestness" argument

By this time, nature lovers, aware of the preceding argument, upon seeing the image of a severe investigator behind the pane of a lab neighbouring their own piece in the field – feeling as out of place in our time as a sixteenth-century man-of-war – may feel somewhat ashamed and ready to retreat, not, however, without a pained look at the setting of their pleasures. Before this happens, let us raise their morale and assure them that their pleasure is neither sinful nor scientifically useless, for, according to Lorenz (apud 3, 288), no man, not even a yogi or any other kind of holy man in Eastern India would be patient enough to gaze at a worm, a spider, a fish, or a child persistently as it is necessary in order to perceive a natural law in their behaviour, unless he could derive some pleasure from this gaze. Indeed, if this statement is true, as it seems to be, we can no longer agree with the "earnest" man's argument, which seems to imply that the value of science is proportional to the suffering it causes its practitioner, in the same manner that we cannot accept that an initiation into yoga practices is a useful requirement for success in a scientific career.

The contemplative laziness of our naturalist is not even a mild form of social delinquency, but, on the contrary, something that seems essential to much of scientific practice, if not for the whole of it. As many have noted, the first man to make a pause in the practical task of moving a stone with a branch to consider how it implied much less effort than using only his bare hands, thus finding out the principles involved in the action of a lever, later to be embodied in those most practical of things – our machines – was a sublime lazybones. We may even say that this idleness seems to be shared by every organic system, and manifests itself as exploratory behaviour, or, according to Berlyne (4, 1), as the activity an animal performs when it has nothing special to do. In fact, this behaviour may be very useful, indirectly, because it may lead the animal to acquire a representation of its environs that will allow it to choose, on the basis of a laziness that seems to be a fundamental feature of all organisms, the shortest and least demanding among the available routes to a vital aim. Paradoxically, it is while working for biological aims that are considered useful that an animal is essentially lazy, and it is in order to acquire an adequate cognitive structure of a situation – an activity that is generally considered secondary and idle – that an animal effectively avoids rest. Looking from another angle, it is because the nervous system does not operate merely toward the fulfilment of an animal's crudest vegetative needs, but also with a view to the record, retention, and cataloguing of events and relationships – a cheap activity in the sense that it does not take too much energy and is usually deemed idle – that an individual may afford to be lazy, that is, to abstain from indefinitely repeating trials and errors in a given situation, and be able to save the enormous effort implied in alternative locomotor actions, etc., in order to fulfil its most vital needs (5, Ch. I).

What the tendency to perform relatively brief or easy activities reveals is that organisms are basically averse to work without reward, and that they only stand and tolerate effort on the lowest level needed for consummation. On the other hand, their surrender to play, contemplation, and thought is an indication that such activities have a consummatory value in themselves.[43] It should be noticed that such activities underlie what we call learning; according to recent studies (1, pp. 9 and 146; 4; 8) they are attached to a drive that is both central and neural and has, according to Thacker (apud 7, p. 9), "the cognitive structure itself, organized and proliferated" as an aim. In short, we may conclude that an advancement in cognitive clarity, in man or other animals, seems to have a consummatory value by itself or to act as a reward.

If this is the case, the contemplative idleness of our naturalist, as long as he actively explores animal behaviour, will eventually bear fruit as regards the advancement of science. After some time under these conditions, he will not fail to find regularities in certain phenomena and wonder why, under certain circumstances, an animal acts this way and not otherwise; and, almost imperceptibly, the observer will be drawn from his contemplative idleness and will conceive hypotheses, effect slight alterations in the environment under observation, and visit an animal at other times and in different places to check whether his hypotheses are true. He may – must, perhaps? – eventually realize that the task of explaining behaviour is even more interesting than mere sensual contemplation[44]. He may even face heat and storms, bogs and marshes, thorns and insect stings, and other things that, taken as a whole, are worse hindrances than those faced by his earnest colleague in a lab. However, facing these hindrances in order to achieve cognitive clarity cannot be totally boring, unless the researcher enjoys the idea of being a martyr to science. Indeed, if this is not the case with the "earnest" researcher we have been alluding to, if he cannot really derive any pleasure from his activity, and only demotivates his students for research – the worst thing that he could do to science – we may suspect that, ultimately, this is because the activity is not driving him towards scientific "insight".

If we admit that the acquisition of an organized and proliferated cognitive structure has a great consummatory value for man, that the

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[43] The fact that man may, according to Tinbergen, spend a long time in the appetitive phase of a hunting behaviour, without the reinforcement of an actual catch, suggests the same conclusion.

[44] Tinbergen (9, 144 ff.) says: "We often feel there is not less beauty, perhaps there is even more, in the outcome of analysis than in mere contemplation. If, during analysis, we do not lose sight of the animal as a whole, then beauty is increased by the beauty of detail". ... "... I must stress that my aesthetic sense has been deriving more satisfaction since I started studying the function and meaning of this beauty".

advancement of science seems to be possible only because the pleasure of building it is one rare and unalloyed pleasure, then we can honestly – that is, without counterfeiting the real motivation of the researcher – consider the first answer we gave to the question posed at the beginning of this article and think of other reasons – more scientifically respectable than a researcher's delight in a close communion with nature – why the naturalistic study of animal behaviour seems to be useful and even indispensable.

All these reasons nowadays hinge on the need of filling in gaps and compensating for shortcomings in laboratory work: in one way or another, they are connected to an increasing dissatisfaction with the incomplete, even distorted, way of apprehending animal processes stemming from laboratory methods.

5 HISTORICAL DEVELOPMENTS IN PSYCHOLOGY THE NATURALIST REBELS AGAINST

This dissatisfaction comes from the fact that, for historical reasons, foreign to the essence of laboratory methods, scientists working in laboratories eventually concentrated on a wealth of detail on a small number of questions that do not exhaust the issue of behaviour and are often not very relevant to what an animal does during most of its life: the way it evolves, how it finds, captures, and uses its prey, how it reproduces and assures the survival of its young until they reach maturity, and how it survives in a frequently hostile world in a way which is often typical and limited to members of its own species. We should therefore turn our attention to this historical development and see the extent to which a naturalistic approach might correct the deficiencies in today's labs and greatly advance comparative psychology.

Everyone knows that comparative psychology was a logical development of Darwin's evolutionary theory, which had the aim of explaining not only physical, but also mental differences among the species (10, p. 5 ff.). The mission of this new discipline, now considered a branch of biology rather than philosophy, was similar to the task performed by an older science, comparative anatomy, in the field of body structures: describe the phenomena of behaviour (originally, mental manifestations) of organic systems, find out the laws governing them, compare them, and determine how they evolved to their present form.

At first, this task was carried out with great difficulty; Darwinians faced the opposition of traditional science and theology; most of them concentrated on the most controversial aspect of evolutionary theory: the continuity of man with other species. Since they still did not have scientific methods, they relied on a resource explored by their own master: anecdotal evidence, popular reports on the shrewdness and other features of animals, which seemed to provide satisfactory proof for the continuity hypothesis. However, even at this early stage, others were really advancing the ecological study of behaviour. It is enough to mention Darwin's work on plant behaviour, and those of other great naturalists, such as Wallace, Houzeau, Bates, and Belt on relatively unknown animals of various countries; as well as those by Huber, Fabre, Wasmann, Emery, Claparède, Forel, and the Peckhams on the behaviour of insects, by Hartmann on apes, by Spinas on the social life of animals, and by Poulton on animal colour.

As early as 1890, naturalistic investigation was gradually acquiring more precision and objectivity in works such as those produced by Lubbock on the behaviour of Hymenoptera, Verworn and Loeb on protozoans and lower metazoans, and Lloyd Morgan on vertebrates. From 1900 on, mammals, which had seldom been subjects of naturalistic studies – since they are warier and have greater mobility, and, therefore, are usually more difficult to observe than invertebrates – came under close examination in seminatural situations, with the use of mazes, problem boxes and other techniques, adapted to the natural tendencies of the animals. Prominent in this period were the works by Thorndike, Small, Kline, Hobhouse, and Yerkes on mammals. Meanwhile, valuable studies on invertebrates were being conducted by Bethe, von Uexkhüll, Piéron, and Bohn, in Europe, and many investigations on animal behaviour continued to be done by Jennings, Parker, Holmes, and Yerkes, in the United States (10, Ch. I).

Until about 1910, therefore, ecologically-oriented developments in psychology were outstanding and, as might be expected, starting to produce more accurate analyses in laboratories. However, as pointed out by G. A. Miller (11, p. 254), just when the scientific study of animal behaviour began to flourish, the investigative trend lost its momentum, first in biology, then in psychology. The systematic description of natural behaviour, the comparison of these species and man, lost its drive. After a short period of progress, comparative psychology was languishing and remained so for more than a quarter of a century.

This change of direction, according to Miller (11, p. 254) was not caused by disbelief in Darwin's ideas, nor by a lack of adequate methods for the naturalistic study, or even by a sudden loss of interest in animals, but simply for the reason that students of natural behaviour became interested in other research areas that seemed more promising. Biologists, with the rediscovery of Mendelian laws in 1900, followed by new developments in cytology, became interested in genetic research; psychologists, on their turn, with the diffusion of Pavlov's study on the conditioning of natural reflexes to new stimuli, became interested in the properties of reflex, considered the basic atom that automatically formed, through conditioning, all behaviours, however complex.

In both cases, it should be noticed, this was coherent with their previous orientations. Indeed, given their usual training, biologists tended to give more attention to behaviours that characterized species rather than individuals and that might turn out to be useful in clarifying phylogenetic relationships and taxonomic problems; in explaining these behaviours, which were taken as inherited, biologists tended to rely on factors internal to organisms, and, among them, those that were genetic seemed crucial. Psychologists, on their turn, coming to science after having been trained in the positivist and empiricist philosophies, and having to deal with educational issues, tended to approach psychology through the analysis of environmental effects: their new interest was coherent with their former orientation, since the concept of reflex, either original or acquired, was essentially an interpretation of how environmental factors gained control over behaviour. It was certainly because of the radicalization of these new directions that we have had this vacuous dispute between nativists and environmentalists in the science of behaviour: unfortunate and vacuous because it obviously stems from an unreal analysis, for in the germinal cell or the initial egg these little packages of chemical agents, the chromosomes, form with the chemical environment of the protoplasm in which they are a system of reciprocal influences that are inseparable from the start. We can also suspect that this rejection of the ecological approach to animal behaviour was, to a certain extent, favoured by the mechanicist and reductionist paradigm of reference that, after its onset in the late years of the last century and early in this century, as a reaction against the loose, anthropomorphic procedures of Darwin's earliest followers, eventually gave in to another excess and precluded inferences about the intervening processes of a psychological sort in the interpretation not only of animal, but also human behaviour, and replaced them with processes based on a mechanistic analogy.

Anyway, although these new orientations in the research of organic processes were undeniably productive to science in general, they were also detrimental to comparative psychology. In fact, given that biologists practically abandoned this field – since the genetic study during those three decades would be more useful in clarifying morphological rather than behavioural aspects; and since these applied only to differences within a same species, for different species usually do not produce fertile offspring, a requirement for studying their differences through the genetic method (12, p. 326) – only psychologists were left, and they, as pointed out by Miller (11, p. 255), had already viewed the Russian discoveries as an excellent opportunity of replacing the ecological approach with an analytical, lab-based method, amenable to measurement and strict control. And more: since psychologists, as pointed out by Miller (11, p. 256 ff.), were interested in reflexes as the basic units of all behaviour, and since a reflex was basically the same thing in any creature, it didn't seem important to them whether studies were restricted to a few animal species. The rat, accommodating and amenable to laboratory conditions, tended to be the animal of choice and was to dominate psychology for decades to come. Paradoxically, the more often it happened, and since the ecological approach cannot be dispensed with in the comparative study of behaviour, the farther they were from a true science of animal behaviour.

It should be noticed that the choice was for the rat, not the solitary wasp, because, as noted by Lashley (13, p. IX), the rat does not have highly specialized and elaborate instincts that could made it inadaptable to manipulation and to the restrictive conditions of life in captivity; and that it was partly because of this choice that the 'anti-instinct' trend, exemplified in the writings of Watson, Dunlap, and Kuo came to dominate psychological theory – a move made easier because biologists and zoologists, who were the scholars best prepared to counter it, had already left the scene.[45]

The anti-instinct movement failed, however, because, according to Beach (apud 14, p. 45), its advocates were forced to adhere to a bifactorial conception according to which all behaviours were either innate and then reflexive, or entirely learned; but the dichotomy could not resist the amassed evidence, and the notion of instinct as a "complex, innate behaviour pattern" was reintroduced in psychology.[46]

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[45] The anti-instinct stand that pervaded American psychology from 1920 to 1940 was in part a thoroughly justified rebellion against the positing of imaginary powers and the tendency to verbal explanation of the 'vis dormitiva' kind in the study of the typical complex patterns of each species (14, p. 44 ff.). In fact, as shown by Fletcher (15, Ch. III), this criticism applied only to the most defective and, unfortunately, widely disseminated conception of instinct – McDougal's – and not to the older conceptions of, say, Darwin, Lloyd Morgan, and Hobhouse. The essence of the concept is now preserved, as shown by Thorpe (7, p. 15), in the idea of "drive", or, rather, "internal drive".

[46] The term "innate" can hardly be avoided, but it is usually misleading. Indeed, if it means "present in the organism at birth", it certainly cannot be applied to certain so-called instinctive behaviours that appear only relatively late in ontogeny. On the other hand, if it means something that is part of the nature or constitution of an organism, one does not know to what it should be applied, since it is not clearly known what results from this nature or constitution in terms of behaviour; in other words, it has not been proven, for any of the so-called instinctive behaviours, whether they are inherent to the constitution of an organism or extrinsically added. Considering them as non-acquired, as it is often pointed out (by Beach also), means to take the null hypothesis as proven (14, p. 61 ff.). Tinbergen (16, pp. 102 and 115), on the light of criticism, has recently recognized that ethologists had not been using the term in a proper way: while it is implied that an "innate" behaviour is "not learned", in the broad sense of not having been influenced by environmental factors – something that obviously cannot be proven (given the ubiquity and inevitability of these factors in organic systems) and has often been refuted (14, p. 63 ff.), ethologists, according to Tinbergen, understood that these behaviours were not built by conditioning after birth, although they might be influenced by some learning, in the sense of some environmental effect, as mentioned above. Though we do not want to overuse a simple footnote, we need to say something that might help to clarify this momentous dispute about the term 'instinct'. The whole issue seems to have originated in a mistaken procedure: instinctive acts would be those that, like the organs in a body, had a taxonomic value (16, p. 170), in the sense that they can define what can be understood as a species or even a genus or an order in zoological systematics; however, it was believed that only those manifestations that were passed on through heredity and, therefore, were genetically determined, had this value; learned activities, therefore, did not; whereas instincts, since they have a taxonomic value, would not, therefore, have been learned. The mistake is in thinking that genetic determination precludes environmental determination, that is, in accepting what came to be known as the 'innate x learned' dichotomy. If, on the contrary, as it is generally admitted today, both determinations are always present and are important in any organic manifestation, either it is an organ or a behaviour, an instinct can also be learned (in the sense of being subject to environmental determination), and learned acts, on their turn, can be innate (or partially determined by genetics) (Cf. Verplanck in 14, p. 62). However, the latter cannot be transmitted through heredity: only the potential for learning them. Nor can instincts, if the biologically appropriate environmental factors required by the genetic factors are absent; if, however, the medium required for their manifestation occurs, they will have taxonomic value – and this medium, given the ecological niche in which each species develops, will inevitably occur. Therefore, what is important for distinguishing an instinctive act from a noninstinctive one is to ask whether it has taxonomic value – not the other way, as it was generally implied – and there are no a priori criteria that can replace inductive research in this task! We might say this is the perspective ethologists are now adopting (16, p. 170 and 173). Anyway, we think that the term "innate", unless it is used in the strict sense it was given by Tinbergen, as mentioned above, should be excluded from the definition of instinctive behaviour.

6 THE CRITIQUE OF PSYCHOLOGY BY ETHOLOGISTS. SCIENTIFIC REASONS FOR THE NATURALISTIC STUDY OF ANIMAL BEHAVIOUR

The reintroduction of the concept of instinct in psychology as well as the ecological approach formerly adopted by comparative psychology is to be credited especially to ethologists: a small group of European zoologists who, thanks to a very accurate naturalistic procedure, produced works of great value and originality which would be highly influential in the scientific world, especially after World War II. In fact, ethologists' studies are not recent: its reputed source is Heinroth, who, in 1910, was the first scientist to attempt the establishment of phylogenetic relations clearly based on the so-called instinctive behaviour of closely related species – an objective that was an undeniable requirement in the line of development founded by Darwin. The term "ethology" initially meant the science of racial characteristics, innate behaviour, and typical customs of animals in nature, but now it is used for the biological study of behaviour (12, p. X; 16, p. 169; 17, pp. 76 ff.). In this sense, a number of researchers all over the world may now be considered ethologists, such as Lorenz (Austria), Tinbergen and Baerends (Netherlands), Russell and Thorpe (England), Darling (Scotland), Nissen, Carpenter and Schneirla (United States), etc.

With ethologists, therefore, we return to the ecological orientation of psychology as it was practiced in the first decade of this century, a position that recognizes the need of initiating comparative science by describing, as fully and precisely as possible, the natural behaviour of as many species as possible. This obviously entails using the naturalistic method and leaving in quarantine, or even rejecting for a while, the usual procedures carried out in laboratories, with all their refined specialization. Indeed, one of the most important and immediate consequences ethology had on the science of animal behaviour was a growing dissatisfaction with laboratory methods as traditionally employed in psychology. This was so because, for the historical reasons we have mentioned, psychologists involved in laboratory work eventually concentrated on the research of reflex and a few correlate functions as the acquired stimuli generalizations and inhibitions, without considering the relevance of these processes for the ordinary life of an animal and whether they were dependent in any other way on other conditions that their procedure would not allow them to see (18, p. 163 ff.).

Indeed, it is relatively easy to show both the narrowing of problems and the accumulation of errors this historical development entailed. It is evident, for instance, that the aforementioned procedures cannot explain how an animal, without the opportunity of previous training in certain situations, if it is in the appropriate biological stage, may, on the first opportunity, as it were, search and find that a certain plant or insect is the normal recipient for laying eggs in its species, or how it may, while going about the field, choose certain materials and then build, just like its ancestors did, a nest with an architecture, location, form, and other features which are precisely those required for the safety and shelter of its future offspring. Clearly, in these activities which are usually called instinctive, the processes of conditioning and associative learning play only an insignificant part – and these activities, we must remember, account for the largest part or for almost all behaviours occurring in nature. Of course, the analysis of stimulation and response procedures as an explanation for all behaviour cannot, according to Thorpe (6, p. XIII ff.), satisfy researchers with a biological orientation, for they know that it is often the case that animal behaviour is not a response to a stimulus in the environment, but, rather, an appetitive search for certain situations or objects: an animal, as if driven from within by a desire or need – this is stressed in the older concept of instinct – actively goes in search of materials, explores a hunting territory, migrates in the breeding season, roams over a wide area in search of a female. Under conditions of intense drive or appetite and in the absence of adequate objects, the so-called instinctive activity may occur "in a vacuum": a bird, for instance, may perform all movements observed in nest building, but without straw or twigs (16, p. 173 ff.; 18, p. 171; 19, p. 101). The question of finding out which given instinct is operating on an animal, and the current stage of its biological cycle, is important when predicting the stimuli to which it will respond and to which it may be conditioned. This is what is taught, for instance, in this particular finding, one among others by Tinbergen that would be equally worth quoting (9, p. 170 ff.); that Grayling butterflies respond to colour when oriented toward food, but act as if colour-blind when oriented toward a sexual partner. This is undoubtedly a naturalistic finding of extraordinary value, the existence in animals of “filtering” mechanisms – the so-called Innate Releasing Mechanisms (IRM)[47] – that allow an organism to release[48] a behaviour in the presence of those stimuli that, among the thousands of stimuli to which it is always exposed, are biologically relevant, in the sense of having acquired an adaptive meaning during the evolutionary process. It was also thanks to naturalistic research that Heinroth and Lorenz discovered that remarkable conditioning process called imprinting: the process through which an animal, during a relatively brief period of its existence, if exposed to an object bearing the right size, shape, and other critical properties which are “innately” determined, may condition to the whole class of this object – as well as to it, individually – in a relatively irreversible way, all responses pertaining to its stage of development and that normally are directed toward members of its own species – such as following, asking for food, etc., as well as other responses, such as sexual, that appear in later phases. Thus, for instance, Lorenz (19, p. 102 ff), by exposing himself to newly-hatched greylag goslings, could make them follow him everywhere and cry pitifully when he was out of sight, as goslings bred in a normal way do toward their mothers. Here, the naturalistic method could reveal certain psychological susceptibilities that clearly predetermine the direction and other characteristics that a learning process may acquire, and these susceptibilities are assumed to be of greater interest to the science of education. Thanks to these discoveries, ethologists have been defying the almost exclusive emphasis of American psychologists on the learning process: according to Tinbergen (20, p. XVI) they are prone to forget that learning is a modification of something that we had better study first, before this modification occurs.

Another reason for the dissatisfaction with laboratory methods on the part of students with an ecological orientation is the deformation of animal behaviour often caused by captivity, a condition that implies deprivation – of social contact with conspecifics and of ample opportunity to

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[47] After recognizing the difficulties presented by the term “innate”, ethologists have recently adopted the abbreviation (I)RM, or simply RM, to refer to this “filtering” mechanism (17, p. 113).

[48] Therefore, sign- or key-stimuli, as conceived by ethologists, are effective not because they produce a certain behaviour, but because they unlock the mechanism that prevents this behaviour from continually manifesting itself, when there is an endogenous accumulation of the specific energy for a certain instinctive act.

explore and handle a diversity of materials. As pointed out by G. A. Miller (11, p. 257), it was found out [in ethology] that social adaptation was crucially important, but, in spite of it, animal society had always been ignored in psychology laboratories, where species were normally housed and tested in isolation. Ethologists have often stated that an animal in these conditions will simply fail to exhibit certain behaviours and, while performing others, may evince a level of stupidity that is not to be seen in its natural environment.[49] Ammophila campestris wasps, for instance, would certainly not exhibit more than a few seconds of mnemonic retention capacity in a test like the one for delayed reaction, whereas in nature, when going through their reproductive cycle, they can, as the Baerends have shown, retain until the following day, after a single visit, how much food is available in each of their multiple underground nests, since the amount of provisions brought in the following visit is based on these quantities (9, p. 109).

Another reason for the discontentment with the psychology laboratory is that analysis is restricted to a few species, and, worse, laboratories tend not to make comparisons even among these few species. When comparisons are made, however, they almost make no sense, for, according to Tinbergen (21, p. 12), given the differences between one species and another one, we can only say that identic experimental techniques should not be used in their comparison, for these techniques would almost certainly not be the same for both. On the other hand, even if we could disregard this argument, the task of comparing each species with all the others according to age, training, etc., in each device and specified series of stimulating conditions, would be an endless task: we have only to consider the number of combinations among more than one million species to feel dizzy. It is only from a biological point of view, like the one adopted by ethology, that comparisons are possible: for, then, they are conducted among closely related species and with the purpose of determining if their similarities are analogies – attained through convergence, as regards their function – or homologies, i.e., similarities originating in a common ancestor. The purpose of behavioural comparison, therefore, should be to help,

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[49] The opposite phenomenon also occurs: Scott (apud 7, p. 401 ff.) suggests that in captivity, since they no longer need to continuously forage, some birds will spend their time in mimicry as a playful activity – something they never do in the wild.

as comparative anatomy does, in the identification of an evolutionary line in the manifestations of organic systems (16, p. 170 ff).

No wonder, then, that ethologists have claimed the movement for themselves and denied psychology the status of true comparative science of animal behaviour. The essential difference separating the two disciplines, that would include all others and be the ultimate source of all the criticism we have mentioned, was expressed with unusual felicity by Tinbergen (20, p. XV ff.) when he said that ethologists are zoologists and as such they are interested in the three major problems in biology: that of the function or survival value of life processes, that of their causation and that of their evolution. Behaviourists have concentrated on the second problem, that of the underlying causes, and practically ignored the others. Many psychologists, improbable as it seems, are not interested in them. Whoever is aware of the extreme importance of insight into adaptiveness, selection and evolution for general biology will agree that this is a serious gap in a science concerned with life processes. The lack of a harmonious proportion in the interest of behaviourists made them neglect true comparative study. Their training as zoologists made ethologists aware of the great value of comparison as an aid to the study of evolution.[50]

These differences between ethology and modern psychology cannot be denied. However, as pointed out by Tinbergen (15, p. 76; 19, p. XV), they have a strong similarity in that both conduct their studies of animal behaviour in an objective manner and, had not it been for an historical accident, they would not have been given different names. Since "ethology" is the most recent term (15, p. 76), one should say it must be punished, according to the taxonomic practices prevailing in biological science, and be considered as one mere synonym for the older term, "psychology", from which would spring, as pointed out by Mayr (apud 17, p. 80 ff.) and as it tends to be the case with other secondary biological sciences[51], two branches, or distinct varieties, which are now being integra-

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[50] Lorenz (apud 17, p. 79) even affirms that a consideration of the survival value is essential in a full analysis of the causes of behaviour: "When I stress phylogenesis so insistently it is because all there is in an organism is not something that exists, but a process, and a process that has been going on since the beginning of life".

[51] This characterization of psychology as a biological sub-science may be opposed by scientists inclined to stress the behaviour of humans as social beings. However, in doing so, they fail to see that society is essentially a biological phenomenon, and that it is a characteristic feature of infrahuman animals as much as it is of man – a

ted: evolutionary psychology, which is truly comparative, and functional psychology.

Whatever the names adopted – the issue of names, after all, does not seem to be of great importance – there are certainly lessons to be learned from the developments we have been considering. Psychologists will certainly not fail to respond to the criticism of ethology and reconsider the reasons – long known by them, but left aside for some three decades in this century – as to why the study of animal behaviour as it occurs in nature is not only scientifically useful, but also indispensable. Basically, these reasons hinge on the fact that this sort of study is the essential, nay, irreplaceable primitive core of a truly comparative biological science. In recognizing how essential and irreplaceable naturalistic observation is, we also recognize that laboratory methods cannot build such a science on their own and now deserve some serious criticism. On the other hand, recognizing this entails that comparative psychology withdraw to an older position – a withdrawal that, strangely enough, is a progress, which means that the 'progress' from this position was not entirely forward, but, in a certain way, only a lateral development, if not a development in a wrong direction. It is clear, then, that none of the new orientations that replaced the ecological approach in this century provides a full explanation of behaviour and cannot be considered a true shortcut or an acceptable substitute for comparison and the direct study of natural behaviour in all its complexity. From the point of view of a truly comparative science, searching for the general laws of behaviour in such directions is certainly like looking for a lost object not where it was dropped, but where lighting makes for a more comfortable search. Finally, there is another lesson to be learned from the criticism of ethology: laboratory psychologists working in comparative psychology cannot complain if, upon sending an invitation to their domains, at the same time as the naturalist, find themselves with a small company of grumpy and not very young people: after all, a party outdoors held by naturalists is better than a party in a stuffy hall.

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fact that had not been recognized before because, as noted above, the tendency of psychology laboratories was to observe animals in individual cages and study processes in a low level of molarity.

7 THE RELATIONSHIP THAT MUST PREVAIL BETWEEN THE NATURALISTIC AND LABORATORY METHODS

It should be noticed, in case we have not been explicit enough, that students with an ecological orientation are not backward individuals, with a prejudice against laboratories. The only thing they want is that the microanalyses carried out in the laboratory arise from field observation; for field observation, however coarse, ensures that investigation will not take directions of lesser significance. Naturalists, of course, (Cf. Lorenz, apud 3, p. 286 ff.; 9, Ch. 16) agree with the following statement by Warden, Jenkins, and Warner (10, p. 30 ff.), quoted for its precision and vigour in describing the relationships between the two methods: "... Obviously, we cannot draw a sharp line between careful field observation and a simple experimental procedure. In a very proper sense, a laboratory may be considered as a limited, controlled field in which isolation and quantitative measurement of certain selected aspects may be carried out". ... "Field observation must keep its place of honour among biological sciences, even more so in comparative psychology. The solution for many important problems depends, partially or entirely, on competent field work. However, it cannot be denied that the development of refined experimental methods is a sign of increasing maturity in a science, an indication of an ability to properly define and solve problems". It seems convenient to add, for clearness, the statement by Tinbergen (9, p. 271) that, in each stage of research, the biologist must be aware that he is studying and temporarily isolating for the purpose of analysis adaptive systems with very special functions – not mere bits.

8 EPILOGUE: SOME CONSIDERATIONS THAT MITIGATE THE ACCUSATION OF "EARNESTNESS"

In fairness, we should mention that a good part in the discontentment with mere investigation of the Pavlovian reflex and a lot of the pressure for the extension of the observational bases of psychology originated inside laboratories. As noted by Thorpe (6, p. XIV), Lorenz's and Lashley's works, the most significant foundations of ethology, began in an intellectual environment that was not satisfied with mechanistic physiological conceptions, an environment that had been partially created by naturalists, but also, in part, by Gestalt psychology, with its study, starting in 1912, of "the more highly developed perceptions of animals and men". Gestalt conceptions would be closely involved in many developments dissenting from reflex-based laboratory work: one has only to mention its influence on Tolman's investigation of purposeful behaviour – a synonym in functional psychology for the appetitive behaviour of ethologists (18, p. 171) – and the ensuing contemporary emphasis on central mediating processes, such as those termed "expectation", "attention", "attitude", etc. It is the need of relying on these central autonomous processes – in the sense of being relatively independent of the afferent activity, reinforcing now one response, then another one – as pointed out by Hebb (22, p. 4), that precludes a conception of behaviour in terms of elementary stimulus and response processes as implied in the notion of reflex. Even in sectors of psychology favouring the S-R position, this impossibility is evident: the investigation, initiated by Skinner, of the so-called instrumental conditioning – which, according to Thorpe (7, p. 85 ff.), is the core of trial and error learning and differs from classical conditioning mainly for the fact that a response is a "voluntary" somatic action of an animal displaying appetitive behaviour. All these developments in laboratory studies apparently were useful in securing a warm welcome to the position advocated by ethologists and in restoring the interest, on a par with the functional view, in the comparative study promoted by them.

On the other hand, one should not forget that the investigation of reflex and related processes in laboratories, although of little value for comparative psychology, has certainly promoted, in functional science, a prodigious amount of specialized and useful knowledge in the area of learning phenomena. Recognizing this means recognizing that such investigation was not totally free from some theoretical laziness. The portrayal of its practitioners as the "earnest" guys in psychology – who, by logic and etiologic fate, should also be classified as scientific bores – must be highly qualified. However, for the modern disciples of Darwin, who are interested in the issue of evolution and yearn for including the most diverse natural manifestations, animate and even inanimate, within a single cognitive expectation, the label applies, at least partially, to those investigators who, because of their restrictive approach, remain partially blind to the beauty and mysteries of behaviour as a biological phenomenon and tend to proceed as if the whole of science were only measurement and technique, sweat and tears: those whom D. L. Miller (23) and Prentice (24) certainly had in mind, who find that operationalism and logical positivism not only lay down the rules for scientific inference, but also forbid theorization and inference, and reduce scientists to the mechanical function of cinematographers that only record events, but do not interpret, nor establish relationships among them, and do not feel the thrill and the bliss in their findings.

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II: SOME ASPECTS IN THE BIOLOGY AND ETHOLOGY OF ANTS[52]

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We, humans, generally feel proud, not without reason, of our condition as social beings. However, in zoological terms, I think we are on a relatively primitive level of social evolution if compared with ants. In fact, among social insects, there is not a single one, not even bees, wasps, and termites, that has had its evolution as predominantly shaped by social adaptation as ants. The evolutionary features of this adaptation may be found not only in the habits of these insects, but also in details of their anatomo-physiological organisation. This feature is so outstanding among ants that it is based on their species, rather than on other social insects, that W. C. Allee, O. Emerson, T. Park, and K. P. Schmidt, in a famous work on animal ecology, ground their claims that insect societies constitute social superorganisms (Cf. Allee *et al.*, 1949, cap. 24). This not only means – as if this were not enough – that a colony of social insects, like other populations, looks like a single organism because they have structure, ontogenesis, heredity, and integration, and form a unit in an environment, as these authors say (*Op. Cit.*, p. 419), but also that it is the colony (an insect society as a whole) rather than the individual organism that is to be seen as the unit on which the most important selective pressures have acted during the evolution of the species.

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[52] Text presented as part of the lecture "General aspects in the ethology of ants and some observational and experimental data on the behaviour of winged female leafcutters in colony formation", during the Second São Paulo Ethology Congress at the Ribeirão Preto College of Medicine, University of São Paulo, 29 November to 1 December, 1984, organised by Dr. Antonio Fernandes Nascimento Júnior and Dr. Sylvia M. Nishida, sponsored by the Ribeirão Preto Biological Society and the São Paulo State Association of Zootechnicians. Annals have not been published. .

The ubiquity and prevalence of the social in the evolution of ants is perhaps the main cause for the hegemony of these insects over all animals now living. As stressed by Wheeler (1910), ants prevail throughout the globe in numerical terms and are naturally found in all areas, except for New Zealand and Antarctica. Ants, in a phrase often used by Forel (1921-1923) are a "strong folk" in two senses. One, that they tend to be numerically abundant, for, until 1968, according to Bernard (1968), 7,600 species had been identified, and the total number of species is probably 12,000 to 14,000 species, according to Brown's estimate, as quoted in Wilson (1971) (apart from extinct species). Besides, many species form colonies of thousands and even millions of individuals. Second, that ant colonies have provided the material conditions or ecological niches for the existence and evolution of hundreds of other animal species. These animals are called myrmecophiles, 241 species of which were found by Bernard (*opus cit.*) living with the 193 species comprising the total ant fauna of Western Europe; this number included 129 beetles, 53 mites, and 23 Diptera; myrmecophiles are to be found among spiders, Hemiptera, other Hymenoptera, springtails, Crustacea, isopods, Thysanura; they also include a cricket and a barkfly, as well as many Lepidoptera, and millipedes. Dr. Karol Lemko, a well-known myrmecologist, while still working at the Zoological Museum of the Agriculture Secretary of São Paulo State, said that in the material collected from a single nest of *Camponotus rufipes* Fabricius, 1775 and sent to foreign specialists for determination, tens of new species had been identified. With Lemko's death I could never ascertain how many species, among newly found and already identified, had been collected in a single nest of an important Brazilian species, but I can imagine the wonderful surprises our land holds for students with an interest in these animals, which maintain an essential relationship with ants: predation, parasitism, commensalism, or symbiosis.

Ant species may be as different in aspect, morphology, habits, and temperament as an antelope is different from a bison, a buffalo, or an Indian zebu. These differences are the visible expression of a network of past relations among the species and special environments mediated by a prevailing, though invisible, factor: the adaptive efficiency of the colony as a whole.

In a beautiful work, Derek Wraggle Morley (1954), based on the knowledge available at the time, tried to retrace the main steps in this evolutionary transformation, from primitive ants to their modern descendants.

Morley took a very well-known species in Europe and characterised its physical aspect and habits: *Formica rufa*. Then, he considered that selective pressures must probably have acted on ancestral ant species towards the complex society he describes. *Formica rufa* is an ant wood with diurnal habits that builds mounds or volutes covered with pine needles and forms large communities of interconnected nests, called "polycalic" by Forel (1921-1923). Though it is an omnivorous ant, its main source of food is the honeydew of sap-sucking insects; day after day, during sunny hours, *Formica rufa* workers, like our *Camponotus crassus* Mayr, 1862, go over bushes and trees herding aphids, coccids, leafhoppers, and other sap-sucking insects, whose excretes of half-digested sap they carry in their crops.

Morley tried to infer the features of more primitive, ancestral ants: most especially those in the genera *Diacamma*, from India, and *Amblyopone, Myrmecia,* and *Promyrmecia*, from Australia.

The most primitive ants, because of their physical aspect – an elongated body, armed with a terrible stinger in their hindmost gaster segment, and protected by a strong chitin armour against predators – and their solitary habits, greatly resemble wasps (scoliid wasps, according to Morley, 1954, tiphiid wasps, according to Wheeler, 1923, and with more support) from which they may have descended some 100 million years ago, at least (Dumpert, 1978, p. 19). Both in outer aspect and habits, there is not much differentiation as regards sex or caste (*Diacamma* may not even have a worker caste). Living in small numbers in roughly scraped holes in the soil or in trunks, each ant goes out to feed independently. Cooperation in the colony would be almost exclusively restricted to defence against intruders, in a response to the alarmed stridulation of companions. Their reliance on olfactory recognition for minimum mutual tolerance would limit the possibility of an increase in population in the nest; ruthless fighting would occur as soon the number of ants reached a few tens. The elementary habit of going out to forage individually and of feeding, generally on nectar, wherever the food was found underwent a remarkable transformation, of great importance for social evolution, as new larvae emerged. On these occasions, they would tend to exchange nectar for prey – usually other insects – and, instead of eating them in the place where they were captured, brought them to the nest, to throw them anywhere and sometimes on the larvae. These larvae were not motionless, but had instead a mobile neck and head, and, though having no legs, were able to crawl towards the food.

Profound changes had to occur both in the morphology and customs of primitive ants before the complex societies of Myrmicinae and Formicinae became possible. It seems that these changes were the result of a selective pressure towards population increase in colonies. We know (Cf. Huxley, 1967) that each attribute of a given species is in a permanent conflict as to change or not in a given direction. For many animals, a particularly important conflict, that has to be faced very early, is whether to increase or decrease in size. Both alternatives have advantages and disadvantages. Even though an increase generally means the possibility of preying instead of being preyed on, for instance, it also means increased breathing and feeding needs, geometrically proportional to linear growth. In the case of ants, this increase is more advantageous to the colony as a whole than to its individuals, so much so that, as it will be seen later on, an occasional instance of individual growth will prove instrumental and subordinate to this objective rather than as a final objective in itself.

Many correlated changes were needed for a proper response to the selective pressure towards colony growth. A first major change was seen in the eggs, according to Morley. In primitive ants, eggs have a dry chorion and are randomly scattered on the ground, like excrement in a warren, where they are left untended. In more developed ants, eggs have a moist chorion, and are frequently licked and transported in clusters, adhered to each other. This would make for easier transportation in the case of climate changes and easier care on the part of adults. Thanks to this modified chorion, eggs would become increasingly attractive, almost as much as larvae had been thanks to the salivary secretion they released when fed.

A second change occurred in the number of eggs produced. For this to occur, fertile females had to undergo an increase in the volume of elasticity of their gasters, in order to hold more oocytes. This increased volume and elasticity were attained by reducing the hardness and rigidness of the chitin plates covering their gasters, and by modifying the membrane linking these plates, leading to more elasticity and the acquisition of a fold allowing for an increased distance between the esclerites or plates as the gaster is expanded. These transformations in the tegument, in their turn, together with the abdominal dilation due to the increased number of oocytes, entailed an increased vulnerability of the fertile female, or queen, to predators. To make up for this increased vulnerability, the queen had to change her foraging habits: it stopped leaving the nest for food, and remained protected inside the nest. This left to the other ants the task of satisfying her needs.

Males, in their turn, to increase their fecundation capacity, tended to increase in number and/or size and adapt their morphology in order to carry more semen and chase females more easily. A consequence of these adaptations was that males became useless in provisioning, maintaining, and expanding the colony.

These transformations in the reproductive castes resulted in increased populations, but also entailed an increased amount of work in order to expand and multiply chambers, clean and feed breeding ants and their offspring. The solution to this economic problem was achieved through the evolution of a worker caste comprising ants with totally or almost totally absent reproductive capacities, now responsible for the increased amount of work in the colony. The development of this caste entailed anatomical, physiological, and psychological changes that made them reproductively non-functional, more cooperative, and fitter to face the modified conditions of the society. Polymorphism, or the presence of subcastes within the worker caste is a visible manifestation of these changes, as in the case of leafcutters (genus *Atta*). The so-called “soldiers” occur where subcastes of an intermediary size have disappeared in the course of evolution and were exclusively replaced with workers with extreme sizes, minims (ordinary workers) and majors – the “soldiers”, which generally differ from minims also in morphological features, such as large heads and mandibles, especially fit for cutting up larger prey or discourage predators, as seen in certain *Pheidole* species (Cf. Goetsch, 1957). Where size variation persisted, as in the case of leafcutters, one can ordinarily observe a work division in which minims tend to eggs, larvae, and pupae, and clean and feed the queen, medians excavate and forage, while majors perform the tasks of dissuasion and defence (Cf. Autuori, 1957; Carvalho, 1972).

An efficient and widely spread adaptation among more developed species to solve the problem of supplying food to a colony with increased population was, as pointed out by Morley (*Opus cit.*, ch. 6 and 7), the development of the "crop" or social stomach, which works as a sort of "shopping basket". More developed forms of ants have two stomachs, one small, individual, and a larger one for the community. Not much food reaches the actual, individual stomach, and, so, according to him, workers would almost always be hungry, even with a full social stomach, and this fact would account for their almost ceaseless activity. Concomitant with the development of the crop, there was a change in the kind of food collected, which became almost totally liquid. This modification was then followed by an increased capacity for regurgitation, made possible by changes in the gizzard or proventriculus. In some species, dilation of the gaster produced accumulation of liquid food in the social stomach, which has been conventionally called (Wheeler, 1910, ch. XX) "semi-replete" or "replete", and which leads in some cases to another innovation regarding the solution of a feeding problem: in certain species that live in deserts and undergo a prolonged period with a lack of liquids, such as *Myrmecocystus hortedeorum*, replete workers remain, during the drought, hanging from the roof of chamber nests, transformed into true living food deposits, obligingly attentive to the regurgitation solicitations from other companions engaged in the tasks of the colony.

The problem presented by the increased needs of room to accommodate and incubate immature individuals, clean and provision the colony has been solved in other ways in different ant species. Thus, for example, army ants, such as the Dorylinae species *Eciton hamatum* and *Eciton burchelli,* very well studied by Schneirla (1956, 1957), kept the habit of solid food in the form of small prey, thanks to the action of nomadism. These ants do not have permanent nests; they simply retreat in the evening to some sheltered spot in the environment, such as a concavity under a stone or a trunk reached in the course of their predatory expeditions. At this point, ants interlink their legs and keep themselves more or less together, thus providing gradually varying temperatures in the gaps between the layers of the cluster, forming incubation chambers that can be selected according to the temperature needs of immature forms. The activities of the colony are organized, according to Schneirla (1956, 1957), round two distinct phases, "nomadic" and "stationary". During the nomadic phase, the ants set out on an extensive predatory raid, which is also a migration, into another part of the terrain, where, at the end of which, they establish their nest of interlinked bodies. During the stationary phase, they remain in a single nest for a number of days, usually under a log or a stone, from which they launch daily predatory raids, progressively extending their range until all hunting spaces in the area are covered during their permanence. During this phase a new generation of callow ants appear, which, upon reaching the stage of inexperienced, newly eclosed ants, provide the stimulus that will trigger a new nomadic phase, characterised by extreme agitation among workers. *Eciton* queens, enormous if compared with workers, become physogastric and, therefore, less mobile during the stationary phase, and thin and fit for longer walks during the nomadic phase. Schneirla (1956, 1957) showed that the reproductive cycle of the queen determines the phases of activity of army ant colonies, but that this cycle, in its turn, is regulated by the attention queens are given by workers under the form of licking and feeding; at the end of the nomadic phase and the start of the stationary phase, when the larvae hatched in the intermediary period of the nomadic phase become pupae, there is a marked decrease in the amount of social stimulation directed to workers, whereupon the queen temporarily gains an attraction value to these same workers, leading to increased attention and overfeeding. This overfeeding, in its turn, triggers the development of a series of oocytes, and, then, to renewed egg-laying in the intermediary period of the stationary phase. Therefore, according to Schneirla, there is an intricate play of reciprocal influences among the queen, immature individuals, and workers, determining the instinctive pattern of army ants. This pattern is deemed wonderfully adaptive, since it may have allowed Dorylinae ants the feat of being, according to the author, the only animal species living in nomadic communities with an exclusively carnivorous diet.

Like Dorylinae, granivorous ants such as *Messor*, and fungus--growing ants such as *Atta* and *Acromyrmex*, have not developed regurgitation as a form of food sharing, even though it is not totally absent. In these cases, a developed social stomach working as a shopping basket is not important, since food sources – granaries and fungus gardens – are inside the nest.

Granivorous ants, such as those in the Old World genus *Messor*, and the genus *Pogonomyrmex* in the Americas, store the seeds of grasses and cereals in chambers inside the nest. The ants then bite into the seed coat and gnaw the kernel, imbibing it with the secretion of their labial glands, thus forming a gum that is converted, first, into maltose, and then, glucose (Dumpert, 1978, p. 248).

Fungus-growing ants include genera which use from caterpillar excrement to dead insects and chewed leaves to build their gardens (Weber, 1972). This fungus breaks down cellulose, thus providing the ants with what is probably their only source of food. It does not live on its own and is found in nature only as an ectosymbiont in the nests of *Attini* ants, which are responsible for their establishment, cultivation, and dissemination (Möller, 1893; Dumpert, 1978, p. 247-254) as a pure crop, free even from other kinds of fungi.

This latter fact seems inconceivable if we remember that millions of spores from other fungi float freely in the air and are brought inside the nest with the materials *Attini* ants use in their gardens. How they can keep their gardens pure and practically free from bacteria and mould has not been totally explained. Such knowledge, I think, may be of great economic value, since our commercial crops are greatly harmed by fungi and bacteria. Leafcutters such as *Atta* and *Acromyrmex*, which are among the most extensively studied *Attini*, must get rid of bacteria and spores through mechanical means, as they systematically lick all the surface of each vegetable fragment before using their mandibles to cut it up and macerate it, and, finally, implant it as a tiny pellet in the fungus bed. It also seems clear that they employ enzymes in their faeces and the secretions of metathoracic glands to carry out this biological control. This might perhaps explain a behaviour I have seen in *Atta sexdens rubropilosa Forel, 1908* workers (popularly known in Brazil as "lemon leafcutter" because of the lemony scent released when they are crushed); these ants process vegetable fragments before attaching them to the fungus bed: this behaviour comprises deliberate and repeated rubbing of their hind leg tarsi against the insertion points of these glands. The evolutionary development of metathoracic glands, the secretion of which protects the chitinous armour of ants against bacteria and fungi spores , is recognised as one of the most important factors in their conquest of a land environment (Cf. Dumpert, 1978, p. 19; Cf. also p. 70 and p. 243 on the antifungal and germ-inhibiting action of their metathoracic glands). The action of this secretion in leafcutters, in conjunction with β-indolilacetic acid, a substance that promotes plant growth, had already been demonstrated, according to Dumpert (1978, p. 250 ff.), by Maschwitz and Koob in 1970 and 1971, respectively.

However, alternative solutions, other than the development of a crop or social stomach used as a shopping basket, have been exceptional, according to Morley (1954). In most ants, the mechanism of reciprocal regurgitation was the most important solution to the problem of providing a colony with food and constitute what Morley classified as the crucial domain in the social life of ants. This mechanism certainly originated in the attraction that ants, including the modern descendants of primitive species, feel towards the salivary secretion produced by their larvae. As if exploring the interest of adult ants in this secretion, the larvae of more developed species, notwithstanding their diminished independence and mobility, increased both the amount and the quality of their saliva, which they freely release on being licked or simply touched by workers.

As already pointed out by Wheeler (1910, p. 5), "there is certainly a striking parallelism between the development of human and ant societies" . Out of the six stages in the development of human society, as claimed by Topinard in 1895, i.e., hunting, pastoral, agricultural, commercial, industrial, and intellectual, ants have attained at least the first three, as stressed by Lubbock (1898). And this parallelism can also be seen in the details of strange solutions both societies share, evolved in order to solve their economic problems. One example is the social parasitism of one species over another, as in the case of *Anergates atratulus*, that lost the worker caste and is naturally found living in obligatory dependence of *Tetramorius caespitus* (Wheeler, 1910, p. 498). Another example is slavery, as in *Polyergus rufescens*, which prey on *Serviformica* pupae for food. Some of these pupae develop into adults inside a *Polyergus* nest and perform all the tasks of its caste, which include looking after the offspring of their raptors and defend the nest against ants from other nests, even ants of their own species. The parallelism between human and ant societies is an outstanding instance of evolutionary convergence because it does not imply homology. It is most interesting, however, and even theoretically relevant, that such disparate, in widely separate orders, have reached, even though in very different ways, a most curious set of solutions to the adaptive problems posed by social living.

An ethology work, in order to be considered satisfactory, should demonstrate how each anatomic, physiological, or behavioural feature of a given species, or even, as in the case of ants, of each of its castes, is connected to the way of life of the species in its characteristic environment, a way of life in which they have a major adaptive significance. By way of example, I consider some of the ways ants establish their nests.

The typical form of colony establishment found in contemporary descendants of primitive ants, represented by the genus *Myrmecia*and many Ponerinae is independent. Queens in these species leave the nest, before or after fecundation, and then dig a chamber in the soil or in a tree trunk or take advantage of a pre-existing hole. They often leave the chamber and their eggs for brief intervals in search of food. In more advanced species, on the other hand, fertile females remain secluded until the birth of the first generation of workers; meanwhile they rely on their own reserves, especially body fat and wing muscles, which are used only for the nuptial flight. Among *Atta sexdens*, this style of colony establishment is taken to an extreme, as the secluded female tends to the brood and also the fungal garden brought from the original colony in their infrabuccal pocket. The queen remains secluded for about three months, without food from outside, until the first generation of workers open the chamber to the external environment and replace the queen in the tasks of provisioning the colony and tending to the brood (Huber, 1908). It provides in this way a paradoxical spectacle, in the words of Ribeiro (1972), in which we see the most intensely social of animals in a totally solitary phase.

In recently evolved species, such as those in the genus *Formica*, queens leave the nest, like swarming bees, with a band of workers that help them to build a new nest with temporary or permanent links with the older one. A new queen appears in the original nest that replaces the former one after fecundation. This way of colony establishment seems efficient and suitable to polygynous species that build communities of many interlinked nests.

This kind of establishment, however, is not restricted to more developed ants, and must have evolved in times, places, and groups of different genera as a convergent solution to a given way of life. According to Schneirla (1958), for instance, among *Eciton* army ants, and also *Neivamyrmex*, which are relatively primitive, colonies are generally established by a division of an original monogynous colony, one with the original queen, and the other with a new queen, selected among those born during the reproductive season. A peculiar phenomenon in these genera is the "sealing off" of the other queens, when workers actively prevent them from marching during the division process. According to Schneirla, "sealing off" seems to be entailed by the probability of failure in the division of the mother-colony, which seems to increase with the number of divisions, as each new branch must be populous enough to support on its own an amount of reciprocal stimulation of its workers until they reach the threshold of excitement necessary to trigger the characteristic raids of the species.

A curious variation in the pattern of colony formation with helpers is found in *Acromyrmex lundi*, a leaf-cutting and fungus-growing ant from Argentina and southern Brazil. In this species, popularly called "quenquém" in Brazil because of its stridulation, a number of queens associate, as reported by Weber (quoted in Dumpert, 1978, p. 152), to found a new colony and establish a unified fungus garden. An equally curious variation in the pattern can be seen in the genus *Carebara*, from northern Africa. In this case, some workers attach themselves to the queen's legs before she takes off; like pygmies attached to a giant, they are flown to the site where they will help to build and consolidate a new nest (Dumpert, 1978, p. 153). This kind of colony establishment seems to originate in the difficulty the huge *Carebara* queens have in dealing with their tiny eggs without the aid of their minute workers.

Among parasitic ants, like *Bothriomyrmex decapitans* and *B. atlantis*, females cannot establish a colony on their own; to do so, they need the logistic support of *Tapinoma nigerrimum* and *T. erraticum* – the species they prey on. The fertilized *Bothriomyrmex* queen lets herself be captured by workers near the entrance to the host nest; once inside it, she looks for the queen, climbs her back and spends some days sawing off her head (Forel, 1921 – 1923; Dumpert, 1978, p. 159; Wheeler, 1910, pp 446 – 448). She lays eggs that will be looked after by the hosts, and, upon their death, the offspring will be established as a pure colony in the nest.

A similar procedure is used by the slave-making *Formica sanguinea* against their prey, a colony of *Formica fusca*. Fertile females of *Formica sanguinea* can establish themselves in a breeding chamber with fertile females of *Formica fusca*, a species that can found colonies independently, and let them tend to their offspring. Later, when the first workers are born, they will kill the now useless *F. fusca* females. There is still another method sometimes used by *F. sanguinea*; a female may take part in incursions in search of pupae of *F. fusca* and, instead of returning to her nest, she remains behind with some remaining pupae, the future slaves that will help the queen to establish a new *F. sanguinea* colony (Dumpert, 1978, 162-163)

Formica rufa queens, studied by *Morley* (1954), are also frequently unable to establish colonies independently or simply prefer to do it parasitically. In this case, the queen looks for a host´s nest, generally those of *Serviformica* ants, such as *Formica picea, F. cinerea* or *F. fusca*, and tries to invade it, facing the vigorous opposition of the workers. She faces the opposition like a cunning myrmecophile, assuming submissive postures and performing placating gestures (wiggling their antennae, for instance). Once inside the queen's chamber, she kills her in the same style as founding *Bothriomyrmex* queens do.

It is significant that temporary social parasitism is to be found among monogynous species, with smaller queens (often the same size as a worker) with no food reserves to face the independent foundation of a colony. Their monogynous habit cause them to be repelled at the entrance of nests of the same species, something that does not occur in the case of polygynous species, like European wood ants. Some *Lasius* species, if not most of them, exhibit temporary social parasitism during colony establishment, when a newly-fertilised queen will look for an auxiliary colony for adoption. This is what happens in *Lasius umbratus*, for instance. After fecundation, she stays in the vicinity of a nest of *Lasius alienus* or *L. niger*, waiting for an opportunity to grab one of the ants, drag it to a hole or tussock, and kill it with her mandibles. Maybe this instance of a "killing urge" is necessary for the *L. umbratus* female to mix its odour with that of the worker in the auxiliary nest, and thus lessen the hostility of *L. alienus* or *L. niger* workers, and then invade their nest. During the invasion, when the *L. umbratus* is invariably dragged by her legs or antennae, she can only wait for the hostility to be replaced with an interest in licking the tip of her gaster, and for them to confirm their preference for her – since they are monogynous – and kill their own queen.

The connection of each peculiarity in colony establishment with the way of life of each species has to be searched for in each case and, especially in the case of the enormous and diverse myrmecological fauna of Brazil, where ethologic exploration has barely started. The same can be said about most behaviours and characteristics of this fauna. Why do leafcutters have uncommonly long legs? What is the function of the grid of hairs that many ants have under their mandibles? The answer to these questions seems obvious when we see a leafcutter carrying vegetable fragments in an upright position, often in windy weather, supported by the tarsi of their long legs, especially the mid and hind pairs, forming a polygon with ends as far as possible from the longitudinal axis of its thorax, thus forming a wider support base if compared with other insects; or when we see desert ants extending their nests and carrying away the thin and unsteady grains of sand with the aid of their psamophores. The task of raising productive issues, from an ethologic point of view, about each ant species or any other animal, and of finding suitable answers for them, depends and will depend for a long time on thorough and patient observation with a comparative concern, in their natural habitat, supported by observation and even experimentation in artificial environments when a greater control of natural conditions is desirable. I doubt that even a long life of diligent study would be enough to clarify the adaptive meaning and the causal mechanism even of the main aspects of a single animal species, however insignificant and simple it may seem. And I think this is so because an organism, according to Lorenz (in Tinbergen, 1955), rather than an existing thing, is a developing process with millions of years behind it, and must therefore have a complex organisation that represents, in a given morphology and behaviour, the evolutionary solution to a most complicated set of adaptive problems. Unfortunately, time works against the projects of ethologists, a rare kind of scientist, living in an age of fast transformation of the natural environments he or she would have to inhabit to observe their "way of life". Many species have already disappeared without our having learnt about the solutions they evolved to solve adaptive problems posed by a given ecological niche, which might perhaps suggest solutions to our own adjustment difficulties. I think that if we could learn with the species still with us, this would be as worthwhile or more than a sentimental or romantic love for nature, a good reason for us to strive, in the interest of humanity, to secure measures for ecologic preservation and the protection of fauna and flora.

REFERENCES

For works mentioned in this text, see References at the end of the main text and Appendix III.

III: THE ULTIMATE REASON FOR TALKING ABOUT PSYCHOLOGY: THE MNEMIC ADJUSTMENT OF AN INDIVIDUAL ORGANISM TO ALTERED ENVIRONMENTS[53]

Walter Hugo de Andrade Cunha

If there were only reflexes and fixed-pattern actions in the behaviour of organisms when observed in their interactions with the environment, we would feel no need of thinking about a psychology. What requires the existence of a psychology – whatever this is – are those behavioural phenomena that apparently cannot be explained either by their anatomophysiological constitution or the nature of the environment in the moment they are seen; under these conditions, when observed without a view as to their causes, they seem to have the character of gratuitousness and arbitrariness. Most human actions – “actions” in its broadest sense, as everything a person “does” (13) – have this character, whether they are observable from the outside, like building a house, watching TV, teaching, playing football, talking on the phone, and driving a car, or veiled and directly observable only by their agents, like perceiving, illusorily or truly, thinking, remembering, or being afraid. Psychologists – whether they are behaviourists, psychoanalysts, phenomenologists, or existential humanists – see these phenomena as having this in common: they are manifestations stemming from the specific history of an individual organism’s interaction with its environment. Given this point of view, the explanation for these activities must be sought in peculiarities of the relationship of each individual organism with its specific past environments.

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Assuming that these manifestations are phenomena determined by the history of an organism's relationship with its environment means assuming that this organism has been modified in its contact with given environments, and that this modification allows us to explain these behaviours. Some of the changes an organism undergoes in its contact with the environment can even affect its later behaviour, but do not entail a psychology: a fever, for instance, or the tiredness and strengthening of muscles after exercise. Triggering a fixed-action pattern also alters the likelihood of its repetition within a given time span since its latest occurrence (7, 8, 13). However, these changes do not take us nearer the gratuitous and arbitrary behaviours mentioned above. They may cause the organism to stop responding to some alterations in its environment; however, they do not explain positive responses to other things or aspects in a situation – balls, telephones, professions, memories – or even responses to the absence of certain things – for instance, the fear responses of chimpanzees to the absence of a companion's body (when only its head is shown) or to the absence of movements in another (when they are shown an anesthetised companion), as studied by Hebb (5, 6), as well as our response when we raise the volume of a radio because of ongoing noise and lower it when the noise ceases. They also do not explain phenomena depending on previous experience, like conditioned salivation, searching for ice-cream in bars in Brazil and in drugstores in the US, as well as evoking, reasoning, withholding, refraining from something, speaking, etc.

When we think about them, we see that these actions are what shows that this organism has escaped from merely reflexive and/or instinctive action or, in other words, action elicited by stimuli or triggered by certain environmental factors or situations typical of each species under certain motivational conditions or organic states.

What sort of organic modification is this that allows these non-reflexive, non-instinctive, apparently gratuitous and arbitrary actions in the face of the construction of the organism and even the physicochemical nature of the stimuli? It must be a modification that will make it respond to more things than the stimuli that are presented to the senses at a given moment, if it can result in a behaviour which is not restricted to the actions of these stimuli.

An organic change that seems to have this property is what I will call the mnemic functional adjustment of an organism to aspects of its actions and experiences, such as altered aspects of its specific environment. I claim in this work that this phenomenon is at the root of every psychological event, since it is an organic change that enables an organism, through a special mechanism, which I will call redintegration of the past, to use its individual experience to release and/or endow its behaviour with the apparent character of gratuity and arbitrariness. In what follows I will present some considerations towards demonstrating – even if in a brief, summarised way – the phenomenon of mnemic functional adjustment (or record) and also the mechanism of redintegration of the past, made possible by the former phenomenon, in an attempt to demonstrate, also, the basic form in which the operation of both mechanisms produces the features of both open or veiled behaviour; in order to explain them, the creation of the special science of psychology has been and still is necessary. Strictly speaking, psychology is the offspring of an important discovery in the evolutionary process: that the use of individual past experience is the only element which can be relied on in nature in order to predict and prepare the future of an organism.

Even in the case of animals as insignificant, in a sense, as minuscule ants, there is, as I have indicated in a previous text (2), experimentally, one difference between the environment as physically or sensorily present and the environment to which an animal responds because of its past history of interactions with the environment. Two facts that could be considered as a whole, among others, illustrate this difference. First, there is the gradual mitigation, and, finally, the complete cessation of modifications to a pre-existing behaviour in a constant or recurrent situation when aspects of this situation are abruptly altered (for instance (2), when I introduce cotton swabs dipped in kerosene at different distances along a terrain, next to a trail of *Paratrechina fulva* (Mayr, 1862), or when the habitual caretaker of a chimpanzee colony suddenly starts to visit their cages in a uniform other than his habitual one (5, 6). Modifications are seen in the form of changes in trajectory – returns, zigzagging, detours or changes in speed (pauses or accelerations) or, still, changes in posture or motor coordination of movements (gaster rearing, antennal movements) in the case of ants; and present themselves in the form of what Hebb called "fear responses" (screeching, bristling, retreating, motor agitation, defecation, etc.) in the case of chimpanzees. The second phenomenon is the recurrence of these behaviour modifications, when the alteration to the environment, now apparently ineffectual (but only apparently, as it will be seen later on), is suddenly modified (when, let us say, the cotton swabs are removed after a long permanence along the trail, in the case of ants, or when the caregiver, after a number of days in his new uniform, resumes the old one or puts on a new one, in the case of chimpanzees).

My basic argument for what I call a functional, or psychological, or, in short, a mnemic adjustment of an organism to altered aspects of its environment, stems from these facts. It seems evident that *it is only because an organism mnemically adjusts to the presence of something existing outside itself – in the sense that it undergoes changes regarding the thing itself – that it can respond both to the absence or suppression of this thing, and fail to respond to its continuous presence with behaviour modifications.*

This organic modification that constitutes a psychological adjustment – and that causes some altered aspects of the environment, after repeated or prolonged exposure, to cease from interfering with a given relationship the organism had been maintaining with the environment (in the case of ants, that of repeatedly marching to and fro between the nest and a food source during the provisioning process; in the case of chimpanzees, their going towards the food offered by the caregiver in his own hand or in a bowl), and, at the same time, also become indispensable to the normality of this relationship – a specific case of an organic alteration biologists call *adjustment.* It is similar to that of certain organisms living in temperate areas that grow protective fur for winter, allowing them to live on under conditions adverse to vital processes; it also turns the recurrence of winter essential; the animal will be unadjusted to its environment conditions if kept away from winter, or if winter does not come. The only surprising thing is that the biological adjustment is carried out with no *apparent* organic change in the former case, which does not mean at all that this particular change, unlike the growth of winter fur, does not occur; it only means that we, psychologists, do not have procedures for experimental intervention to deal with it directly, as necessary in order to determine its physicochemical, physiological, and neurological nature.

If, as a tendency, behaviour modifications abate as a given alteration in the environment is continued or repeated (as a tendency, that is, in those cases in which an organism does not abandon a situation, but persists instead in a previous form of regulation), this must be so because each alteration in the environment modifies an organism in such a way that each new alteration will progressively be the less of an alteration, until a point is reached, in this series of alterations, when it will cease to be so (when a liminal critical point is reached). The adjustment mechanism should be one through which a change in a series of changes would cease to be so over time, and a non-change, on the other hand, would become a change. Now, for this to be the case, it is necessary for the organism to respond, each time, not to the alteration in the environment directly, but to the relationship of similarity and difference with the general situation prevailing in the environment so far. The condition for behaviour modification to occur, therefore, would not merely be the occurrence of an alteration in the environment, but an alteration in what the organism might be adjusted to.

It seems essential that we consider what goes on in a suddenly altered environment when an organism has already adjusted to it, in order that we can perceive how adjustment allows for the continuous, uninterrupted behaviour manifested so far. When a swab dipped in kerosene is removed from the vicinity of a trail, we notice that ants approaching the site do it as if the swab were still there, up to the point where, their behaviour being the same, they should find the swab. At this moment their march is interrupted as if something prevented them from going on. In the same way, if I suppress the food at the end of a trail, I see that the approaching ants proceed as far as the vicinity of where the food should be, and then erratically walk round the area, with intensified motions of their antennae. What happens then, I think, is that their behaviour manifests a sort of *inertia*, in the sense that it is a continuation of the behaviour presented so far towards a previous environment to which they had adjusted, until the occurrence of an aspect differing from the environment they had adjusted to.

I suppose that if the environment as it has been before an alteration is enough to encourage the behaviour that had prevailed so far, this is so because the partial environment then attained is similar enough to the previous environment in order to make it work as if the latest environment were present in its entirety: as if it had been redintegrated, therefore, out of a present fragment. An organism responds to a present aspect as if it were facing not only this aspect, but also others that usually follow it. Behaviour in a given moment will therefore be seen as pre-released, pre-adjusted, or pre-regulated, in such a way that, on the occurrence of this aspect, inertia will take place. The impression one has of these cases as seen from the outside, or the impression we introspectively have when we are the agents of this behaviour, is that the organism is anticipating through its responses the environment that will soon be presented, when, in fact, this is being triggered by aspects of past environments, redintegrated out of their confluence with a fragment of this environment in the present. When an organism seems to be judiciously choosing its steps towards a result or target "X", in fact, the assumed anticipation of "X" and of the steps preceding it will be an indication of how the present environment has given place to a behaviour directed by this organism towards a past environment, redintegrated out of the environment now present.

Psychological adjustment, therefore, is an organic change that, when an already experienced, unaltered part of an environment is presented, one other part accompanying this same environment, though absent, or at least not as yet present to the senses, is then brought back into existence, or, rather, back into work, thus allowing this organism to respond in advance to this part, even if absent to the senses, as if it were actually present. This phenomenon – of bringing back into existence, or, rather, back into operation, out of a part of a previous, actually present situation, one other, not as yet verified as present to the senses – I shall call *psychological redintegration*, or *adjustment*, or, for short, *redintegration.*

One should not restrain the phenomenon of redintegration , as formulated here, to the meaning old psychology gave it, that of being recall in terms of reduced cues or response to minimal cues and that Munn (1956) thus defined in the glossary appended to his book:: "Redintegration: Recalling a whole experience, or making an appropriate reaction, in terms of some fraction of the original circumstances".

This phenomenon refers at most to one of the possible effects of what I now understand as the mechanism of adjustment redintegration, which I have thus called so far, however, in recognition of the importance that this early usage has had in my conception of this mechanism.

Finally, and summing up what has been said above, one sees that adjustment is gradually achieved. This gradation indicates that, in the contact of an organism with a given environment, what is at work is the relationship of the present environment with the previous adjustment to the environment brought into the situation by the subject. Given this relationship, some alternatives result for each encounter of an organism with a specified environment. If the relationship is one of difference, new behaviour modifications will occur, and a new adjustment process will start working. If it is one of identity, or great similarity, the behaviour exhibited so far by the organism towards the previous situation will evince inertia in the new situation, something that leads one to assume an adjustment redintegration mechanism at work: the organism will act towards aspects of the environment other than those actually present or acting on the senses at the moment, aspects that will be reintegrated into the former on the basis of their previous adjustment. If the aforementioned relationship is one of only partial similarity, the organism will exhibit an ambivalent behaviour – responses determined by inertia and responses that are modifications of the previous behaviour – such as illustrated in the familiarity-non-familiarity conflict in the case of my ants when faced with a cotton swab by their trail, or with its suppression, or in Hebb's chimpanzees, suddenly disturbed by their usual caregiver dressed in a different uniform. For greater clarity, I will report a similar conflict. I see my bedroom, after some pieces of furniture have been removed. How strange it looks! Such empty spaces! I think this is so because what "actually corresponds to my present bedroom", that is, to a given sensory impression, is being related to the record of how the bedroom had previously been in order to give room to my present perception. In other words, the bedroom as it had been is within me, it is the "presence of the absent", as Merleau-Ponty (9) said, and the present bedroom is different; it is roomier. If I do not realise, when facing my usual bedroom, that it also appears in the relationship with the bedroom and everything I had previously recorded, that it appears to me as an objectively existing environment, this is because there is no change in the relationships – except for the temporal ones – previously maintained between it and these other objects. Because these relationships are confirmed, point by point and from moment to moment by my actions regarding them, I do not realise that the aspects of this bedroom, and of the objects in it, with their uses, distances, and possibilities for manipulation, come from my previous adjustments not only to this bedroom and its objects, but also to different objects (it is hard to demonstrate the latter point; it is suggested in facts like this: the mere perception of a tree before me seems to entail everything that is not the tree, in such a way that all my past is involved in the event: it is not glass, it is not amber, not a cloud, neither oil nor ice, etc., even though it may evoke some objects rather than others: for instance, boats, other trees, pictures of trees, logs). These previous adjustments allow me to perceive something that I have only glimpsed as having weight, softness, temperature, solidity, etc., that is, perceptible qualities that still do not correspond to stimuli acting on the senses at the moment.

Having different histories, therefore, means having undergone different processes of adjustment to altered environments; it can also mean the ability to establish, for a sensorily active aspect of an object or action, a set of redintegration instances that may be common to other people, but which, on the other hand, may and even must have certain specificities, enough to explain the apparently gratuitous and arbitrary character of the acts to be seen. One other illustration will help clarify these points: let's say I'm driving a friend home. I park in front of a gate. It cannot be said that, psychologically, my friend and I each see a different thing. After all, we both notice it is an iron gate; its bars are strong enough to keep us from entering and they must be somewhat cold to the touch. But it would be naïve to assume that just because we notice these facts, we are psychologically facing the very same thing. The gate, for my friend, is a limit or point at which some concerns will cease, and others will begin. For me, however, the gate is merely an object to be examined from an aesthetic or practical point of view, a model or style I may someday use to install gates in front of my own home. It is not the physical constitution of the gate – whether it is made of iron or bronze – that will clarify the different significances it has for us, in the same way that introspection in its presence will not, however carefully carried out, do it for the way we perceive it, and the sensations, feelings, and other objective or subjective "mental elements" supposed to constitute this perception. In order to understand this difference, I have to place it within the context of our individual lives. More specifically, since this is beyond my reach, I will at least be able to observe how my friend behaves towards it: whether he will go past it in compunction, head bent down, or whether with ease and joy; whether he will kick it or caress it, and so on. I can certainly see whether I would do the same while passing by it, and whether I would have to do it by virtue of its own nature or not. It is evident that we both respond to more than that facet that excites our sense organs in a given moment, and that this something is, admittedly perhaps, what each one of us redintegrates, through this sensory contact, from adjustments we have undergone on being exposed to it and other things in the past. And it is only this redintegration and these adjustments that apparently remove, or can remove, the apparently gratuitous and arbitrary character of our acts towards such an object, or even towards and object not previously experienced. In fact, each tree that I see when I enter a forest is the same old object that I carry within me as an abstract possibility waiting for an opportunity to be fulfilled.

I certainly do not have the room to demonstrate how everything that is not a reflex nor a fixed-action pattern in the behaviour of an organism is, in the final analysis, either dependent on, or originated in an adjustment to altered environments, and this entails a mechanism for the comparison between records and materials to be recorded, allowing for the possibility of redintegration of the past out of the present, or, if one prefers, of assimilation of the present into the past. I will only mention that the classical conditioning of Pavlov's dog seems merely to be, in the final analysis, the expression of redintegration made possible by the fact that Pavlov associated bell and food in such a way that the former would entail the latter for an animal subjected to the association. I will also mention that conditioning at work is what demonstrates, for instance, how a light turned on in a cage to indicate that an operating lever will bring water or food also redintegrates the whole situation and becomes the elicitor of an original response in an animal deprived of water or food.

Similar principles to those described above, adjustment and redintegration, were obviously implied in a certain way by Tolman (14, 15) under the concepts of cognition and expectation, or by Piaget (12), under the concepts of accommodation and assimilation. Even before these authors, something of my doctrine was already present in authors like Proust in *In Search of Lost Time*, or Dilthey, in his concept of the "acquired nexus of psychic life" (1, 4). Here, I have only tried to formulate some facts pointed out by these authors, as well as others, in such a way as to make them more intelligible and amenable to the experimental treatment of psychology, considered as more of an empirical and positive science than it has been the case so far.

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ABOUT WALTER HUGO DE ANDRADE CUNHA

Walter Hugo de Andrade Cunha was responsible for the introduction in Brazil – and perhaps Latin America – of Ethology and Compared and Animal Psychology studies. He launched them in 1961, at the Psychology Institute of the University of São Paulo (IP-USP), where he founded and ran a pioneering laboratory devoted to these studies.

Photo courtesy of SBP.

He lectured from 1958 till his retirement in 1984. In 2015, the University of São Paulo conferred upon him the title of Emeritus Professor[1], in view of his extensive and sustained contribution to the development of Psychology, Ethology, and Psychobiology.

In 1956 he graduated from the Faculdade de Filosofia, Ciências e Letras (FFCLH-USP) with a degree in Philosophy. He was hired by the university as an assistant to Dr. Annita de Castilho e Marcondes Cabral, at the Psychology Chair. Under her supervision, he completed his doctoral studies at the same college. His thesis, "Explorações no mundo psicológico das formigas: uma investigação de algumas modificações de comportamento de *Paratrechina fulva Hymenoptera Formicidae*" [Explorations into the Psychological World of Ants: an investigation concerning some modifications in the behaviour of *Paratrechina fulva Hymenoptera Formicidae*], submitted in 1967, was the first one in Brazil dealing with Animal Psychology. It was published by Ática in 1980.

In June 1961, he completed his graduate studies in Experimental Psychology at the University of Kansas (USA). Upon returning to Brazil, he founded and directed the Laboratory for Compared Psychology, where he undertook ethological research and developed a pioneering teaching program for subjects in Ethology and Psychology.[2]

As a result of negative experiences with teachers, from his primary to secondary school days, he was disappointed with traditional teaching methods. Therefore, he developed

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[1] He was honoured also as a Professor by USP in 2004, when the University celebrated its 70th anniversary, and by the Sociedade Brasileira de Etologia (SBEt) on two occasions: in 2013, as the founder of Ethology in Brazil, and in 2019, on the occasion his 90th birthday.

[2] For instance: "Instinct", "Animal Behaviour Observation", "Animal Societies", "Animal Behaviour Investigation", "Purpose and *Umwelt* in Animals", "Behaviour and Evolution", "Theories and Systems in Psychology" and "The Conceptual Framework of Psychology".

a unique teaching system that fascinated his students, including myself, even though it entailed more time and work.[3]

Thanks to his innovative studies, methodology, dedication and enthusiasm in teaching and supervising dissertations and doctoral theses, many of his students, who came from many different areas of Brazil, would become advocates of his academic ideals.[4]

He was an active member of the Sociedade Brasileira para o Progresso da Ciência [Brazilian Society for the Advancement of Science] (SBPC), Sociedade Brasileira de Etologia [Brazilian Ethological Society] (SBEt), Sociedade Brasileira de Psicologia [Brazilian Psychological Society] (SBP), and Sociedade Latino-americana de Psicobiologia [Latin American Society for Psychobiology].

Antônio Jayro da Fonseca Motta Fagundes
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[3] Described In: CUNHA, W. H. A. (1974) Acerca de um curso de pós-graduação destinado ao treino da observação científica no domínio das ciências do comportamento [On a post-graduation course directed to the practice of scientific observation in the realm of behavioural sciences]. *Ciência e Cultura,* v. 26, n. 9, p. 846-853.

[4] For details and further information about this native of Minas Gerais state, born in Santa Vitória, then a district of Ituiutaba, on 15 November 1929, I recommend two sources:

(1) Centro de Lógica, Epistemologia e História da Ciência da Universidade Estadual de Campinas (CLE-Unicamp), entry Walter Hugo de Andrade Cunha. (Retrieved at: https://www.cle.unicamp.br/index.php/content/walter-hugo-de-andrade-cunha. Access on 18 May 2020). Walter Hugo donated to CLE all his personal archives, which include videos with testimonials and photographs.

(2) FUCHS, H. (1995). Psicologia animal no Brasil: o fundador e a fundação [Animal Psychology in Brazil: the founder and the foundation]. *Psicologia USP*, v. 6, n. 1, p. 15-42. [Also available at: http://pepsic.bvsalud.org/scielo.php?script=sci_arttext&pid=S1678-51771995000100003. Access on 18 May 2020]. The almost 300 pages of issue no. 1 in this volume of the Journal, authored by eight of his former students, comprise parts of 1 dissertation and 5 theses, a sample of the works developed under his supervision.

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