ANIMAL BEHAVIOUR · VOLUME 1

CAUSES AND EFFECTS

EDITED BY T.R. HALLIDAY
AND P.J.B. SLATER

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SERIES INTRODUCTION

As Niko Tinbergen, one of the founders of ethology, pointed out, if one asks why an animal behaves in a particular way, one could be seeking any one of four different kinds of answer. One could be asking about the evolutionary history of the behaviour: why did it evolve to be like it is? One could be asking about its current functions: through which of its consequences does natural selection act to keep it as it is? Thirdly, one might be interested in the stimuli and mechanisms that lead to the behaviour being performed: what causes it? Finally, one might be asking about development: how does the behaviour come to be as it is during the life of the individual animal? A complete understanding of behaviour involves investigation of all these questions, but in recent years there has been a tendency for ethologists to specialise in one or other of them. In particular, the functional analysis of behaviour has almost become a separate discipline, variously called behavioural ecology or sociobiology. This fragmentation of the subject is unfortunate, because all its facets are important and an integrated approach to them has much to offer.

Our approach in these books has been a more wide-ranging one than has been common in recent texts, with attention to all the kinds of explanation that have traditionally been the concern of ethologists. Aimed at students, each volume will provide a comprehensive and up-to-date review of a specific area of the subject in which there have been important and exciting recent developments. It is no longer easy for a single author to cover the whole field of animal behaviour with full justice to all its aspects. By asking specialists to write the chapters, we have tried to overcome this problem and ensure that recent developments in each area are fully and authoritatively covered. As editors, we have endeavoured to make sure that there is continuity between the chapters and that no significant gaps have been left in the coverage of the theme specific to each book. We hope that students who are inspired to further study by what they read will find the Selected Reading recommended at the end of each chapter a useful guide, as well as the more specific references which are gathered together at the end of each book.

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T.R.H.

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CONTENTS

INTRODUCTION

What causes an animal to behave in a particular way? As Aristotle realised, this question can be posed at several different levels. Those that we might identify at the present day would include the evolutionary or functional question of why a behaviour pattern is included in the animal's repertoire, and also the developmental question of what influences during the lifetime of the individual have led it to behave in this particular manner. This second approach is dealt with in Volume 3 of this series. In this volume, however, we are concerned with a third class of cause, which Aristotle termed the efficient cause and which we now often refer to as the immediate cause of an animal's actions. This is the most common usage of the term cause, and covers only factors which lead to behaviour in the short term, excluding more long-term antecedents such as selective forces, inherited tendencies and aspects of past experience. Here, then, we are asking what external stimuli, internal states and mechanisms lead to the performance of the behaviour that we see.

Those who study the immediate causes of behaviour can take many different approaches, as the chapters of this book will make clear. Perhaps the most fundamental distinction is between those who remain at the behavioural level and those who seek answers in physiology. To study behaviour at its own level is to treat the animal as a 'black box', modifying the stimuli that impinge upon it and seeing how these affect its behavioural output without being concerned too deeply with the exact nature of the intervening mechanisms. Both external stimuli, such as length of day or presence of other animals, and internal stimuli, such as hormone levels or gut content, can be altered in this way and just how they affect behaviour may be studied. This enables behaviour to be predicted, to be changed and its causes to be understood without any direct knowledge of the mechanisms within the animal for translating the various inputs into the output. To others, answers such as this are unsatisfying: they want to know exactly what is going on to produce the behaviour in terms of hardware, to analyse the neural circuitry between sense organs and muscles responsible for it. Only then will they feel that the behaviour has been 'understood'. This is the essence of the reductionist approach: seeking to explain each level of organisation in terms of that below it. At an extreme it could be claimed that human psychology should ultimately be understandable in terms of the behaviour of atoms. This is obviously absurd, but is it absurd simply because it is impracticable?

Reductionism does have its enthusiastic adherents, and there are those who argue that studying the causation of behaviour is ultimately a matter for neurophysiologists (e.g. Wilson 1975). However, there are enormous pitfalls. Quite apart from the sheer complexity of the matter, is the point that each level of organisation tends to have so-called 'emergent properties' which could not be predicted from the level beneath. As Marr (1982) put it, in a stimulating review of levels of approach to understanding vision:

> 'Almost never can a complex system of any kind be understood as a simple extrapolation from the properties of its elementary components'.

In contrast to this we can take the following remark by Barlow (1972), made at a time when our knowledge of the nervous system was advancing rapidly and appeared to hold the key to most things:

> 'A description of that activity of a single nerve cell which is transmitted to and influences other nerve cells and of a nerve cell's response to such influences from other cells, is a complete enough description for functional understanding of the nervous system'.

Barlow's remark was clearly intended to provoke research and discussion but it embodied the optimism of that time, when sensory physiologists were going deeper and deeper into the nervous system and it seemed that they might almost emerge at the other side with an 'explanation' of behaviour. Such an enterprise is, however, doomed to failure for the practical reason that translating between levels is a very complex process and for the more theoretical reason that properties emerge so that questions of interest at one level may have no counterpart at that beneath. This is not to say that the neural mechanisms underlying behaviour are of no interest, it is just to point out that they may be extremely hard to unravel (as is proving to be the case) and that understanding them is only part of the answer to understanding the causes of behaviour.

A point related to the merits of reductionism is the question of how mechanistic behaviour is. The answer to this question from someone who studies behaviour depends strongly on the complexity of the animals they work on. Certain aspects of behaviour, like reflexes in ourselves and in other animals, are virtually automatic. The neural machinery is simple, perhaps involving only two or three cells, and the response is near constant and highly predictable. In some animals, especially amongst invertebrates with small repertoires of rather fixed behaviour patterns, much of the behaviour may be like this. For example, it may not be too great a simplification to summarise the behaviour of a spider confronted by a visual stimulus by the rule: if it is small eat it, if it is large run away from it and if it is intermediate in size mate with it. However, as animals become more complex, with numerous possible modes of behaviour, these cannot be subject to simple rules which do not change with time. In other words, the problem of changing motivation crops up. To those who wish to study behaviour from a mechanistic point of view this can be a nuisance and more consistent animals must be used. Take Ewert (1974), for example, justifying his choice of the toad for experiments on visually guided behaviour:

> 'In response to specific stimuli one can repeatedly elicit predictable reactions, such as snapping at prey, fleeing from an enemy, clasping during courtship and making particular wiping motions after tactile stimulation. (The fickle European frog, in contrast, undergoes short-term changes in motivation and is not suitable for behavioural experiments.)'

Where one person's interest ceases, another's begins; to those interested in understanding the intricacies of motivation, the frog has virtues that the toad lacks! Indeed, for most vertebrate behaviour there are short-term changes in responsiveness which make it hard to obtain consistent results. Some such changes may be for relatively trivial reasons, such as adaptation of sense organs to the relevant stimuli or fatigue in appropriate muscles, but often these can be excluded as the senses and muscles are used for other activities. Some more central change must then be responsible. It may not be surprising that an animal which has just eaten to satiation is not interested in food, but why should a male stickleback chase a rival one day but pay scant attention to him the next? Understanding such changes is the bread and butter of motivation study and, at least amongst vertebrates, changes in motivational state are a very important determinant of whether or not an animal will respond when a stimulus is presented to it.

This book is concerned with mechanisms and with motivation, but it is not a book about physiology. Reference will, of course, be made to physiological factors, such as levels of hormones, glucose and ions in the blood, and to characteristics of the nervous system. But the focus throughout is on behaviour, and these subjects are raised only where they help us to understand behaviour rather than as central topics. While our authors offer very different views and perspectives on many issues, they are united in approaching behaviour at its own level rather than simply as a projection of physiology.

The first three chapters are concerned with the more physical aspects of behaviour, Land with sensory systems, Dawkins with movement patterns and Collett with how the two are coordinated so that the animal behaves in an appropriate fashion. Animals can glean information about the world in which they live in numerous different ways, for various sorts of stimuli impinge upon them and can be used to guide their actions. Most commonly, pressure waves stimulate hair cells within the ears to create the sensation of sound, electromagnetic radiation over a limited range of frequencies is picked up by eyes and used to create a visual picture of the world, and chemicals, especially from other animals and from food, are sensed by smell and by taste. The main aim of Chapter 1 is to survey the properties of the senses and show how animals can use them to extract information about their surroundings. In common with subsequent chapters, Land takes a comparative approach. When discussing the senses this is especially interesting for two reasons. First is the remarkable variety of ways that evolution has generated for picking up information of a particular sort and translating it into a form usable by the nervous system. Eyes make a good example: though all perform similar tasks, for subtle reasons related to their exact uses and the medium in which they operate as well as the phylogenetic relationships of their possessors, they come in many different designs. Second is the fact that animals are by no means limited in their senses to those we possess ourselves. They may sense a broader range of frequencies that we can, as with bees that see the ultraviolet patterns on flowers, snakes that sense the infrared radiation from their warm-blooded prey and bats that orientate using high-frequency sounds far beyond the limit of our hearing. In other cases the sense may be of a different quality altogether, as with the magnetic sense of birds, bees and bacteria and the electrical sense of some fish.

Having gleaned from their senses what is going on in the world around them, to what use do animals put the information? This is the main theme of Collett's chapter. It may seem surprising that he starts with examples from single cells, as many people would not think of such lowly organisms as 'behaving'. It is, however, salutary to consider the sophisticated and adaptive ways in which bacteria and protozoa can alter their movements in relation to stimuli from the world in which they live, without so much as a nerve or muscle to assist them! Nevertheless, one can only get so far by simple reactions to whether or not a particular sense is stimulated. In most animals subtle changes in the sense organs lead to equally subtle changes in behaviour, detection of the appropriate sensory events involving collation of information from many receptors and the response involving particular combinations of many muscles which may, at other times, take part in quite different actions. Collett discusses these relationships. In some cases they appear to involve the straightforward application of simple rules which translate sensory cues into appropriate action so that behaviour can be matched to environment elegantly and economically. Only with the intervention of prying scientists do things go awry and so give us an insight into the rules that guide the animal's actions. In other cases, especially amongst mammals, one must invoke more than just simple rules: here several senses may fall into register with one another within the brain to give the animal a multimodal picture of where it stands in relation to its world, and the animal must learn about that world and retain a mental map of it to match its actions to it. Rudimentary stimulus–response reactions will not guide an animal to an unseen water-hole or to the best place of refuge from a predator regardless of where it happens to be on its territory when the danger arises.

In considering the motor activities of animals, Dawkins moves us into a realm which has for long been central to ethology, and provides a bridge to the chapters on motivation which follow. If we watch an animal moving around in its environment and going about its daily business of feeding, drinking and grooming, it is easy to be overawed by the complexity of it all. How can one start to analyse something so diverse? One of the great contributions of the early ethologists was to recognise that some order existed in the midst of this diversity, and that animals had a repertoire of stereotyped behaviour patterns that could be spotted each time they occurred and were the same throughout a species. Thus all horses walk by moving the two legs which are diagonally opposite each other at the same time, but all giraffes, surprisingly for an animal so tall, move the two legs on the same side at once, swaying from side to side to keep their centre of gravity above the pair on the ground. Later work has revealed that various attributes of such Fixed Action Patterns, including their fixity, were not as hard and fast as had been supposed. Dawkins discusses these problems and others concerned with defining units of behaviour. She then goes on to look at the organisation of these basic units into higher-order sequences of actions and at theories underlying this organisation, notably the idea that some behaviour is goal-directed and the idea that related actions fit together in an organised manner because there is a hierarchy of control. The idea of hierarchical organisation was espoused most strongly by Tinbergen (1951) who, in a first flush of enthusiasm for the possibility of making links between behaviour and the nervous system, devised a hierarchical model incorporating centres which he hoped might have physiological manifestation within the brain. As Dawkins shows, life is not that simple and, while advances have certainly been made in understanding the neurophysiological basis of behaviour patterns and the sequences into which they fall, she argues strongly for the 'whole animal' approach and for the understanding of behaviour this can give us.

While single actions may appear in much the same form every time an animal performs them, sequences of different activities are seldom repeated in exactly the same order. In other words, behaviour is probabilistic rather than deterministic in its structure: a good reason why it appears to be so complex. This is also a good reason why changing motivation often has to be invoked as a factor to explain the structure of behaviour.

Although the study of motivation deals with many different topics, it is most convenient to split them up into the factors affecting the occurrence of single systems of behaviour, as discussed by Halliday in Chapter 4, and the interactions between systems, which McCleery covers in Chapter 5. Both these subjects have received a great deal of attention from ethologists, and views on them have changed markedly over the past few decades. Once again, rather sweeping generalisations by early ethologists provided a stimulus for research which, in its turn, showed just how inadequate these theories were. As far as the motivation of sets of related behaviour patterns was concerned, the first theory proposed was Lorenz's (1950) 'psychohydraulic' model known more colloquially as Lorenz's water-closet. This pictured 'action specific energy' as accumulating and being expended like water in a tank, and is discussed as a starting point by both Halliday and Toates. It is a naive first approximation to what may perhaps be going on in some systems, but it trips up on a number of important facts. Two of these deserve mention here. First is the assumption that different behavioural systems are likely to have similar underlying mechanisms. We know that, like Lorenz's model, the tendency to feed and drink rises with time elapsed since these patterns were last performed. We would expect this, as these actions correct physiological deficits which are bound to accumulate. But would we expect the same of grooming, sex, aggression or egg-rolling in geese? In his book *On Aggression* (1966) Lorenz clearly does have such a model in mind. However, recent research has shown the application of such general theories to be dangerous: one of the wonderful things about animal behaviour is how finely tuned it has become through natural selection to the requirements of each species. Different systems may behave quite differently depending on the exact requirements of their possessors. A second problem with Lorenz's model is that it makes no provision for the behaviour to be influenced by feedback from its own consequences. As Toates points out in Chapter 6, the application of control theory to behaviour patterns such as feeding and drinking has been especially fruitful, and feedback diagrams help us to predict behaviour with a fair degree of accuracy. Except in the most stereotyped of behaviour patterns, animals continuously monitor and modify their behaviour in the light of its consequences: they stop drinking, for example, when they have accumulated sufficient rather than, as Lorenz's model would predict, when they have taken a certain number of gulps.

Generally speaking, human beings can walk and chew gum at the same time. Amongst most animals, however, it is unusual to find the performance of two different behaviour patterns proceeding simultaneously. A bird tends to be either flying or preening or feeding or singing, although there are of course exceptions. This makes the analysis of behaviour much easier but it leads to a whole range of problems in understanding motivation. How should an animal decide what to do at a particular time? If it is hungry and itchy, there is a prospective mate nearby and a predator is looming, should it escape, mate, feed or groom? These are the sorts of problems which McCleery discusses in Chapter 5. For some species a fixed hierarchy of priorities provides a reasonable description of changing motivation: in the snail *Pleurobranchaea,* for example, egg laying suppresses feeding, and escape takes priority over both. In most species, however, priorities change and different acts are more likely at different times. Earlier ethologists pictured drive systems vying with each other for expression, with the possibility that where two were in conflict a third might be disinhibited, so that unexpected behaviour appeared in the form of a displacement activity. But internal drives and conflicts between them are not very fruitful hypotheses because they can account for almost anything one might observe: if you expect the animal to groom it is doing so because its grooming drive is high, if not it is doing so because other drives are in conflict and grooming has been disinhibited. Because of such difficulties with intervening variables which cannot be observed, drive theories tend to have fallen from favour. However, the problems remain and McCleery describes the more sophisticated and precise modern theories which have been formulated to cope with them.

The problems of motivation, whether they deal with the occurrence of a single behaviour pattern such as feeding or with sequences of different actions, are complex, some would say intractable. Devising models of how systems may work has always been helpful, regardless of whether or not the model is thought of as having any physiological reality. Building models can be quite an eye-opener and is now an easy matter for anyone with a little knowledge of computer programming. We know the system has certain properties and we build these into our model. How does it behave? Usually not very well at first, but we can modify it in one way or another to make it more realistic. We can incorporate further features if these prove necessary but sometimes, to our surprise, we need not do so: unexpectedly a property of behaviour emerges from the model without having been predicted, or the model behaves in a particular way when tested and we find that the same manipulation of a real animal has the same effect. Models are a marvellous way of helping us to think about really complex things and, by moving back and forth from animal to computer, we can discover just what is needed to predict behaviour when this might otherwise be beyond our capabilities. Toates shows some of the potential of the modelling approach, referring back to some of the problems discussed by Halliday and McCleery. His discussion of drinking will be a revelation for anyone who thought that all one need postulate is thirst!

CHAPTER 1
SENSORY STIMULI AND BEHAVIOUR

M.F. LAND

1.1 Introduction

It is the information supplied by senses that guides an animal's present and future actions, and it is the variety, quantity and quality of this information that to a large extent determine the complexity and flexibility of the animal's behavioural repertoire. In the simplest cases a sense organ may supply no more than a statement about the intensity of a particular form of energy. The paired eyespots of a planarian, for example, tell the animal which direction is the lighter, but no more, and the action resulting from this knowlege is a movement either towards or away from the lighter region. As the next chapter will show, the simplest of information can thus be used to guide an animal to a suitable habitat. Similarly, a sudden decrease in light intensity may be used by a fanworm or a clam to indicate the imminent presence of a predator, and the animal will withdraw into its tube, or close its valves. Although there are many examples of behaviour of this kind, where it seems possible to establish a straightfoward one-to-one link between a change in a stimulus and a recognisable kind of motor activity, with more sophisticated sense organs and phylogenetically more advanced animals this is usually not possible. There are several reasons for this, and they are all pertinent to the problem of how animals use their senses.

In the first place, most sense organs supply far more information than can be made use of at any one time (consider, for example, that the human eye alone has about 120 million receptors, each capable of allowing discrimination between at least ten intensity steps). At any one time, therefore, most incoming sensory information is redundant or unusable. There can be no question of a simple reflex link between complex receptors and