I
Introduction

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Levels and processes

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Behaviour is studied in many ways because people become absorbed in different types of problem. Some want to know, for instance, what a pattern of behaviour is for, while others want to know how it is controlled. Nevertheless, styles differ even when a problem is shared. The research of some people is driven by clear and explicit theories. Other people suppose that when enough information has been collected, the explanations for behaviour will stare them in the face. Some push a theory for all its worth until it overwhelms the opposition or collapses from weakness. Others, revelling in curiosity, enjoy the diversity of individuals and species. The opposition between these contrasting styles is easily overstated for they complement each other and, when those who work in different ways find a way of coming together, their union is often highly productive.

'Coming together' is perhaps a good way to describe the overall character of this book. One message, emerging strongly from it, is that ideas should flow in both directions between different levels of analysis. In that sense the stance differs sharply from a commonly held position that the people studying behaviour should pose problems for the neuroscientists who, having done their work, should pass on the project to the molecular biologists (e.g. Dudai, 1989). In the same vein, the study of social structure should not simply be reduced to the study of relationships. Both should be helped by the knowledge and the understanding obtained at the other level; likewise for the studies of social relationships and individuals' behaviour.

A second theme of the book is that, at all levels of analysis, scientists studying behaviour are faced with dynamical systems that have an awkward way of altering their characteristics when conditions change. The way to understand such systems is by studying them as processes, not by taking snapshots or by abstracting linear causal chains. In the study of behavioural

development, for instance, an approach, which now seems outmoded, was to make manipulations in early life and examine the long-term effects on adult behaviour. As the manipulations of the environment were combined with the use of strains of different genotype (e.g. Cooper & Zubek, 1958), the claim that differences are due solely to a particular aspect of experience or solely to genes was made less frequently than before. Nevertheless, even to the present day, influential voices are to be heard arguing that, if something is known about genetic and environmental variation, then it is possible to use standard statistical techniques to show how genes and the environment contribute to differences in a particular characteristic. The conclusion emerging from such thinking is that the genetic and environmental factors *add* together to produce their effects on behaviour (e.g. Loehlin, Willerman & Horn, 1988). However, even if the dynamics of development could be plausibly reduced in this way, major aspects of the interplay between the developing individual and its environment are easily missed by the analytical techniques used to derive such conclusions (Bateson, 1989; Wahlsten, 1990). The general point that recurs frequently in this book is that understanding is significantly improved when the processes involved in the development and integration of behaviour are studied directly. This places a spotlight on the behaviour of individuals.

The mood of a great many of the chapters in this book is a wish to understand how things are put together. Instead of explaining patterns of behaviour in terms of their parts or their origins, the drive is to understand the rules that make the processes work. The assumption is that getting to grips with the organisation of behaviour is the precursor to obtaining principles. At the very least, the questions that need answering are being formulated. In this introductory chapter I discuss briefly the contents of each essay in the scientific part of the book before returning to the themes that run through the whole book and the way they link to Robert Hinde's own interests.

Bateson and Marler

The chapters in Section II, which is about behavioural development in animals, deal primarily with two favourite and famous ethological examples, imprinting and song-learning in birds. In Chapter 2 my general concern is with how the undoubted complexities of development might be made more tractable by uncovering principles that make sense of that complexity. In order to illustrate how this might be done, I look at the particular case of imprinting. The features of the animal existing at the time when it normally starts to learn the characteristics of its close kin crucially affect the process by which an animal's social preferences develop in the way they do. Even though the hypothetical underlying rules for the developmental process are

rather simple, what happens to the bird is not reducible to internal and external contributions that add together. An important conclusion is that as developmental processes are studied, the old nature/nurture dichotomies, which were always difficult to handle empirically, lose any usefulness that they might once seem to have had.

In Chapter 3 the interplay between the developing animal and its environment is disclosed in another way by Peter Marler who reviews the marked species differences found in the development of song in birds. Closely related species differ in how much they learn, the sounds which they are most likely to learn about and the sounds which they are most likely to make when they have been exposed to the same conditions. Songbirds also differ in when they learn most readily and in subsequent inventiveness in generating new patterns of song. Marler argues that all this evidence points strongly to the pervasive influences of genetic factors in generating those differences. Since he is dealing with learning, his examples also emphasise the importance of understanding the rules that underlie developmental processes. These rules have to develop, of course, and may well take on peculiar characteristics in special environmental conditions. Nevertheless, a crucial difference between different species will be those genes that influence the character of the features in any one set of circumstances. In essence, then, Marler exploits differences between species in getting at the way developmental processes work.

Fentress, Horn, Hutchison, Andrew and Rosenblatt

Section III deals with the neural and endocrine mechanisms underlying behaviour. In Chapter 4 John Fentress underscores the main themes of the book when he considers the rules of connection between behavioural and neural analysis. He regards what he calls the bi-directional perspective, looking up as well as looking down, as crucially important. This approach is now becoming an important part of neuroethology. Fentress recognises that the major problem facing scientists in this area is to put together properties that have been isolated for purposes of experiment and yet which must be interconnected in the free-running animal. He has led the way in showing how systems can sometimes operate autonomously and sometimes affect each other. The difficulty is, as he points out, that once a system has been abstracted, it is treated as though it cannot interact with another one. Even so, he is optimistic about the outcome of attempts to reassemble the integrated organism. The next chapters show why.

In Chapter 5 Gabriel Horn gives examples from imprinting in domestic chicks of how the interconnections between different levels of analysis are being made in practice. Problems of the organisation of behaviour, which had not even been thought of before the neural analysis of imprinting had

been carried out, are now being posed. The neural analysis has not only thrown light on the neural bases of recognition memory, but also has made possible the dissociation of the mechanisms involved in the initial preferences from the mechanisms involved in narrowing chicks' preferences to a familiar object. How do the development of predispositions and the specific effects of experience on preferences interact? How is mate choice affected by the lesions which have a highly specific effect on filial imprinting? Is it possible to dissociate the recognition memory aspect of imprinting from the operant and classical conditioning aspects which are known to accompany it? What are the functions of the memory systems storing representations of the imprinting object in different locations in the brain? All these questions have been or are now being studied at the behavioural level as a result of the research at the neural level.

Another example which further elaborates the general point made by Fentress about approaching problems at both the behavioural and neural levels is found in Chapter 6. John Hutchison links behavioural analysis of courtship with the biochemical techniques of neuroendocrinology, illustrating this interplay with the results of his own long-term work on birds and mammals. The male hormone testosterone is a precursor, broken into different metabolites by enzymes in brain cells. These metabolites affect behaviour differently. Whether or not a behaviour pattern is expressed depends on the brain enzymes, which in turn depend on the animal's state. Since the animal's state depends on environmental conditions, the advantages of bringing together expertise from different levels of analysis are obvious. Hutchison points out, furthermore, that the principles involved here are as important in development as in the control of adult behaviour.

The new knowledge about the various actions of testosterone on behaviour is also strikingly illustrated in Chapter 7 by Richard Andrew's account of his own studies of information processing and storage in domestic chicks. Surprisingly, the male hormone testosterone makes birds and mammals less distractable. The effect seems to be produced in two ways. Andrew suggests that the androgenic component of testosterone increases the persistence with which motor patterns are performed, while the oestrogenic component increases the time for which the representation of an event is held in working memory. The second, very interesting effect relates perhaps to increased span of attention found in humans with high circulating levels of testosterone. Andrew makes the general point that in science, surprising novel phenomena should be seized eagerly and studied with the best tools available. Further support for this stance is provided by the discovery of asymmetries in brain function of chicks at the behavioural level which Andrew reports and at the neural level which Horn reports in his chapter. No theorist, as far as I am aware, had anticipated these discoveries.

In Chapter 8 Jay Rosenblatt reviews the intensive research which has been conducted on the control of maternal state in rodents and then looks to the ways in which these ideas may be generalised to primates. Thanks in large part to Rosenblatt himself, rapid progress has been made in understanding the hormones and other neuroactive substances that stimulate the onset of maternal behaviour, the neural substrates on which these substances act and the stimulation from the young which maintains maternal behaviour. His own research on rodents is a fine example of working simultaneously at different levels. As in the case of the work described by John Hutchison, Rosenblatt shows how events external to the animal can trigger hormonal changes and modulate the effects of the hormones. Much less is known about primates, but it seems that, unlike rodents, hormones probably do not increase maternal responsiveness in the final stages of pregnancy. By contrast, primates are likely to be similar to rodents in the way that young animals can stimulate and maintain maternal behaviour. This comparison shows the extent to which more general principles of the organisation of behaviour are starting to emerge and where they are limited to a particular taxonomic group.

Clutton-Brock, Rowell and Simpson

Tim Clutton-Brock opens Section IV with a chapter on another aspect of the reproductive behaviour, the mating system. One of the consequences of the great growth of primate studies over the last 20 years has been that detailed knowledge is available now about a great array of species. This allows the comparative approach which Tim Clutton-Brock uses in his chapter. In Chapter 9 he examines the association between sex differences and the maximum number of mates that a male may have at any one time. He points out that the character of the mating system may have ramifying consequences for many other aspects of the biology of the species, partly because the conditions with which the two sexes have to cope are so different in those species in which a male may have many mates and the female only has one. Although Clutton-Brock is concerned first and foremost with functional issues, the extent of sex differences has an important developmental slant. A predisposition to behave in a particular way that differs from the other sex may be amplified or heavily damped by environmental conditions. This is particularly striking when the behaviour of the male depends on such factors as his body condition and the social environment. For instance, the Gelada baboon males may develop to twice the size of the females and defend harems against other males, or they may be the same size as females, look like females and never fight another male (Dunbar, 1984).

In Chapter 10 Thelma Rowell examines the emergence of ideas about social behaviour which have been strongly influenced by thinking on the different levels at which such behaviour may be analysed, namely individual interactions, social relations and social structure. Such work must start from treating animals as individuals, which has not been standard practice in those branches of biology that have been concerned with universals. She points out that a degree of complexity and continuity in the relationships of primates is now accepted in a way that would have been unthinkable thirty years ago. Even so, analysis at the highest level of social structure presents enormous practical difficulties of observation when studying animals in the field and she sees an as yet largely unbridged gap with the lower levels.

In Chapter 11 Michael Simpson argues that one individual may signal to another that it is likely to devote time, aid and resources to another when a variety of possible partners are available and when coordination between individuals is of mutual benefit in biological terms. He suggests that, when a non-human primate directs certain types of behaviour, such as grooming, selectively at a particular individual, such actions are the equivalents of 'promises or declarations of future commitment to a relationship' in humans. An individual signalling in this way benefits when its commitment enhances its value in the eyes of a potentially valuable partner and, thereby, helps to keep that partner. By selecting some human examples to illustrate his views about commitment in social behaviour, Simpson shows how such knowledge projected into other animals can provide valuable insight.

Bowlby, Stevenson-Hinde, Rutter, Dunn and Radke-Yarrow

The section on human behaviour begins with three studies of a specific problem, the long-term effects of the relationship between the mother and her child. John Bowlby saw the great potential of bringing the insights of psychoanalysis together with the concepts and methods of ethology, particularly when examining the lasting influences on social behaviour of the attachment of children to their mothers. In Chapter 12 Bowlby provides a lucid overview of where attachment theory now stands. His perspective on the field which he founded is very welcome. The ethological part of the theory was originally couched in terms of what was then thought to happen in the case of imprinting, namely an instantaneous, irreversible bond formed at a critical stage in development. Views of imprinting have changed a lot since then. The process is thought to be much more flexible and considerable attention is now paid to the additional steps which are involved when early experience leaves an impact on adult behaviour (e.g. ten Cate, 1989). Views of human developments have also changed a great deal.

In Chapter 13 Joan Stevenson-Hinde examines the relations between attachment and temperament. Typically they have been set in opposition, an unfortunate dichotomy reminiscent of other old debates in the study of development, so that temperament is seen as part of nature and attachment as part of nurture and the two sum together. Stevenson-Hinde rejects that approach. She argues that they are much more helpfully seen as separate systems and the child's behaviour represents the dynamic interplay between them. In this respect, her argument is very similar to that of Fentress and mine in earlier chapters.

The question of how the long-term effects on adult behaviour might be produced by the mother–child relationship is considered next. In Chapter 14 Michael Rutter takes a fresh look at the idea of maternal deprivation. In a comprehensive sweep of the modern literature, he examines the way in which the influence might be mediated. The linking processes involve the way children relate to people they encounter later in their development and, as a consequence, particular outcomes are only obtained in particular conditions. Rutter explicitly rejects the likening of this picture with the old one of imprinting in birds and, in my view, he is right to do so. This is not only because developmental concepts have been changing in both fields of research, but also because the nature of the mediating events and the influences on adult behaviour are turning out to be markedly different in the two cases. In birds, the early experience does lead to an internal representation of the familiar object which may control sexual behaviour at a later stage. In humans, Rutter suggests that the breakdown of the mother–child relationship in early life makes institutional rearing of the children more likely. This is often followed by a return in adolescence to a discordant family environment and escape from that to an ill-considered marriage, which then breaks down. In those circumstances, the young mother provides as inadequate a basis for a relationship for her own child as had been provided for her.

In Chapter 15 Judy Dunn examines the contributions to studies of child development that have come from ethological work on animals by Robert Hinde. At the methodological level she values highly the approach of observing directly the mutual influences on each other of children and mothers in their own world. At the conceptual level, she picks up the issue discussed by Rowell in the previous section and focuses on the framework that divides social behaviour into levels. She argues convincingly that no headway will be made in understanding the social development of individual children without an appreciation of the links between their individual characteristics, their relationships and the social norms of the wider group.

In Chapter 16 Marian Radke-Yarrow is concerned with the methods and conceptual apparatus needed in the study of child development. She points

out that the perspective of the child influencing the world in which it develops as well as being affected by it is widely agreed upon by those working on development. However, the ways in which the data are collected have not been well adapted to studying the dynamics of developing relationships. While a mathematical crank can be turned in order to generate a picture of the causality, it is not at all difficult to think of subtle forms of interplay that would readily elude such statistical analysis. The fashioning of methods appropriate to the tasks is crucial. As a remedy she sees the need to characterise and measure carefully the environments in which children develop and the direct measurement of mutual influences. Like many others writing in this book, she emphasises the importance of studying the individual. She points out that, by doing so, access to the points of rapid change is much more likely – always an advantage when trying to understand the processes underlying development (see Hinde & Bateson, 1984). She also emphasises a point that recurs many times in the book, namely the need to draw together in collaboration people who have worked in different disciplines.

Hamburg

Section VI is devoted to a survey of the relations between behavioural knowledge and the problems created by humans' aggression towards other humans which culminates so disastrously in modern warfare. In Chapter 17 David Hamburg starts his analysis by dealing with non-human primates with a view to examining the precursors of human conflict. He emphasises that uncovering the likely course of evolution only provides a part of what is needed to have an understanding of human capacity to adapt to new conditions. Even so, by gaining a picture where humans came from, how they got there and how different present circumstances are from the ones in which the species evolved, the hope is that it may be able to modify the most dangerous aspects of human behaviour. The knowledge of the ways in which non-human primates respond to members of their own social group, as compared with members of other social groups, does give an important insight into human behaviour by pointing to the link between attachment and aggression. Dehumanisation of the adversary plays an important role in justifying violent behaviour that is rarely, if ever, considered against members of one's own group. The next step is to understand the conditions when such behaviour is likely to be expressed so that thought can be given to controlling those conditions. Violent behaviour is particularly likely to come to the fore when individuals perceive a conflict of vital interest between their own group and others, an unacceptable difference in privileges and status, or differences in attitudes that threaten their own self-respect.

Hamburg emphasises that in making progress in a matter that should concern everybody, collaboration between different disciplines is crucial.

Hamburg's emphasis on collaboration draws attention to a third theme that runs throughout the book. The emphasis on different levels and on studying dynamics require more knowledge and expertise than any one person can usually command. The obvious conclusion is that links must be made between different disciplines and specialists have to learn to work with others who speak what seems to be at first mutually incomprehensible scientific languages.

Changes in approach

The contents of this book invite comparison with *Growing Points in Ethology*, a collection of essays edited by Robert Hinde and myself 15 years ago (Bateson & Hinde, 1976). The two books have ten authors in common and both emerge from the same stable. The wits of the time nicknamed rather cruelly the earlier book as 'Groaning Points' or 'Growing Pains' because many chapters made them work harder than they would have liked. *Growing Points* was published just after E. O. Wilson (1975) produced his great book on sociobiology. The appeal of evolutionary theory, in which sociobiology was embedded, was that it seemed to make a complicated subject manageable. However, after 15 years in which concerns for the function and evolution of behaviour have been dominant in studies of animal behaviour, the major practitioners are beginning to appreciate the need for knowledge of the mechanisms (e.g. Clutton-Brock, 1990). In this sense they are rediscovering the wisdom of the founding fathers of ethology who saw the value of keeping both the 'how' and 'why' questions in play at the same time.

In what sense has research on the mechanisms of behaviour pulled the field together? It would be nice to say that a thorough understanding of rules underlying the development and integration of behaviour has been achieved. If that were the case the life of the student wrestling with a formidable literature would be made a great deal easier. The size of this book suggests that such a happy state has not yet been reached – the book might have been a lot thinner if it had! Even so, I think that at the least the questions that must be answered in order to provide a sense of coherence are much more clearly formulated than they were.

Apart from this trend, four differences between the two books stand out – at least to my eye: the growth of neuroethology, a reduction in the space given to functional approaches to behaviour, a new readiness to take subjective insights into human behaviour and apply them along with the objective approaches to animals, and a big increase in the proportion of