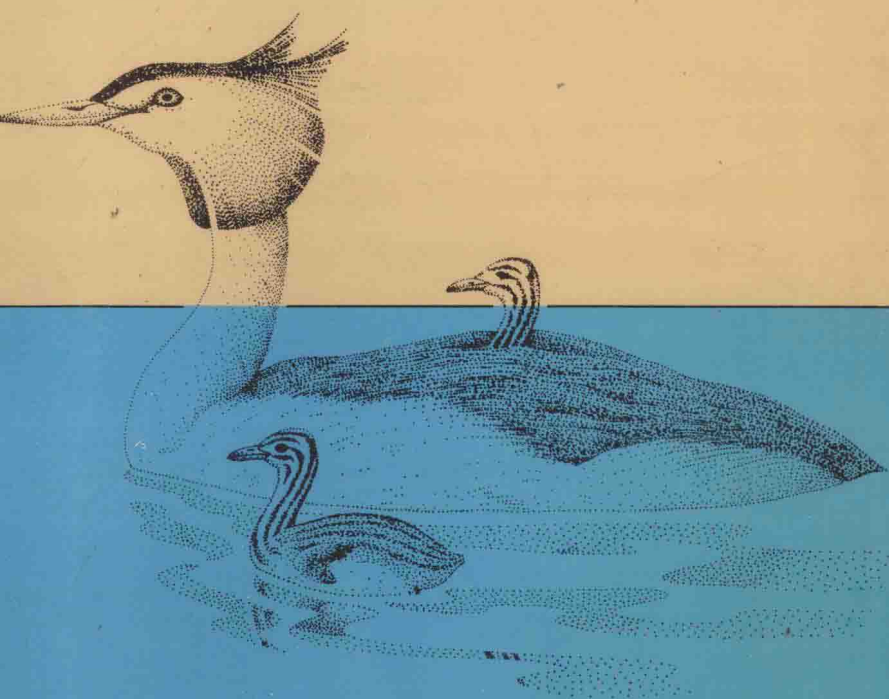


# Animal Behaviour

A Series Edited by T. R. Halliday  
and P. J. B. Slater



3

## Genes, Development and Learning

Blackwell Scientific Publications

ANIMAL BEHAVIOUR · VOLUME 3

# GENES, DEVELOPMENT AND LEARNING

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

BLACKWELL SCIENTIFIC PUBLICATIONS  
OXFORD LONDON EDINBURGH  
BOSTON MELBOURNE

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Blackwell Scientific Publications  
Editorial offices:  
Osney Mead, Oxford OX2 0EL  
8 John Street, London WC1N 2ES  
9 Forrest Road, Edinburgh EH12QH  
52 Beacon Street, Boston,  
Massachusetts 02108, USA  
99 Barry Street, Carlton,  
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First published 1983

Photoset by  
Enset Ltd, Radstock Road,  
Midsomer Norton, Bath, Avon  
Printed and bound in  
Great Britain by  
Butler & Tanner Ltd,  
Frome and London

Distributed in the USA and Canada by  
W.H. Freeman & Co., San Francisco

British Library Cataloguing in  
Publication Data

Genes, Development and Learning.—  
(Animal behaviour; v. 3)

I. Animals, Habits and behavior  
of  
I. Halliday, T.R. II. Slater, P.J.B.  
III. Series  
591.15 QH432

ISBN 0-632-00904-7

ISBN 0-632-00885-7 Pbk

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GENES, DEVELOPMENT AND  
LEARNING

# ANIMAL BEHAVIOUR

A SERIES EDITED BY

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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.

We thank Bob Campbell and Simon Rallison of Blackwell Scientific Publications for their help and encouragement throughout the preparation of these books, Clare Little of Oxford Illustrators for her fine work on the illustrations and, most important of all, our authors for their readiness to accept a well-defined brief, to meet deadlines, and to accept our editorial changes and promptings.

1983

T.R.H.

P.J.B.S.

## ACKNOWLEDGMENTS

Both of the editors and, in most cases, some of the authors of other chapters have commented on each chapter in draft. In addition, the authors of individual chapters would like to thank the following for their comments: Kevin Connolly, Richard Dawkins, Arthur Ewing and Aubrey Manning (Chapter 1); Robert Hinde and Joan Stevenson-Hinde (Chapter 2); Wolfgang Schleidt (Chapter 3); Jerry Hogan and Sara Shettleworth (Chapter 6). Marty Chalfie kindly allowed his unpublished findings to be quoted in Chapter 1.



# CONTENTS

Series Introduction	vii
Acknowledgments	ix
Introduction	1
1 Genetics and Behaviour	11
LINDA PARTRIDGE <i>Department of Zoology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT</i>	
2 Genes, Environment and the Development of Behaviour	52
PATRICK BATESON <i>Sub-Department of Animal Behaviour, University of Cambridge, High Street, Madingley, Cambridge CB3 8AA</i>	
3 The Development of Individual Behaviour	82
P. J. B. SLATER <i>Ethology &amp; Neurophysiology Group, School of Biology, University of Sussex, Brighton BN1 9QG</i>	
4 The Development of Social Relationships	114
NEIL CHALMERS <i>Department of Biology, The Open University, Walton Hall, Milton Keynes MK7 6AA</i>	
5 General Principles of Learning	149
N. J. MACKINTOSH <i>Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB</i>	
6 Learning as a Biological Phenomenon	178
T. J. ROPER <i>Ethology &amp; Neurophysiology Group, School of Biology, University of Sussex, Brighton BN1 9QG</i>	
References	213
Index	239

## INTRODUCTION

What influences shape behaviour during the lifetime of the individual animal? Of all the questions that can be asked about animal behaviour, those concerned with development have traditionally been the most contentious, partly because of differences in the emphasis of those looking at behaviour from different viewpoints. Ethologists, and especially those who worked on 'lower' animals, were impressed by the fixity of the behaviour that they studied, and by its remarkable adaptiveness. Trained as biologists, they appreciated that natural selection was responsible for this precision, and they tended to stress the genetic determinants of behaviour. 'Innate' behaviour was seen as arising fully formed the first time the animal required it and, at an extreme, development was sometimes seen as a subject for embryologists, of little relevance to behaviour (e.g. Lorenz 1965).

Diametrically opposed to this viewpoint was that of many psychologists, particularly those of the behaviorist school in America. They were interested in learning and intelligence, and in general laws which, though elucidated by work on animals, might be applicable to the study of humans. Their stress was thus on flexibility not fixity and on environmental not genetic determinants. To take an extreme view, J.B. Watson, the founding father of behaviorism, once wrote:

'Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in, and I'll guarantee to take any one at random and train him to become any type of specialist I might select—doctor, lawyer, artist, merchant-chief and yes, even beggar-man and thief, regardless of his talents, penchants, tendencies, abilities, vocation and race of his ancestors.' (Watson 1930).

This was a strong claim, and Watson knew he was overstating his case, but he did so as an antidote to the fervour of those who believed that genes or 'breeding' were what really counted.

As must always happen with opposing viewpoints as extreme as these, it was just a matter of time before confrontation occurred,

and this was followed by inevitable compromise. Confrontation came when a number of North American psychologists, notably Hebb, Lehrman and Schneirla, wrote criticisms of the emphasis placed by ethology, then largely a European science, on innate behaviour. Hebb (1953) had little sympathy for either extreme. He pointed out that to ask the extent to which a behaviour pattern was hereditary and the extent to which it was environmentally determined was:

'... exactly like asking how much of the area of a field is due to its length, and how much to its width. The only reasonable answer is that the two proportions are one-hundred-per-cent environment, one-hundred-per-cent heredity. They are not additive; any bit of behaviour whatever is *fully* dependent on each.'

Such criticisms were well taken by most ethologists, and the more extreme forms of environmentalism also became less common amongst psychologists. A final round was fought between Lorenz (1965) and Lehrman (1970) but, by then, the whole dispute seemed to have tired itself out. The convention was to believe in a close and continuing interaction between genes and environment during the course of development. Ethologists had come to accept that environmental influences, including learning, might have a profound impact on the development of fixed and species-typical behaviour; for their part, psychologists came to appreciate the powerful way in which natural selection could lead to constraints on learning, making some animal species more capable of particular tasks than are others. The important task for both was to determine exactly *how* genes and environment interact with each other during the course of an animal's development.

Can one simply say, then, that the learning-instinct controversy is dead and that one need worry no more about it? Unfortunately this is far from being the case: the issues involved have a nasty habit of popping up elsewhere as soon as one thinks they are demolished, like the figures in a fairground shooting booth. It is certainly not a trivial matter; in everyday life the stress that people place on genes as opposed to environment in explaining their own behaviour and that of others has an immense impact on their attitude to life and to one another and is a major determinant of where they stand on the political spectrum. Amongst those whose writings may influence people, an extreme position on

this issue, especially one which favours genetic determinism, may be positively harmful. Two recent examples illustrate this. One is the race and intelligence controversy, fired especially by an article by Jensen (1969) in which he argued that North American whites were intrinsically more intelligent than blacks. This was bound to be an unpopular viewpoint in that greatest of all environmentalist nations, but it was also logically unsound. Quite apart from the problems of measuring intelligence and the fact that tests devised to do so are likely to be more easily carried out by people of some cultural backgrounds than those of others, there is the problem of what is meant by heritability, this being the measure of inheritance used. It is not a measure of how much genes and environment each affect behaviour. As Hebb pointed out, that is a meaningless question. It is a measure of how much the *variance* in behaviour is attributable to each, originally devised for the selective breeding of plants; only where a good deal of the variance in a character was genetic could such selection be successful. The heritability measure is discussed further by Bateson in Chapter 2. Suffice it to point out here that the measure is as much affected by environmental differences as by genetic ones: heritability of a trait in one environment may be quite different from that in another.

The second example concerns sociobiology, that field of study on the border between ethology, ecology and evolution devoted especially to functional and evolutionary questions. Being concerned with the evolution of adaptive behaviour, and because natural selection can only work on genetic differences, this field is bound to stress the heritability of the behaviour patterns with which it is concerned. In some cases this point has, however, been overstressed in very much the same way as genetic influences on intelligence have been. This is curious, for while heritability may vary within wide limits, it is hard to conceive of any trait in which it would be negligible and which would not therefore be susceptible to change through natural selection. This, rather than strong genetic determination, is all that is needed for evolution to take place. Adaptiveness does not require behaviour to be genetically fixed. Yet E.O. Wilson, the leading figure in sociobiology, repeatedly stresses genetic determination as if behaviour was fixed and inflexible. To take an extreme example:

'Are human beings innately aggressive? This is a favourite question of college seminars and cocktail party conver-

sations, and one that raises emotion in political ideologues of all stripes. The answer to it is yes.' (Wilson 1978).

With such naive misunderstandings around, it is no wonder that others go to the opposite extreme and that those who study development sometimes despair! In this book, however, we are not grinding a genetic nor an environmental axe but trying, in a series of essays, to give something of the flavour of the field of behaviour development today. It is a field of immense importance, as we hope to have indicated in this introduction, both for our understanding of animal behaviour and how it comes to be as it is and also, more broadly, for various philosophical and political issues. Each of the six chapters is written by a different person. Although the last two chapters, those on learning, are the only ones written by trained psychologists, the impact of the recent dialogue between ethology and psychology will be apparent throughout. The assiduous reader will certainly find some points where chapters disagree, or where emphasis is different. This is inevitable in an active and fast-moving field, and we have left some overlap in coverage between chapters to allow such differences in perspective to persist. However, we trust that no reader will detect polemic. The emphasis is on an integrated and wide-ranging approach which will serve as both an introduction to, and a progress report on, what is one of the most exciting fields of behavioural research.

In the first chapter, Partridge describes recent developments in the genetics of behaviour. In the past, behaviour genetic analysis used often to consist of selection experiments to determine whether variance in a particular behaviour pattern had a genetic basis, and of a rather general comparison between animals known to be genetically different to see how their behaviour differed. But selection experiments nearly always work; as we pointed out above, it is hard to conceive of any behaviour pattern uninfluenced by varying genetic factors. Thus, these selection experiments were able to show, amongst other things, that the ability of rats to master mazes could be markedly raised or lowered by a few generations of selective breeding (e.g. Tryon 1940). Attempts to look at differences between genetically distinct animals came up against the problem that the relationship between genes and behaviour patterns is an exceedingly complex one, with each gene affecting many characteristics and each characteristic being

influenced by many genes. Recently, however, as Partridge points out, new techniques have made possible more detailed study of how genes influence development. Two especially exciting examples that she discusses are the way in which it has become possible to study the precise effects of single-gene mutations on the simple nervous system of roundworms, and the use of mosaic individuals in fruit flies to pinpoint the structures responsible for the abnormal behaviour of mutants. Studies such as these, though often involving rather gross changes in the nervous system and behaviour patterns which are highly abnormal, are beginning to give an idea of the exact ways in which genes affect development.

Partridge also discusses the extent to which genes may be thought of as controlling development, but comes down firmly against attributing control to any particular one of the sources of information that affect the growing animal. She does not share Bateson's enthusiasm, expressed in Chapter 2, for culinary analogies and, as a result, the reader must choose whether or not to agree that development is like the baking of a cake. Suffice it to say here that no analogy should be taken too far, as both authors would, of course, agree. Waddington (1935) likened development to the Whitemoor marshalling yard of the London and North Eastern Railway, where trucks were rolled downhill through a series of points, the position of each of these progressively restricting the siding, or end-point, that they would reach. In some ways this was a good analogy with the narrowing of possibilities that accompanies ontogeny, with changes tending to occur at particular stages or sensitive periods. But, of course, as Bateson's discussion will make clear, the idea of tracks with no possibility of later transfer between them is altogether too limiting when we consider behavioural development. The cake analogy also breaks down if looked at in detail, but it neatly expresses the idea that the finished product in development is utterly dependent on a number of quite distinct factors whose contribution cannot be simply teased apart.

In Chapter 2, then, Bateson describes current views on how genes and environment interact to give behaviour. He shows just how far ethologists have progressed since the days when behaviour was thought to be either learnt or innate. But he also demonstrates that we have moved on from the opposite extreme, in many ways equally naive, that everything interacts with every-

thing else in the course of development. There *are* rules which affect development (the existence of sensitive periods provides a striking example) and, indeed, development is to some degree regulated, so that some sudden gust cannot blow it permanently off course. Just what constraints there are on the outcome is a fascinating problem, and one with which the remaining chapters are all, to a greater or lesser extent, concerned.

Chapters 3 and 4 both consider the trajectories taken by growing animals: just what factors do affect the ways in which behaviour develops? Slater examines behaviour at the individual level and, in particular, whether or not experience of the situation to which it is adapted has a role in shaping it. In an unpredictable world, specific environmental inputs can help to gear the animal to the exact situation in which it finds itself. The development of the vertebrate visual system provides an example here, the genetic constraints on which were earlier discussed by Partridge. At the opposite extreme are behaviour patterns, of which anti-predator responses are the most obvious, which must be right the first time they are called upon. Experience of one sort or another can certainly affect their development, but it cannot be experience of encountering a hungry predator because that may have a lethal outcome. As in any discussion of behavioural development, bird song provides a key example of how genes and environment interact. It is referred to in several chapters but discussed in most detail by Slater. Although the learning of song from others is widespread, there are strong differences in strategy between species when one looks more closely; why this should be so is still a matter for speculation.

The way in which individual animals come to eat the right food, to avoid being eaten themselves or to sing an appropriate song is a complicated enough matter, but the development of relationships between animals is a good deal more so. Here it is not just how an animal adapts its behaviour to a largely indifferent environment, but how it modifies what it does in the light of the behaviour shown by others which may in turn be changing what they do in response to it. The development of relationships between animals is the subject covered by Chalmers in Chapter 4. The classic example here is that of imprinting, originally described as the process whereby young birds become attached to their mothers and may subsequently seek to mate with individuals which look

like her. Recent research suggests, however, that one should differentiate between filial imprinting, involving the attachment to the mother, and sexual imprinting, which affects the choice of mate. The latter tends to take place rather later and to be affected by the young bird's experience of others as well as of the mother. Chalmers discusses imprinting in some detail, building on some of the points outlined by Bateson in Chapter 2.

The relationship between a young bird and its mother is a relatively simple case compared with those found in the social groups of many mammals. Here it is not simply a matter of the young animal following and maintaining contact with a single individual, but the infant must form relationships of different sorts with many individuals, and these may change as it grows older. Where two active participants are involved, it is not easy to work out who is responsible for changes which take place but, as Chalmers describes, there has been tremendous progress in this area, especially with experimental work on primates. This is an important topic, for mother-infant relationships in primates have similarities to those in humans and may help us to understand the reasons why these sometimes go awry.

The final two chapters are concerned with learning, a range of processes which have an important part to play in development and which continue, later in life, to enable adult animals to adapt their behaviour to changes in their surroundings. Mackintosh considers the great variety of different phenomena that we call learning. Some, such as sensitisation and habituation, are relatively simple and are found throughout the animal kingdom. Others, such as the more complex forms of associative learning that have been studied in detail in the laboratory by learning theorists, have been mainly described in higher animals. As Mackintosh points out, learning is certainly not a unitary phenomenon and it is, indeed, rather difficult to provide a definition of it which is unexceptionable. His chapter considers just what learning is and what forms it may take. While stressing diversity, he is at pains to point out that similar processes may be going on in a wide variety of different situations. One should not therefore throw up one's hands in horror at all attempts to generalise as, perhaps we might add, ethologists have recently been rather prone to do.

In the final chapter, Roper takes a lead from pointers Mackin-



tosh provides to consider the biological importance of associative learning in greater depth and to make links between psychological and ethological work on learning. How has recent research, and especially that dealing with constraints on learning, left the extremely broad generalisations about learning that psychologists used to be so fond of making? Roper identifies two such generalisations: the principle of equipotentiality, which suggests that any animal should be able to learn anything within the limits of its sensory and motor equipment, and general process theory, suggesting that associative learning follows the same laws in all species. From this rather different perspective he approaches topics described in earlier chapters, such as imprinting and song learning, and asks what light the study of them has shed on learning and the psychologist's view of it. It is clear that learning must now be regarded as an adaptive phenomenon, a product of natural selection like any other attribute of an animal, and that, as such, broad generalisations about it can only be true in the loosest way. That this is so is perhaps most clearly illustrated by the changed view of learning that had to follow the discovery of learnt food aversion in rats. An animal which becomes ill several hours after eating a type of food will avoid eating it again: eating and illness are associated, but the time interval between them is far in excess of the close temporal proximity previously thought to be essential if learning was to take place. Examples such as this suggest that learning is best viewed as a collection of specialised abilities rather than as a single general process. Similarly the ethological literature is replete with examples to illustrate how far short the principle of equipotentiality falls as a general description of the abilities of animals.

One of the messages of this book is that the process of development is not as simple as it once seemed. The broad generalisations of early ethologists, and the different range of ones which psychologists put forward, were attractive and easy to grasp. But they were born out of ignorance at a time when few species had been studied in any detail. Some of these early ideas did, however, play a useful role as working hypotheses. Now that a substantial body of research has been conducted on behavioural development we have the information to see just where they fall short and we are able to replace them with more considered and firmly founded accounts of how development takes place. There is