THE LIFE OF MAMMALS

BY

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PREFACE

WHEN presenting any subject it has to be decided whether to accept a conventional method, known and widely accepted, or to try to invent a better one. The latter is the more exciting course, but a compromise is safer for the author and kinder to his readers, who want to learn the subject as it is. This book attempts to have the best of both methods. It presents mammalian anatomy, physiology, histology, and embryology as they are, and at the same time tries to show what in the future they may be. It begins with a discussion of biological method, which may seem to be a strange and difficult subject to the scientist, who is apt to leave these matters to philosophers. I recommend even the beginner to read it before he passes to the detailed work of the rest of the book. It may show him how many parts of the subject are imperfect and how they can be illuminated by use of a new language that considers the body as a self-controlling machine. This idea is not new but in developing it I have been pleased to find how interesting it makes the consideration of the structure and function of many parts of the body. I have not been able to apply the methods of information theory fully or exactly, but I hope that others may come to do so and to find in the study of control the clue that unifies many parts of Biology.

As one tries to treat the whole organization of life in this way it seems that a new science is growing with every word. This is very exciting, but the average student of biology or medicine cannot wait for a new science to be born. He must learn now, and the book attempts to give an orthodox presentation that will be acceptable by the most conventional, while yet showing how new approaches can be incorporated.

The book is meant to be used as a systematic aid to the student of mammals and man who has already some general familiarity with biology. It should serve as a companion to a course of practical study of dissection and of histology and embryology. Drawings of dissections and sections are included with the hope that they will be found useful in the laboratory. The book was first drafted some years ago when I was writing the *Life of Vertebrates* and in a sense it forms part of that work. But it became clear that a Life of Mammals of somewhat different scope might be useful not only to zoologists beginning their course but to others as well.

Most students first learn about mammals through dissecting the rabbit or the rat and the book therefore gives special attention to these species. For the medical student these mammals are an introduction to the study of man and I have tried to present their biology in a way that will be useful for this purpose. In particular the sections on the skeletal and muscular systems and on neurology are meant to provide an introduction to those subjects as they are treated by human anatomists and physiologists. Too often the zoologist who trains future medical students is unfamiliar with the methods and terminology that his pupils will meet later. One aim of this book is to bridge the gaps between the basic and the medical aspects of biology. Unfortunately the book ignores altogether many aspects of mammalian life that many would wish to study, for example ecology. It provides only a framework or scheme for the study of mammalian life, within which much else could be incorporated.

It is impossible for any work of this sort to be authoritative and original as well as comprehensive. I have tried to cover the ground but have had no hesitation in lingering longer in the fields that have interested me especially. I doubt whether anyone suffers by learning from a book in which he can discern the personality, interests, and foibles of the author. Perhaps some of the complaints about the aridity of science come from the attempt to produce giant comprehensive textbooks written by collections of depersonalized authors. One of the chief lessons for any intending scientist is that the facts that he is told may be wrong and that points of view differ and change. This is no excuse for making mistakes, as I have no doubt often done; but let a critic realize that the anxiety involved in uttering such a work is formidable. References appropriate to each chapter are given at the end of the book. Recent references have generally been preferred and this has meant omitting classical ones. A contemporary survey, even if of little originality or critical worth, is often the most useful reference from which to work backwards through the literature.

Any system of arrangement of so vast a subject-matter will seem to be in some way illogical. The plan adopted assumes that the student will first dissect the parts of the mammalian body and learn the microscopic appearance of the tissues at the same time. Having dealt with the skeletal and vascular systems he will study the individual organs, and last the nervous system, receptor organs, and endocrines. During this work he will often want to know about development, but in practice the study of embryology is distinct and is here treated separately at the end.

In due time we shall learn how to combine macroscopic and microscopic studies with those of biochemistry and biophysics. All that I have been able to do here is to issue reminders that there is a connexion and to suggest possible means of unification.

Preparation of such a treatise involves collaboration by many people. I should like to thank most warmly all those who have given help, directly or indirectly. Many have read sections dealing with their own specialities and are mentioned separately below. Others have allowed their illustrations to be copied or have provided the material for new pictures. The figures have been drawn from life or redrawn from other figures by Miss E. R. Turlington and Miss J. I. D. de Vere. Their faculties of observation, care, and skill have been disciplined continually by a consideration of the needs of the user. The production of such representations is an integral part of the work of biology, for which we cannot be too grateful. Mr. J. P. Stanier and Dr. E. G. Gray have helped with innumerable tasks of editing, assembling of figures, and of bibliography. Finally, it is a pleasure to record my thanks to the Secretary and Staff of the Clarendon Press for their skilful and willing collaboration in the preparation of the book.

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I

THE CONTROL OF LIVING SYSTEMS

1. The methods of biology

IT is easy to say that the purpose of any biological inquiry is to study the life of the organisms concerned, but this implies that we must begin by discussing what we mean by 'life' and by examining the methods that are available for investigating it. In an earlier time it would have been enough to say that this book about the life of mammals is an account of the structure, function, and development of the mammalian body; but a description like this in terms of the old and apparently obvious sciences of anatomy and physiology is no longer adequate. In order to make full use of recent advances we must inquire more closely into what is involved in the use of such terms as 'structure' and 'function'.

2. The development of the language of biology

No investigation of this sort can begin without making decisions about the terminology that is to be used, and this introduces questions that are usually dealt with by logicians and philosophers. It is not satisfactory for anyone to say that being a scientist he is not interested in such matters; if he does not discuss them the result will be that he proceeds to use uncritically the words he has learned. Adequate representation by one person to another about any subject-matter depends upon agreement about the use of symbols.

For our present purpose we have to make a brief study of the words that are used for the description of living activities. Words have many functions and it would be impossible here to give a proper account even of the sorts of words that are commonly used by biologists. Nevertheless some consideration of the problem helps to show the significance of recent changes in biological terminology and allows us to reorganize our knowledge more satisfactorily.

Animals may be said to remain alive by taking action that foreshadows or predicts the probable course of events (p. 18). They can do this because the body, and especially the brain, contains a record of past sequences and associations. Use is made of this record by comparing each new situation with it so that, if the comparison is sound,

an accurate forecast results. As each individual life proceeds an increasing store of 'knowledge' about probable sequences of events is built up and this is drawn upon in each new situation, so that actions that ensure survival can be made in circumstances that resemble those of the past.

In man the individual is able to improve his store of knowledge by drawing upon the experience of others, and one of the functions of words is to ensure this transmission of information. One individual can tell another about the probable outcome of a situation by showing him that it is like some other one that is already familiar to the receiver.

The process of description thus consists in one person adding his experience to that of another. A basic problem for any developing science, therefore, is to decide what comparisons are likely to prove effective for conveying information about the subject-matter.

Certain principles controlling the efficiency of such communication can be recognized. The effectiveness of comparison of a new situation with a given object or process depends upon the familiarity of the recipient with that object. If I say that an animal or a river is raging or acting fiercely this conveys to the listener much about the probability of its future behaviour, because he has studied fierceness in human behaviour and is able to forecast what a fierce system will do. The accuracy of his forecasts will also depend, however, upon the adequacy of the comparison. He may, for example, be led to act as if it was more complete than it is, as if he tries to placate the fierceness of the weather with an offering that would appease a man. Effective description, therefore, requires to be made by comparisons that are understood by all people and yet are exact, including neither too much nor too little.

Fully effective comparisons have hitherto only been available for some of the simpler phenomena of the physical world but they present an ideal to which biological science can strive. In trying to provide a system that enables others to learn how living organisms behave we need to use terms that relate to a wide range of human experience and yet are adequate to describe all the many complexities of living systems. This is not an easy task. The language of the physical sciences is exact and general and biology uses it where possible, but where physical language is not able to describe some aspect of living other words may have to be called in. Some scientists would say that unless the language of physical science can be used by biology no progress can be made. Apart from the compromise with honesty that would be involved in leaving out many of the observations, biologists who have to make practical application of their science clearly cannot adopt this view. A

doctor cannot neglect to treat a diseased brain because language for speaking about that organ is inexact.

A more profitable approach is to consider so far as we are able the types of comparison that have been made in the description of aspects of living, in order to discover the principles of the growth of biological language. Then we can apply these principles in the attempt to make further improvements in methods of description. Anyone who does not find new words such as those adopted in this book to his taste can of course suggest others that he thinks will describe the phenomena more fully. Criticism of the use of the new categories here suggested, such as 'information' and 'representation', is only justified if others are provided that will cover the same data.

The history of the origin of language is obscure and will perhaps never be discovered. Many animals produce signs or sounds that 'release' particular patterns of sexual or avoidance behaviour in others. Communication about events in the world around presumably depended at first on the transmitter's producing behaviour that in some way represented an external situation and elicited in the recipient behaviour appropriate to those events. A parallel can be seen in the 'language' of bees, where the 'dance' of a worker returning to the hive is so related to the direction of the honey found that other bees, following the dance, move off in the right direction (v. Frisch; Haldane, and Spurway, 1954). We do not know how signs and sounds were first used by men to indicate external situations. Onomatapoeic sounds and gestures with the hands and face still serve to make representations in this way, arousing appropriate responses in the receiver. But it is a long way from those signs to communication by our elaborate set of symbols.

It is impossible to discuss here the whole question of the development of language. We cannot even hope to follow adequately the complicated question of the evolution of biological terminology. Johannesen (1950) has shown that in languages as distinct as Arabic and Old Indo-European there are certain common features in the terms used for parts of the body. Thus in such languages many of the words for the head refer either to the direction upwards, or to the curve of the vault of the cranium, or to the act of slaughter for butchery, or augury. The fact that so much of early language centres around terms of direction had led Paget and Johannesen to the theory that the basic activity involved is gesturing with the tongue and hands. Today, even in arguments about complicated mathematical matters, a speaker will often use his hands in the attempt to arouse an appropriate response in the brains of the listeners.

The point for our present discussion is to recognize that communication about some object or situation new to the receiver involves the making of comparison with one that is familiar. We see many examples in anatomy of comparisons that are made to call attention to the shape of organisms or their parts. These comparisons are not necessarily of much relevance to the study of the whole life of the organism concerned. For example, many anatomical terms indicate comparison with familiar objects of everyday life—the neopallium (new cloak) of the brain or the navicular (boatlike) bone of the foot.

3. Person language

A very powerful means for describing any system is to compare it with the face and its gestures, that is to say with a chief part of the human communication system itself. Every child learns in its early life the significance and names of the expressions of the face and the words that go with these. To react correctly to these expressions is the first essential of social life, to which the child is bound in order to obtain the means of subsistence. All normal human beings therefore can react appropriately when they hear, for example, that a fire or an animal is acting gently. This comparison with human features and human behaviour is the basis of a whole system of language in which the behaviour of entities is described by speaking as if they contain agents that act like human beings. We may call such a system *person language* and it has given rise to the most elaborate structures of animism and religion. It has been used extensively in biology, for example in the medicine of the Middle Ages, which attributed humours and spirits to each organ, speaking as if each contained a resident creature with properties resembling those of a person.

Such language has considerable descriptive power but it lacks generality. We can describe a disturbed condition of the liver as due to excess of its depressing humour but this tells us little or nothing further about this humour or its relationship to others except that they all produce actions that are in some way like those of whole men. As a system of biology, therefore, the method is circular (tautologous); it describes actions of the parts only in terms of those of the whole.

4. Language and tools

The language of science has been developed by making comparisons of events not only with human beings but with other aspects of nature and in particular with the tools that man has evolved. It is obvious that the most powerful and widely understood descriptive language in

any generation will consist of words that refer to the means by which men at that time get their living. These will be the words that produce in others the most effective reactions. At a time when systems for ensuring co-operation between men were even less perfect than they are now, person language, based on attention to the human face and communication, held greater power than any other. Now that we operate by the use of a variety of tools and machines it is by reference to these, as well as to human co-operation, that the greatest effect can be achieved.

5. Tool language in biology

The development of the terminology of biology in the modern period has therefore involved the gradual introduction of methods of representation and description of living things in terms of tools and machines, rather than by comparison with human beings. At the same time the new tools themselves have been used for the investigation of living bodies, revealing aspects of them that were completely hidden to the unaided senses. We cannot now trace this history in detail but endless examples come to mind. After the taming of fire and understanding of its properties the actions of parts of the body came to be described in terms of inner fires. When cooking had developed the organs were said to produce various concoctions (Lat. *coquere*, to cook). With the development of windmills and clocks the body was likened to a machine, built with a certain 'structure' and with parts having 'functions'. When chemistry developed, men recognized the presence of elements and compounds in the body and applied chemical techniques to find out more about them. The discovery of electricity and of electrical machines led to analysis of the electrical properties of the body. Finally we shall have much to say about the effect upon biological description of the invention of machines that control themselves, performing calculations and storing information in their memory systems.

The process of development of tools and language for them is obviously a complicated one, which cannot be adequately described in a few sentences. Human populations seem to produce continual cycles of inventions. Tools are framed in order to imitate some function previously performed by the body. Familiarity with these tools leads to description of actions of the body in terms of some of them, and application of the tools themselves to biological study then produces further discoveries about the living organism. More elaborate tools are devised to imitate the newly discovered actions and the cycle repeats.

As our language and tools have evolved they have produced continually more perfect ways of forecasting the general course and the details of the future and providing means to meet it. It is characteristic of science that it has learned to extract certain general rules that apply to all phenomena and enable very exact forecasts to be made. Alchemists acquired a wide knowledge of the special properties of materials, but their general comparisons and theories were defective and of little power compared to the generalizations of modern chemistry, such as the laws of mass action and the periodic system.

Biology today has a great mass of information about particulars, but it is still provided with few generalizations that have power to forecast the characteristics of the behaviour of all living material. In the attempt to see how such generality may be achieved we may look briefly at some aspects of the history of biology in the recent past. Even a superficial study may show us how we can build upon existing knowledge and organize it around general principles. Inevitably our view will be limited by the terminology at present available. Study of the history of the subject should at least show that terms are valid only in their own day and context, and that this validity can be measured only by their effectiveness in forecasting—ultimately by whether the terms enable the race that uses them to make predictions by which it survives.

6. Naturalists' language

One very good way to study the life of any type of organism is to watch the behaviour of the creatures, to describe what they do under various circumstances. This is essentially the method used by naturalists and psychologists, and it is certainly useful in providing forecasts. If you have watched a rabbit warren or a household carefully you will be able to say rather exactly what the inhabitants are likely to do. Yet to restrict biology in this way to natural history and the observation of whole animals would be to ignore the method of analysis that has been developed by science during the past three or four hundred years. Some tremendous generalizations have been discovered by naturalists, notably the fact of evolution, but in recent times most of the advances in biology have been achieved by examining the many parts into which organisms can be divided and comparing the actions of these parts with those performed by man-made tools. The development of the subject has depended upon the application of new technical methods for revealing these parts and of new verbal methods for describing them. This method of analysis of what goes on inside