ANIMAL BEHAVIOUR

Ecology and Evolution

C. J. Barnard

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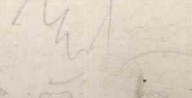

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To Siân, my Parents
and Ken and Pegi

PREFACE

The study of animal behaviour, particularly from evolutionary and ecological viewpoints, has been one of the major growing points in biology over the last 10 to 15 years. The degree of quantitative rigour in theoretical, observational and experimental approaches to behaviour has increased dramatically. As more of the rapidly growing research literature becomes a basic requirement for students reading animal behaviour at undergraduate level, there is a need for a readily comprehensible text, covering all major aspects of behaviour study, to accompany their courses. This book, based on my first, second and third year undergraduate lectures at the University of Nottingham, is designed to meet that requirement.

The book begins with a discussion of the physiological and anatomical bases of behaviour: the relationship between nervous system structure and function and behaviour; hormonal effects on behaviour; biological clocks; perceptual mechanisms; and stimulus filtering. This leads to a consideration in Chapter 2 of how the animal integrates internal and external stimuli in making decisions about its behaviour and the way natural selection has shaped decision-making processes and the organisation of motivation. The first two chapters therefore deal with the instigation or causation of behaviour within the animal.

Chapters 3 and 4 deal with developmental aspects of behaviour. Chapter 3 discusses behaviour genetics, including the relationship between specific genes and behaviour, the heritability of behaviour patterns, the site of gene action in the body and the evolutionary consequences of a genetic basis to behaviour. This is followed by an examination of the role of experience and learning and the interaction of genetic and environmental factors in ontogeny.

In Chapters 5 to 10, the book moves on to examine how an animal's decisions are modified by its ecology. Once the animal has decided to feed, for instance, an enormous number of environmental variables, such as the distribution, abundance and quality of different prey types, climatic factors, competition and the risk of predation influence the way it must organise its feeding behaviour. Models, experiments and observations concerning the ecology of habitat choice, migration, foraging behaviour, predator avoidance, reproduction, social behaviour and communication are discussed in detail with emphasis placed on the rationale behind theoretical predictions and the testing of these predictions in the field and laboratory. Throughout, an attempt has been made to put ideas and results across in simple, readily comprehensible language and to avoid couching them in their less accessible mathematical format. Nevertheless, interested students are encouraged to follow up particular points in their original form in the literature.

The book concludes with a discussion in Chapter 11 of some key evolutionary concepts mentioned in previous chapters: coevolution, arms races, levels of selection and evolutionarily stable strategies (ESSs). The last two are discussed in detail because there is still a good deal of confusion about them in the research literature; it is particularly important in an undergraduate textbook, therefore, to make their meaning clear. All chapters close with an enumerated summary to reinforce their important points.

A number of people have very kindly helped in the preparation of the book over the past twelve months by reading and criticising one or more of the chapters. I am particularly indebted to Patrick Green, David Parkin, Geoff Parker, Richard Cowie, John Lazarus, Ian Duce, Hilary Stephens and Des Thompson, and to Geoff Parker, Peter Davies and Colin Galbraith for permission to reproduce their excellent photographs. I should also like to take this opportunity to express a much longer-standing debt of gratitude to Rex Knight, Professor A.J. Cain, Dr R.G. Pearson, Geoff Parker and John Krebs, all of whom at one time or another, through discussion or advice, have enormously stimulated my interest in the study of evolution and behaviour. I am grateful to Marlies Rivers, Dawn Thompson, Katherine Lyon and Wendy Lister for typing the manuscript and to Tim Hardwick of Croom Helm Ltd for suggesting the book in the first place and for advice and encouragement during its production. Finally, my very special thanks go to my wife Siân for her immeasurable support and assistance as always and to my daughters Anna and Lucy for patience with an absentee father.

1 PHYSIOLOGICAL MECHANISMS AND BEHAVIOUR

Behaviour is the tool with which an animal uses its environment. Through behaviour the animal manoeuvres itself in an organised and directed way and manipulates objects in the environment to suit its requirements. In order to behave, the animal must act as an integrated and co-ordinated unit. It must juggle a bewildering array of stimuli from inside its body and from the external environment and organise the information into a series of commands to its muscles. In Chapter 2 we shall examine this process of integration and see how internal and external stimuli from the environment are translated by the animal into behaviour. Before we can do that, however, we need to know something about the sources and processing of information in the animal's body. Animals have evolved complex systems of cells and chemicals whose task it is to detect, transmit, integrate and store environmentally supplied information for later use in making decisions. They consist of (a) various types of sensory cell which pick up different changes in the environment, (b) a more or less complex system of nerve cells which transmits and integrates information from sensory receptors, (c) chemical messengers which transmit information on a more leisurely time scale than the nervous system and (d) muscle cells which transform information from the nervous system into actions. In this chapter, we shall examine these components to see how they interact to produce behaviour.

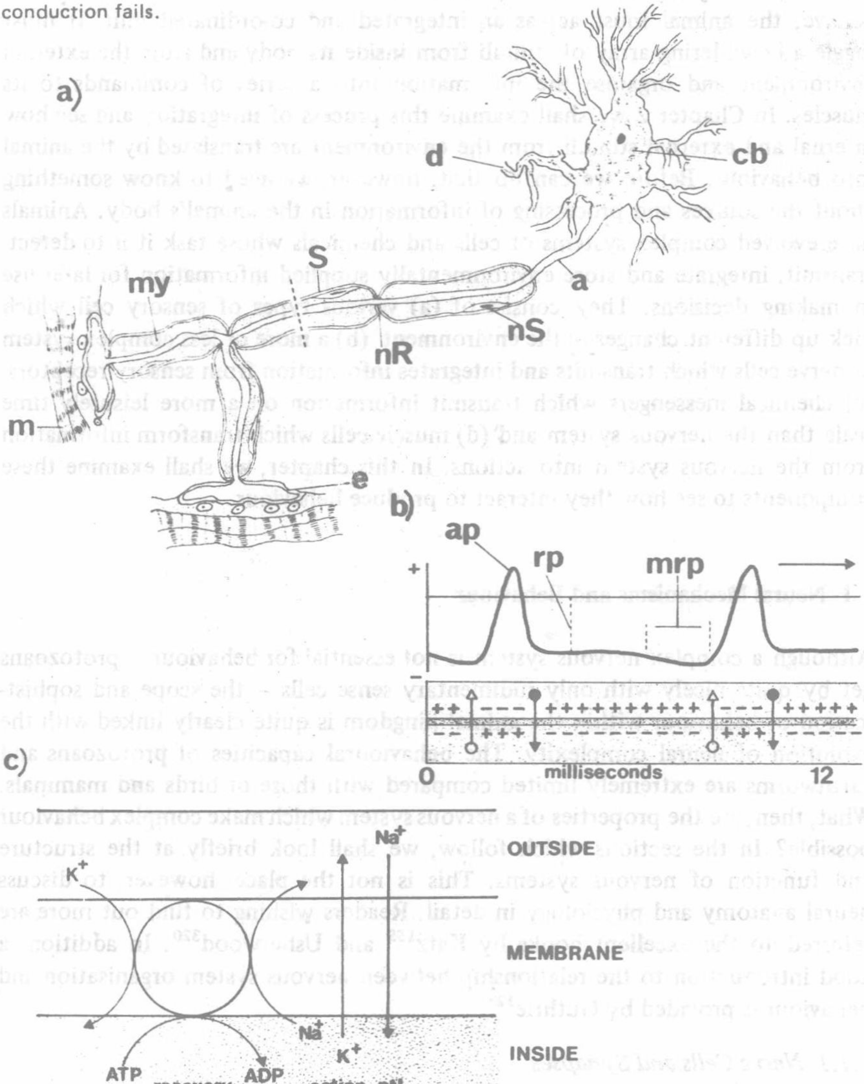
1.1 Neural Mechanisms and Behaviour

Although a complex nervous system is not essential for behaviour – protozoans get by quite nicely with only rudimentary sense cells – the scope and sophistication of behaviour within the animal kingdom is quite clearly linked with the evolution of neural complexity. The behavioural capacities of protozoans and earthworms are extremely limited compared with those of birds and mammals. What, then, are the properties of a nervous system which make complex behaviour possible? In the sections which follow, we shall look briefly at the structure and function of nervous systems. This is not the place, however, to discuss neural anatomy and physiology in detail. Readers wishing to find out more are referred to the excellent books by Katz[155] and Usherwood[320]. In addition, a good introduction to the relationship between nervous system organisation and behaviour is provided by Guthrie[123].

1.1.1 Nerve Cells and Synapses

Nerve Cell Structure. True nervous systems are only found in multicellular animals. Here they form a tissue of discrete, self-contained nerve cells or *neurons*.

Figure 1.1 (a) A Motor Neuron Connecting with Muscle Fibres. cb, cell body; d, dendrite; a, axon; nS, nucleus of Schwann cell; nR, node of Ranvier; S, Schwann cell; my, myelin sheath; m, muscle fibre; e, end plate. (b) The Relationship between Ion Flow and Membrane Potential during an Action Potential in a Non-myelinated Axon. rp, resting potential; mrp, minimum refractory period; ap, action potential; solid circles Na^+ ions; open circles, K^+ ions. (c) Net Ionic Movements during an Action Potential and the Recovery Phase. Ion flow during an action potential is energetically downhill and occurs spontaneously, while recovery requires a metabolic pump. Poisoning of the pump does not prevent propagation of action potentials, but eventually ion concentration gradients become dissipated and conduction fails.



Source: Modified after Adrian, R.H. (1974). *The Nerve Impulse*. Oxford Biology Readers.

Like any other type of animal cell, neurons comprise an intricate system of cell organelles surrounded by a cell membrane (Figure 1.1a). Unlike other animal cells, however, they are specialised for transmitting electrical messages from one part of the body to another. This specialisation is reflected both in their structure and their physiology.

A neuron has three obvious structural components. The main body of the cell, the *soma*, is a broad, expanded structure housing the nucleus. Extending from the soma are two types of cytoplasm-filled processes called *axons* and *dendrites*. Axons carry electrical impulses away from the soma and pass them on to other neurons or to muscle fibres. Dendrites receive impulses from other neurons and transport them to the soma. All three components are usually surrounded by *glial cells*. Although glial cells are not derived from nerve tissue, they come to form a more or less complex sheath around the axon. In invertebrates, the glial cell membranes may form a loose, multilayered sheath in which there is still room for cytoplasm between the layers. In this case the arrangement is known as a *tunicated axon*. In vertebrates the sheath is bound more tightly so that no gaps are left. The glial cells are known as Schwann cells and are arranged along the axon in a characteristic way. Each Schwann cell covers about 2 mm of axon. Between neighbouring cells there is a small gap where the membrane of the axon is exposed to the extracellular medium. These gaps are known as the nodes of Ranvier. Axons with this interrupted Schwann cell sheath are called *myelinated* or *medullated* axons. The formation of the myelin sheath enhances enormously the speed and quality of impulse conduction.

Nerve Cell Function. The basis of the neuron's ability to conduct electrical impulses is the distribution of electrically charged atoms (ions) inside and outside the cell. In squid neurons, for instance, the concentration of potassium (K^+) ions is some 20 times greater inside the cell than outside. Sodium (Na^+) ions, on the other hand, are about 10 times more concentrated outside the cell. While both ions tend to diffuse towards equilibrium along their concentration gradients, diffusion is counteracted both by the low permeability of the cell membrane to Na^+ ions (which have large hydration shells) and by a metabolic pump which transfers the ions against their gradients. The net result of this ionic imbalance is a negative *resting potential* across the membrane of some 60-70 mV, depending on the type of neuron.

When the neuron is stimulated, the membrane suddenly becomes highly permeable to Na^+ ions at the site of stimulation (Figure 1.1b). As Na^+ ions flood into the cell, they reduce the membrane potential at that point. When the change in potential reaches a certain threshold, there is a massive influx of Na^+ ions which results in a sharp depolarisation to around +40 mV, known as an *action potential*. The formation of an action potential at one part of the membrane stimulates an increase in Na^+ permeability in the adjacent part and a wave of depolarisation courses down the axon. The rate of action potential