

1 Introduction

1.1 Nervous systems and the study of behaviour

People in antiquity seem to have had no idea that the brain was in any way connected with behaviour. Even that great practical biologist Aristotle was mistaken in his ideas. He observed the rich vascular supply of the brain and concluded that it was an organ for cooling the blood. The ancient Egyptians were positively cavalier in their attitude: when the body of a monarch was being prepared for mummification, the brain was extracted with a spoon and thrown away. The brain was considered unnecessary for the future life, but the entrails were carefully preserved in a jar and kept beside the mummified body.

Modern opinion emphasises the paramount importance of the brain as the source of an individual's behaviour and personality. This trend has gone so far that many a successful work of science fiction has been based on the idea that the brain might be kept alive or transplanted, and that by this means the essential personality of the original individual might be preserved after the rest of the body has been disposed of. This vast change in prevailing opinion about the brain is, of course, due to the anatomical and physiological research of the last 200 years, which has revealed the nature and importance of the central nervous system.

Our present understanding of the way in which nervous systems control animal behaviour owes much to a group of biologists working in the middle of the twentieth century, who pioneered an experimental approach to analysing behaviour. The approach they adopted came to be known as **ethology**, and one of early ethology's most thoughtful exponents was Niko Tinbergen. In an important paper, 'On aims and methods of ethology' (Tinbergen, 1963), he defined ethology simply as 'the biological study of behaviour'.

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Tinbergen himself made an impact on ethology by concentrating on field observations or on elegantly simple experiments carried out on intact animals. But he expected that the results of this work would be integrated with a neural analysis as this became available. This is seen clearly in his book synthesising ethology, entitled *The Study of Instinct* (1951), in which he referred to contemporary research in neurophysiology and formulated his concepts in terms of the nervous system as far as possible. He expected that the biological methods of ethology would yield 'concrete problems that can be tackled both by the ethologist and the physiologist', and he wrote of 'the fundamental identity of the neurophysiological and the ethological approach'.

The long-term goal of such an approach is to analyse patterns of behaviour in terms of the activity of the underlying neural components. Hence, this field of research is sometimes given the title of **neuroethology**, a term that first came into use in the 1960s. Neuroethology tries to combine the approaches of both ethology and neurobiology so as to understand the neural basis of behaviour. Often, this involves examining groups of receptors or networks of nerve cells in order to elucidate the interactions relevant to behaviour. In some cases it is possible to bring both neurobiological and ethological analysis to bear on a single phenomenon, as Tinbergen expected.

In the chapters that follow, selected examples are considered in which neural analysis has been carried out in a way that is helpful to an understanding of animals' natural behaviour. As far as possible, attention is concentrated on specific case histories in which a connection has been established between a particular group of nerve cells (also termed neurons) and a particular pattern of behaviour. This field of study is developing rapidly and enough has been accomplished to enable initial conclusions to be drawn about the operation of many basic areas. These studies and conclusions form an essential and fascinating part of ethology, the biological study of behaviour.

1.2 Scope and limitations of neuroethology

As might be expected, neuroethology has been most successful in tackling those elementary components of behaviour with which ethology itself began. The simple kinds of behaviour that first caught the attention of the

founders of ethology are often also the kinds of behaviour most readily analysed in terms of the underlying neural events. One good example is intraspecific communication, which requires both that the sender delivers a clear signal and that the receiver has the appropriate sensory apparatus to analyse it. The interactions between predator and prey have also been the subject of many neuroethological studies because the neural mechanisms involved must be simple in order to be swift. When life-or-death decisions have to be made in a small fraction of a second, there is just not time for elaborate neural circuits to operate.

A good many of the cases that have been analysed successfully involve **dedicated systems**. A dedicated neural system is one that is largely devoted to a single, important function such as escape (see Chapter 3). Dedicated systems are easier to analyse than multipurpose systems, not merely because they tend to be simpler, but more importantly because their behavioural function is clearly known. As neural systems become more flexible in the tasks that they can perform, it becomes more difficult for experimenters to determine what is behaviourally important in their neurophysiological recordings. In a multipurpose system, it is difficult to discern which of several possible functions is pertinent to neural activity recorded in a dissected animal. In a dedicated system, any recorded activity is likely to relate to the one and only behavioural function, provided the system is in a healthy state.

For example, the large amount of neurophysiological work that has been done on hearing in cats has been of little interest to ethologists because it is so difficult to correlate particular properties of the auditory system with particular episodes in the animal's normal behaviour. It is almost impossible to know what a cat is listening to at any given moment, simply because its hearing is used for so many purposes. By contrast, in the study of hearing in bats, we know precisely what the animals are listening to: they are listening to themselves. The auditory system of bats is largely dedicated to analysing the echoes of their own cries as part of the system by which they find their way around (see Chapter 6). Knowing this central fact, the physiological properties of nerve cells in the auditory system are readily correlated with their behavioural function in the intact animal.

Whether or not the system under study is a dedicated one, it obviously makes the neuroethologist's task easier if the absolute number of nerve cells involved is small. Unfortunately, most of the higher vertebrates have

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very large numbers of nerve cells in even the smallest subsection of their central nervous systems. By and large, therefore, neuroethologists have looked to the lower vertebrates and the invertebrates for suitable study material. Among the invertebrates, the arthropods show behaviour that is complex enough to be interesting yet they also show a remarkable economy in the number of nerve cells involved. Whereas mammals may employ hundreds of nerve cells to excite a single muscle, for example, arthropods usually make do with no more than half a dozen (see Chapter 7). It does not necessarily follow that, because the number of nerve cells involved is smaller, the neural principles of operation will be simpler. But working with a smaller number of nerve cells does increase the chances of discovering the principles in the first place.

1.3 Neural implications of ethological results

The behaviour of an animal is to a large extent the product of activity in its nervous system. The patterns of behaviour that are recognised in ethological studies must therefore reflect the underlying organisation of the nervous system. In the case of the elementary components of behaviour studied by the early ethologists, this correspondence may be fairly close. Consequently, a careful study of behaviour patterns at the level of the intact organism will often produce results that provide valuable clues about the underlying neural organisation.

Consider the classic case of the egg-retrieval behaviour found in many ground-nesting birds, which was first studied in the greylag goose (genus *Anser*) by Lorenz and Tinbergen in the 1930s. A nesting goose employs a stereotyped sequence of movements to retrieve an egg that has become displaced from the nest. The bird leans out of the nest, places its beak beyond the egg, and then draws the beak back towards its chest so that the egg is rolled back into the nest. Superimposed on this movement towards the chest are little side-to-side movements of the beak, which serve to keep the egg in place. This sequence of movements is used by all members of the species for egg retrieval; none uses an alternative method. Indeed, a very similar pattern of movement is found in other birds, such as the herring gull (*Larus*), on which many tests have been carried out (Fig. 1.1). Stereotyped movements of this kind were originally called **fixed action patterns**; nowadays, more general terms like **motor pattern** are used instead by most ethologists.

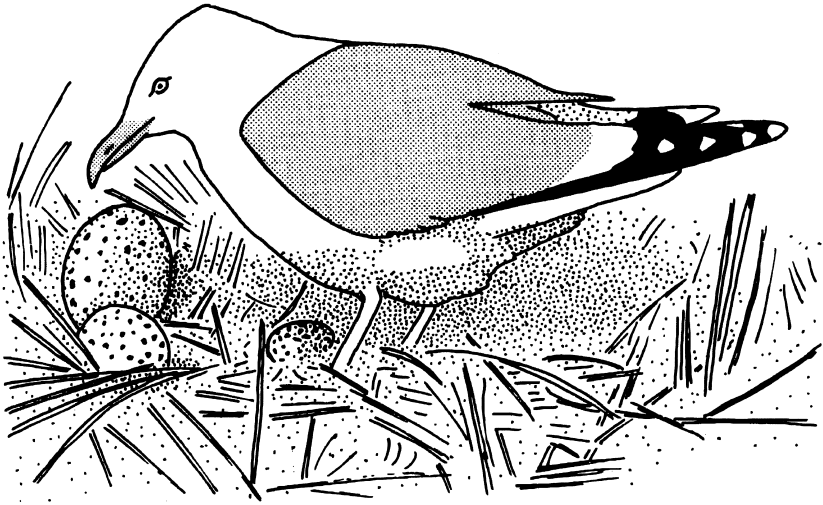


Figure 1.1 Egg retrieval in the herring gull (*Larus*): an incubating gull will retrieve an egg that has become displaced from the nest, using a stereotyped pattern of movement. Here, the retrieval response is being used to test what the gull perceives to be an egg. Two different models, both of which differ considerably from the real egg in the nest, are placed on the rim of the nest to compare their effectiveness in eliciting the retrieval response. (Redrawn after Baerends & Drent, 1982.)

It was noticed that many such motor patterns seem to occur in response to specific stimulus situations in the natural environment. During the 1930s, ethologists developed the technique of using models, in which one feature at a time could easily be varied, to find out what features of a situation are important in triggering an animal's response. Lorenz and Tinbergen found that the greylag geese would retrieve wooden models painted to resemble natural eggs. The goose would still retrieve the models when they were made the wrong shape, such as cubes or cylinders, or when they were made the right shape but the wrong size, including models that were much larger than a normal egg. It was evident from these results, and many others, that only certain features of the natural stimulus are needed to produce a response. These essential features were called **sign stimuli** or, where they were found in the context of social behaviour, **social releasers**.

Ethologists rightly sought to account for the fact that animals often respond to only a small selection of the available stimuli by postulating neural mechanisms in the responding animal. Response selectivity might

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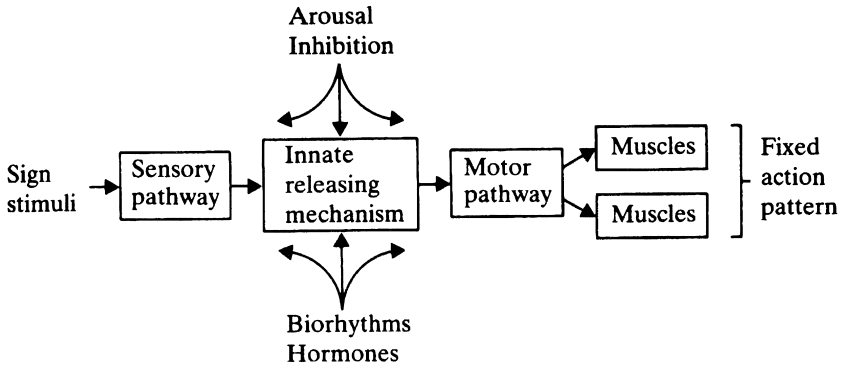


Figure 1.2 A flow diagram showing early ethological concepts of the mechanisms involved in a simple behaviour pattern such as egg retrieval. (Redrawn after Shepherd, 1983.)

be due partly to the capacities of the sense organs, but it was already known that an animal may respond to a specific sensory cue in one behavioural context and not in another. Hence, the occurrence of sign stimuli must also be due to stimulus selection by more centrally located mechanisms processing the information received from the sense organs. The term **releasing mechanism** was coined for this central processing and, because it was assumed to develop independently of experience with the sign stimuli, the adjective innate was attached to it, giving innate releasing mechanism (IRM). The adjective innate is not much used by modern ethologists, but the term releasing mechanism continues to call attention to an important phenomenon of behaviour.

The way in which the various components might interact to produce a behaviour pattern is illustrated in Fig. 1.2, which represents the results of the early ethological period. In egg retrieval, the visual stimuli from around the nest are passed from the sense organs along a neural pathway to the central nervous system, where the releasing mechanism responds to the sign stimuli that indicate 'egg'. This central mechanism then releases or triggers activity in the motor regions of the nervous system that generate the fixed action pattern for retrieval. This sequence is not invariable in its operation but is enhanced or prevented by other factors. Thus, the releasing mechanism is inhibited in the short term (arrows from above in Fig. 1.2) when the bird is away from the nest foraging or escaping from a predator, and in the long term (arrows from below) retrieval cannot be elicited

outside the breeding season, which is controlled by reproductive hormones.

Further insight into this phenomenon has been made possible by the detailed studies of egg retrieval in the herring gull carried out by Baerends and his colleagues (Baerends & Drent, 1982; Baerends, 1985), who placed two egg models side by side on the rim of the nest and then watched from a hide to see which of the models the gull retrieved first. Thousands of these tests were made, carefully varying only one feature at a time, in order to determine what the gulls' preferences were. It was found that the gulls preferred larger eggs to smaller ones, green eggs to any other colour, speckled eggs to uniformly coloured ones, strongly contrasting speckles to weakly contrasting ones, and natural egg shapes to abnormal ones. This last preference was not nearly as strong as might have been expected, and a cylindrical model was almost as effective as an egg-shaped model of the same size and colour.

These results show that the gulls do, indeed, respond selectively to a limited number of stimuli, which match a real gull's egg only in a rough way. It is not even necessary for all the stimuli to be present for a response to occur. The stimuli that are present add together independently to determine the overall effectiveness of an egg model in producing a response. For instance, a smaller green egg will be as effective as a larger brown egg; if speckling is then added to the green egg, it will become more effective than the larger brown egg. One consequence of this property is that models can be made more effective than the real object they represent. A gull will retrieve a model 50 per cent larger than normal, green and with black speckling in preference to one of its own eggs; such a model is what ethologists call a supernormal stimulus.

The experiments with models show that this releasing mechanism involves perception of a number of simple visual cues, which add together quantitatively to determine the degree of 'egginess' as far as the gull is concerned. Clearly, these properties reflect the way in which visual perception occurs in the gull's nervous system, and the flow diagram shown in Fig. 1.3 tries to incorporate this. The response to a limited number of simple cues may well reflect the occurrence in the early stages of the visual system of units that respond selectively to visual cues such as colour, contrast, edges and shapes (represented as selectors, S_1 to S_9 , in Fig. 1.3). The way in which the separate cues add together suggests the presence of a more central unit

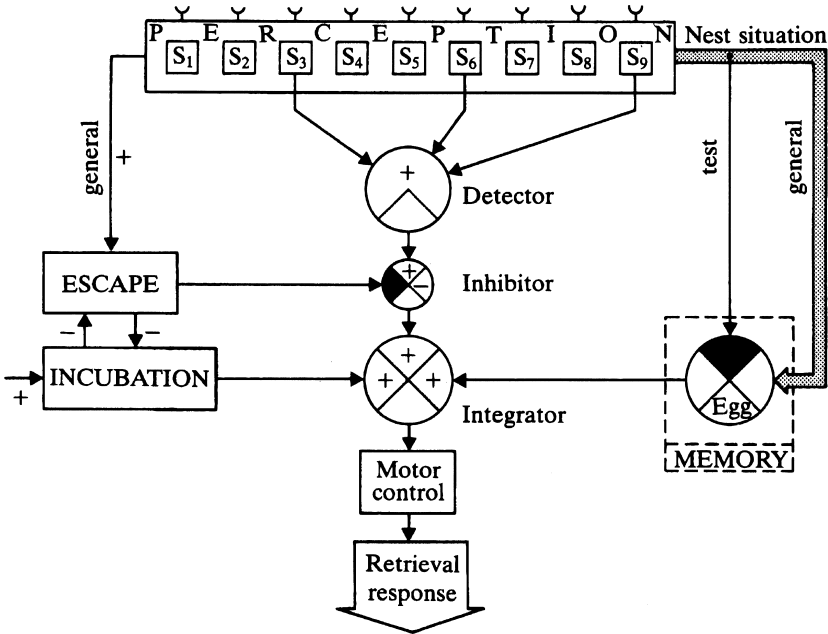


Figure 1.3 Releasing mechanism for egg retrieval in the herring gull: a flow diagram based on experiments with egg models. The boxes represent major systems or operations and the circles indicate sites where summation of inputs occurs. Visual perception (top) is represented as a series of selectors (S_1 to S_9) that respond to particular features of the stimulus. Some of these feed on to a specific detector for egg recognition, which in turn feeds on to the motor control for egg retrieval. This response is maintained during the period of incubation but may be overridden by other factors such as the need to escape (left) or the bird's memory based on experience with real eggs (right). (Redrawn after Baerends, 1985.)

that combines information from a specific set of selectors so as to act as a detector for specific objects in the environment, in this case an 'egg detector'. Units that correspond closely with this description are found widely in the visual systems of both vertebrates and invertebrates, as shown in the following example of prey detection in toads (see also Chapter 5). It is easy to see how these units could be excited more strongly by a supernormal combination of stimuli than by the natural combination.

1.4 Sign stimuli in amphibians

The way in which frogs and toads recognise their prey provides another example of a releasing mechanism. In this case, the ethological results are even more compelling because they have been combined with a neurophysiological study of the same system. This combined approach clearly shows how the selective properties of nerve cells (neurons) are involved in releasing particular patterns of behaviour (Ewert, 1985, 1987).

In the visual world of a frog or toad, just a few, simple criteria serve to categorise moving objects as prey, enemy or lover. Once the visual system has placed a given object in one of these categories, the animal reacts accordingly. These reactions can be used to analyse the criteria involved in prey recognition because the animals are readily deceived by small cardboard models moving in front of them. A special study of prey detection has been made in the common European toad (genus *Bufo*), using such models to analyse the behavioural responses of the intact animal and the responses of specific classes of neuron in the visual system. The natural prey of *Bufo* consists of small animals such as beetles, earthworms and millipedes. If one of these animals appears in its peripheral visual field, the toad responds by turning its head and/or body so as to bring the animal into the frontal visual field. The toad then walks towards the prey in order to capture it.

The sign stimuli, by which the prey is recognised, can be analysed quantitatively in the laboratory. A hungry toad is confined in a glass vessel, from which it can see a cardboard model circling around (Fig. 1.4 *a*). If the toad interprets the model as a prey animal, it tries to bring it into the frontal visual field, and in doing so turns around jerkily after the moving model. The number of orientating turns per minute elicited by a given model, compared to the number elicited by others, can therefore be taken as a measure of the resemblance between that model and prey, from the toad's point of view.

In this experimental situation, the toad is not much impressed by a small 2.5×2.5 mm model, which elicits only a few orientating movements. However, the stepwise elongation of this shape in the horizontal dimension (Fig. 1.4 *b*, shape *x*) greatly increases its releasing value. That is to say, elongation of the model in the direction of movement increases its resemblance to prey, up to a certain limit, and this long, small stripe has been called the

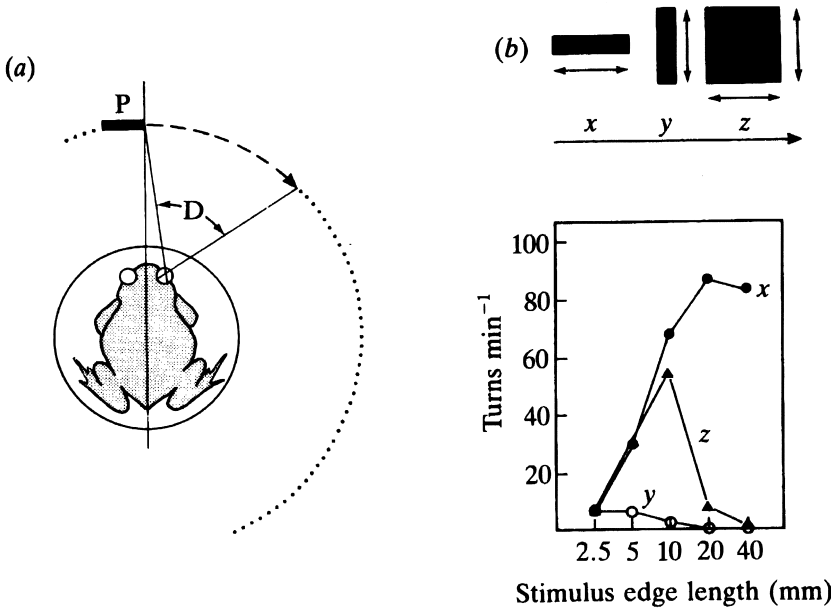


Figure 1.4 Analysis of prey recognition in the toad (*Bufo*). (a) The experimental set-up, with the toad confined in a glass vessel and a prey model (P) circling around it. The toad turns to follow the model when it has moved through a sufficient angle, the effective displacement (D). (b) The response of the toad to moving models of three shapes (x, y, z) as these are enlarged in one dimension (shapes x, y) or two dimensions (shape z). The toad's response is measured by the number of times it turns to follow the model in 1 min. (Redrawn after Ewert, 1980, 1983.)

worm configuration. If the small, square shape is elongated in the vertical dimension (Fig. 1.4b, shape y), its releasing value decreases to zero. In fact, the toad often interprets it as a threat and freezes in a defensive posture. This shape has been called the antiworm configuration. If both dimensions of the model are lengthened equally, so that the toad is presented with squares of increasing size (Fig. 1.4b, shape z), the prey-catching activity initially increases but then declines rapidly to zero. This is probably the result of non-linear summation of the horizontal (worm) and vertical (antiworm) edges.

The toad's ability to distinguish between worm and antiworm does not vary with other stimulus parameters, such as the colour of the model or its velocity of movement. It is also independent of the direction in which the