

# Nerve cells and animal behaviour

SECOND EDITION

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# 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'.

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 sonar 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.

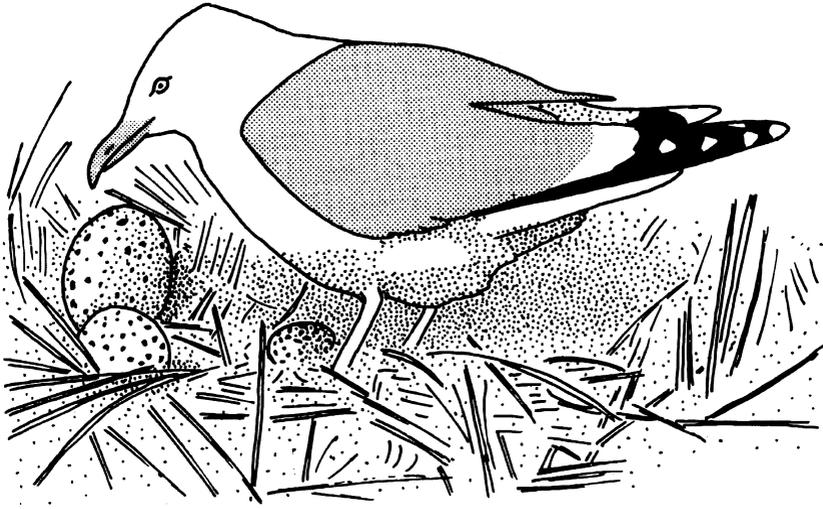
Whether or not the system under study is a dedicated one, it obviously makes the neuroethologist's task easier if the absolute number of nerve cells involved is small. Unfortunately, most of the higher vertebrates have

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

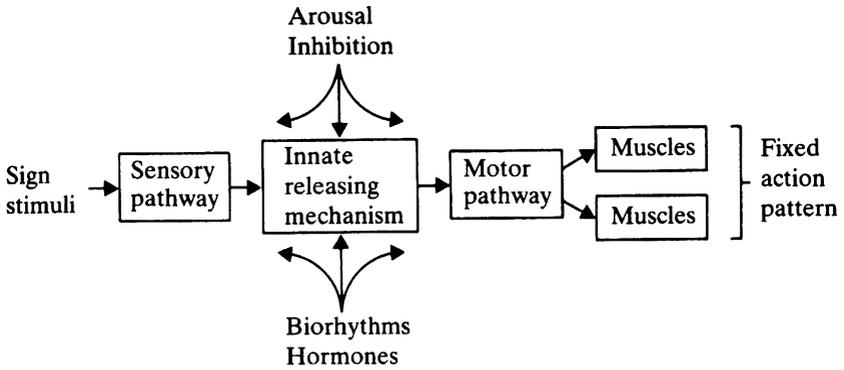


Figure 1.2 A flow diagram showing early ethological concepts of the mechanisms involved in a simple behaviour pattern such as egg retrieval. (Redrawn after Shepherd, 1983.)

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

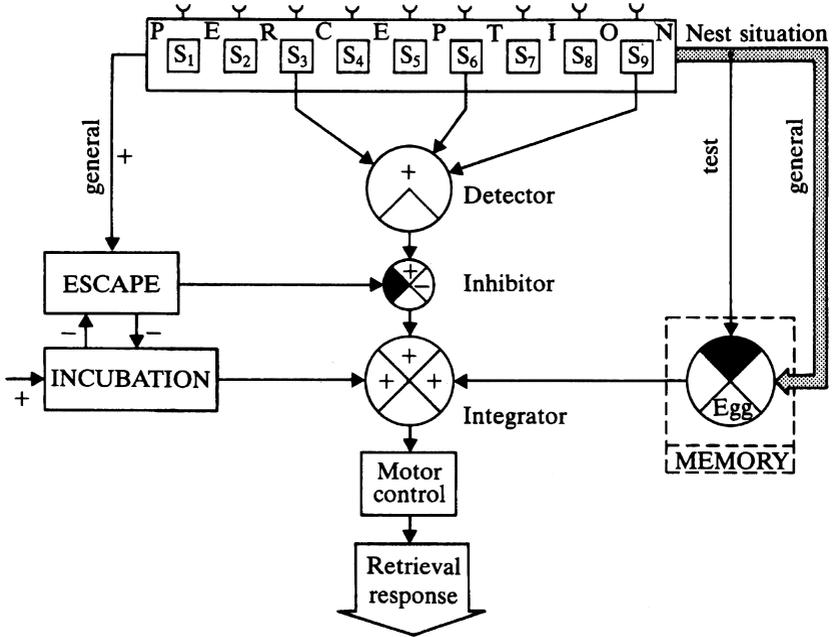


Figure 1.3 Releasing mechanism for egg retrieval in the herring gull: a flow diagram based on experiments with egg models. The boxes represent major systems or operations and the circles indicate sites where summation of inputs occurs. Visual perception (top) is represented as a series of selectors ( $S_1$  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  $2.5 \times 2.5$  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

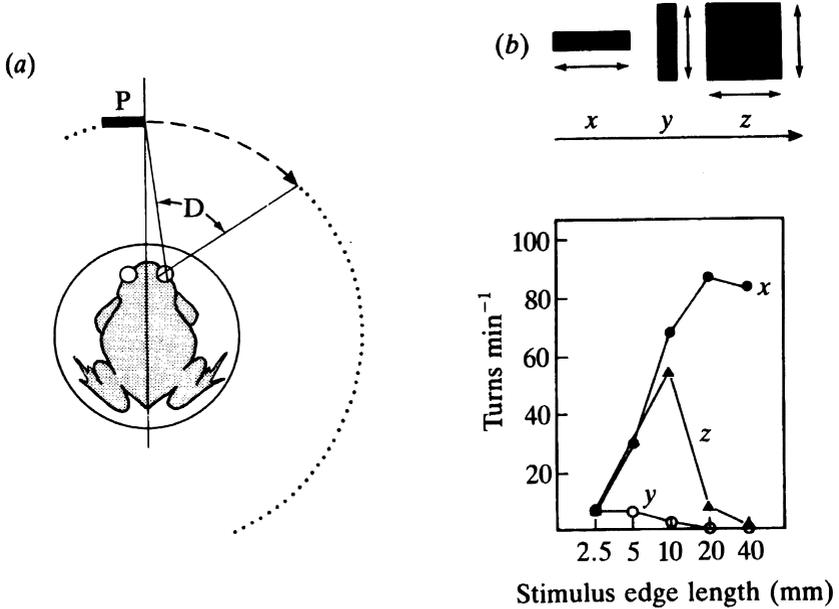


Figure 1.4 Analysis of prey recognition in the toad (*Bufo*). (a) The experimental set-up, with the toad confined in a glass vessel and a prey model (P) circling around it. The toad turns to follow the model when it has moved through a sufficient angle, the effective displacement (D). (b) The response 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

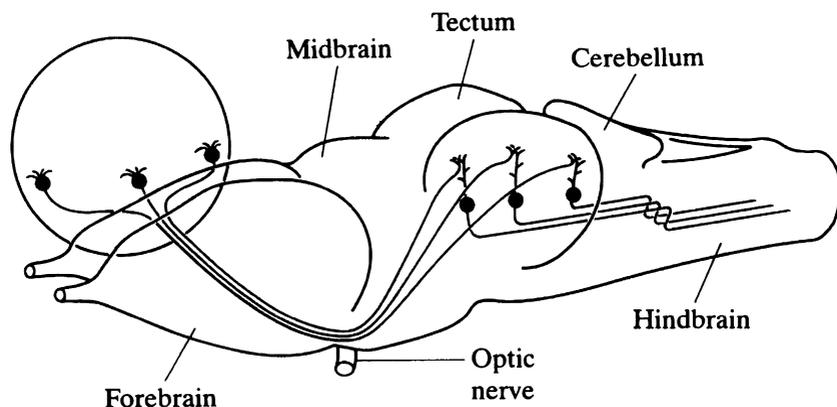
stimulus traverses the toad's visual field. If the models are moved past the toad in a vertical direction, then the vertical stripe elicits prey catching and the horizontal stripe elicits no response or a defensive posture. Thus, the worm/antiworm distinction is based on the combination of just two stimulus parameters: the elongation of the object in relation to its direction of movement. These parameters, then, are the sign stimuli that release prey-catching behaviour in a hungry toad, and it is obvious that they correspond only very approximately to a real worm. Nevertheless, they will normally enable a toad to distinguish correctly between potential prey and inedible objects in its natural environment.

### 1.5 Neuroethology of a releasing mechanism

As with other vertebrates, early visual processing in amphibians takes place in the neuronal circuits of the retina. The neurons of the vertebrate retina (see Fig. 2.4, p. 25, and Box 5.1, p. 107) are arranged in a way that provides for both lateral interaction and through transmission. The through route of the visual pathway is made up of receptors, bipolar cells and ganglion cells.

Recording with microelectrodes shows that the receptors respond in a simple way to changes in the intensity of light that falls on them as part of the image formed by the eye. These responses are mirrored by the bipolar cells, each of which receives input from several receptors. In turn, the ganglion cells each pool input received from a large number of bipolar cells. The ganglion cells are able to respond to more complex features of the image because of the way information from the receptors is processed and combined on its way to the ganglion cells. Ganglion cells can be divided into several different classes on the basis of the type of feature to which each is most sensitive. Some are most sensitive to objects of a given angular size, others to objects moving in a particular direction or to the difference in brightness between adjacent areas of the image. This information is passed along the optic nerve to the brain (Fig. 1.5), where these basic parameters are used to distinguish between mate, prey and predator.

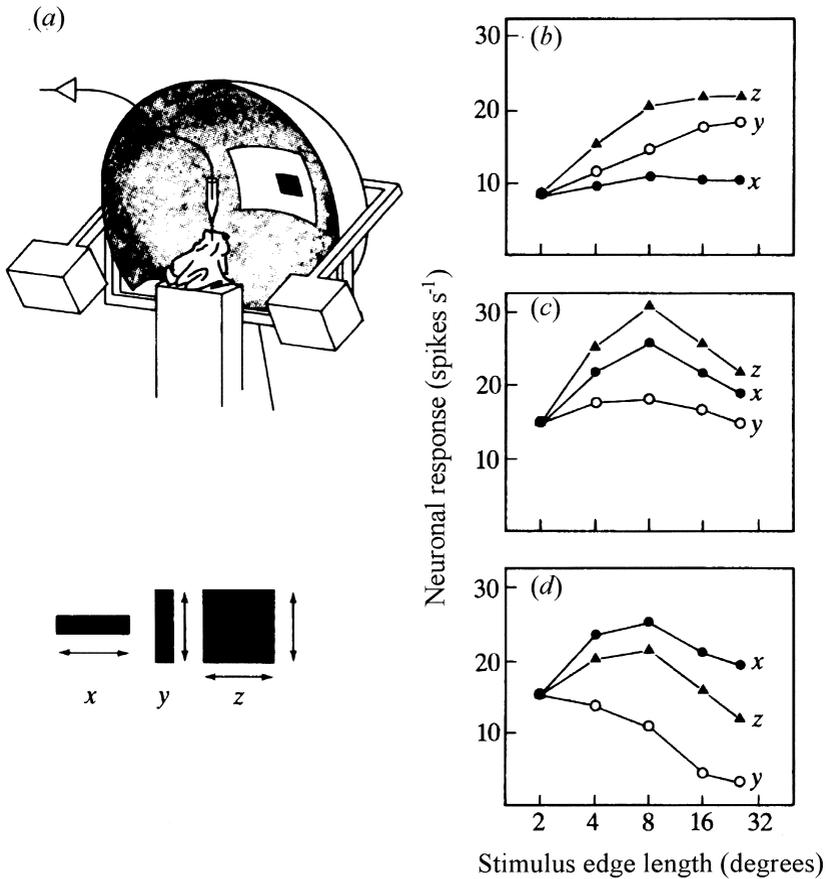
The majority of retinal ganglion cells are connected to the optic tectum, a specialised region of the midbrain visible as a large bulge on either side (Fig. 1.5). A smaller number of ganglion cells are connected to the thalamus, which is the most prominent part of the posterior forebrain, and to the pretectal areas of the midbrain. These connections are spread out in an



*Figure 1.5* The layout of the main visual pathways concerned in prey detection in the brain of an anuran amphibian. The axons of most ganglion cells travel from the eye to the optic tectum on the opposite (contralateral) side of the brain, via the optic nerve (other cranial nerves are not shown). Feature-detecting neurons of the optic tectum send their axons to the motor regions of the contralateral hindbrain.

orderly manner in the superficial layer of the optic tectum, with each ganglion cell keeping the same relative position with respect to its neighbours that it has in the retina.

The responses of the tectal neurons can be recorded by probing the deeper layers of the optic tectum with a microelectrode (Fig. 1.6). Like the ganglion cells, the neurons of the thalamus and tectum can be divided into different classes according to their patterns of response. Of the thalamic and tectal neurons that have been investigated, at least three classes show differing responses to moving stimuli of worm and antiworm configurations. The thalamic Class TH3 neurons respond best to squares; stripes with the antiworm configuration elicit a lesser response, and the worm configuration elicits the least response of all (Fig. 1.6*b*). In the optic tectum, the Class T5(1) neurons also respond best to squares, but when tested with stripes, they prefer the worm to the antiworm configuration (Fig. 1.6*c*). Another class of tested cells, the Class T5(2) neurons, distinguish much more clearly between the worm and antiworm configurations, with the worm configuration eliciting the greatest response, the squares a lesser response, and the antiworm by far the least response (Fig. 1.6*d*). Among all the neurons tested so far, the response pattern of the T5(2) neurons shows



*Figure 1.6* (a) Set-up for recording the responses of neurons in the brain to moving visual stimuli. The toad is held in a fixed position and its brain is probed with a microelectrode for recording the spikes in single neurons. Each stimulus is moved in front of the toad by means of the perimeter device. (b) The response of thalamic Class TH3 neurons to increasing angular size of the same three shapes (x, y, z) used in the behavioural tests (Fig. 1.4). (c) The response of tectal Class T5(1) neurons to the same three shapes. (d) The response of tectal Class T5(2) neurons to the same shapes. (a redrawn after Ewert, 1985; b-d redrawn after Ewert, 1980.)

the best correlation with the sign stimuli for prey-catching behaviour (cf. Fig 1.6d and Fig. 1.4b).

It is evident from Fig. 1.6 that the responses of the Class T5(2) neurons could be accounted for if they receive excitatory input from Class T5(1) neurons and inhibitory input from Class TH3 neurons. The fairly strong

response to the worm configuration in Class T5(1) neurons would be minimally inhibited by the poor response to it in the Class TH3 neurons, resulting in a strong response in the Class T5(2) neurons. Similarly, the poor response to the antiworm configuration in Class T5(1) would interact with the moderate response in Class TH3 to give a very poor response in Class T5(2).

This possibility has been tested by removing the input from the Class TH3 neurons, which can be accomplished by severing the pathway that is known to run from the thalamus to the optic tectum. Whether this lesion is done permanently by microsurgery or temporarily by local application of a neurotoxin, the effect on Class T5(2) neurons is dramatic. The responsiveness of these neurons to all visual stimuli is increased and selectivity is lost, with the neurons responding best to squares and failing to distinguish clearly between stripes in worm and antiworm configurations. This shows that the normal selective response of the Class T5(2) neurons is dependent on inhibition from thalamic neurons, including the Class TH3 neurons.

When a toad with a pretectal lesion is allowed to recover from surgery and is tested behaviourally, its responses closely parallel those of the T5(2) neurons: the operated animal responds vigorously to all shapes, preferring squares and failing to distinguish clearly between worm and antiworm configurations of stripes. Such a close correspondence between the responses of the Class T5(2) neurons and of the whole animal suggests that these neurons are directly involved in prey detection and hence in releasing prey-catching activity. This is confirmed by means of a small telemetry system that enables the experimenter to record from and stimulate single neurons in the optic tectum of a freely moving toad. Recordings made with this system show that activity of Class T5(2) neurons precedes and continues during the orientation of the toad towards the prey. Having recorded in detail from a particular T5(2) neuron, it can then be stimulated by passing a tiny current through the microelectrode, and this consistently elicits orientating movements that are directed to the appropriate part of the visual field.

If they are involved in prey detection in this way, one would expect the Class T5(2) neurons to be connected, directly or indirectly, with the motor circuits in the hindbrain of the toad. Various histological methods demonstrate that a number of the connections arriving in the motor regions on one side of the hindbrain do come from the contralateral optic tectum (see

Fig. 1.5). That these include the Class T5(2) neurons is confirmed by physiological methods. Localised stimulation of the appropriate neural tract in the hindbrain sends signals travelling back up to the optic tectum, where they can be recorded in individual T5(2) neurons with a microelectrode.

Thus, the Class T5(2) neurons provide an excellent example of specific brain cells that are involved in releasing a simple, important behaviour pattern. On the basis of the stimulus parameters selected by the retinal ganglion cells, the neurons of the optic tectum are able to respond to specific parameter combinations that carry information relevant to the toad's way of life. The specific combination of visual parameters to which the T5(2) neurons respond carries information enabling the toad to distinguish between its natural prey and inedible objects. These response properties of the T5(2) neurons do not identify worms or beetles, but rather they underlie the sign stimuli that elicit prey-catching behaviour in a hungry toad.

### 1.6 Control theory and nervous systems

In the attempt to pursue analysis of the mechanisms of behaviour to the neural level, most of the concepts used are drawn either from general neurobiology or from ethology itself. An additional strand of thought that has made a useful contribution is cybernetics or control systems theory, developed to provide a formal analysis of human control systems. It is often useful to treat the nervous system of a behaving animal, or some part of its nervous system, as a control system through which there is an orderly flow of information, with definite input and output elements.

This approach has provided a helpful terminology and way of thinking about the mechanisms of behaviour. With the advent of powerful computers, it has also become possible to use this approach for constructing models that mimic the interactions among groups of neurons. When used carefully, this provides a means of testing whether circuits work in the way that is predicted from physiological recordings. This is particularly useful when large numbers of neurons are involved because it is rarely possible to monitor activity in many neurons simultaneously.

An example of a useful concept from control theory is that of **feedback**; this takes place when an event or process has consequences which affect the occurrence of that event or process. In control systems, feedback is usually negative, which means that action is taken in response to a

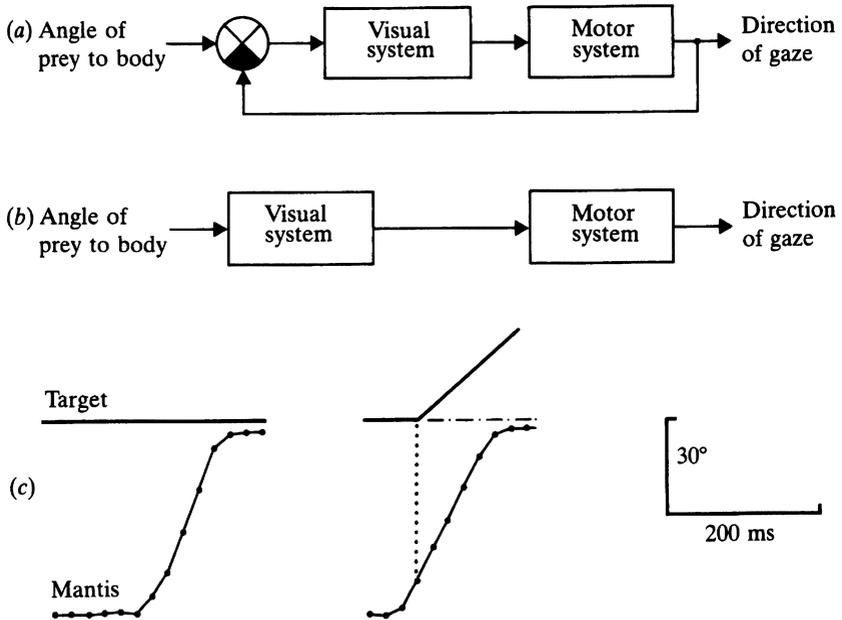


Figure 1.7 Orientation to prey in a mantis (*Tenodera*), illustrating movements with and without feedback. (a) A flow diagram of visual tracking of prey with feedback. (b) A flow diagram of rapid visual location of prey without feedback. In (a) and (b) the boxes represent major systems or operations and the circles indicate sites where summation of inputs occurs. (c) Rapid location of prey, as in (b), analysed from videotape, showing orientation towards a stationary target (left) and towards a target that moves off at a constant angular velocity after the mantis has started to turn (right). (c redrawn after Rossel, 1980.)

disturbance so as to correct that disturbance. This usually involves a special mechanism like a thermostat, by means of which the output of a system is fed back to regulate the input. Many behaviour patterns also have this self-regulatory character. In egg retrieval, the movement of the beak towards the chest seems not to involve feedback because it is so stereotyped and because it continues to completion even if the egg is removed during the movement. However, the side-to-side movements that keep the egg centred on the beak certainly appear to involve feedback of some kind; they tend to disappear if the bird is retrieving a cylindrical model, which rolls smoothly and so does not need centring.

The distinction between movements that do and do not involve feedback

is made clear by the visual orientation to prey in a praying mantis. The insect follows potential prey with movements of its head or body so as to keep the prey in the centre of its line of vision. In this behaviour pattern, visual information triggers a movement of the praying mantis, and this results in an altered visual input, which in turn influences the subsequent movement. Hence, the flow of information forms a **closed loop**, with output feeding back to the input (Fig. 1.7*a*). However, a different situation obtains when the mantis first locates the prey. As soon as a suitable object appears in the visual field, the mantis turns towards it with a rapid movement that is not influenced by feedback from the visual system. Even if the object is experimentally removed during the turn, the mantis still continues turning until it faces the place where the object originally was. Hence, in this case, the information flow forms an **open loop**, without feedback (Fig. 1.7*b, c*).

In common with ethological concepts considered above, such concepts from control theory do not in themselves provide an explanation in terms of underlying mechanisms. Rather, they are, in computer terminology, 'software' explanations that specify the job done and the relations between the different components of a behaviour pattern. For a full understanding of the mechanisms of behaviour, these concepts obviously need to be coupled with a detailed analysis of the underlying neural 'hardware'. Once a neural analysis is accomplished, or at least is underway, then the 'software' concepts come into their own as a vehicle for showing how the neural 'hardware' is organised so as to generate a given behaviour pattern. To take a simple example, flow diagrams such as that in Fig. 1.3 have been borrowed from control theory as a vehicle for summarising behavioural mechanisms. If such a diagram is based on known neural components, whose physiological properties have actually been studied, rather than on hypothetical 'black boxes', then the diagram becomes a truly effective way of summarising the link between the nervous system and behaviour (see, for example, Fig. 3.7, p. 60).

## 1.7 Conclusions

The biological study of animal behaviour was put on a sound footing by the early ethologists in the middle of the twentieth century. These ethologists pioneered techniques for investigating the natural behaviour of animals, including the use of simple experiments in conjunction with field

observations. In the course of this work, they developed a number of key concepts that have helped to guide efforts to understand the mechanisms of behaviour.

One such concept is that of the motor pattern, which is a relatively stereotyped sequence of movements and is easily recognised as part of an animal's ongoing behaviour. The recognition of these motor patterns in the animal's natural behaviour clearly implies that there is a corresponding pattern in the underlying organisation of the animal's nervous system, which generates these movements. Another concept is that of the releasing mechanism, which may be envisaged as a kind of neural filter tuned to recognise specific sign stimuli in the environment. The nervous system must be organised so as to sort out different stimuli and to make decisions about which motor pattern to put into action at any one time. The egg retrieval response in nesting birds provides a good example of the development of these two concepts.

The way that particular nerve cells can be identified as playing specific roles in the control of behaviour is well illustrated by the T5(2) neurons in the brains of toads. The close correspondence between the responses of these neurons and the sign stimuli for prey catching in the toad (*Bufo*) suggests that these cells are part of the natural releasing mechanism for prey-catching behaviour. This conclusion is backed up by lesion experiments, which alter the responses of these nerve cells and the behaviour of the intact animal in similar ways.

Much recent research in neuroethology is aimed at understanding how nerve cells are organised into circuits that perform specific functions in behaviour, such as filtering out sign stimuli or generating a particular motor pattern. This work involves tracing the flow of signals from one nerve cell to the next, and is most easily done where particular nerve cells can be uniquely identified. An essential first step along this path to understanding how nervous systems underlie behaviour is to examine the relevant properties of the fundamental units of the nervous system, the nerve cells.

### Further reading

Alcock, J. (1998). *Animal Behavior, an Evolutionary Approach*, 6th edn.

Sunderland, MA: Sinauer Associates. A useful textbook, which includes some neuroethology, setting it nicely in the context of the varied questions that can be asked about the mechanisms and evolution of behaviour.

Manning, A. & Dawkins, M.S. (1998). *An Introduction to Animal Behaviour*, 5th edn. Cambridge: Cambridge University Press.

Another good textbook, which gives neuroethology its place among the diversity of subject matter and levels of analysis included within the study of behaviour.

Ewert, J.-P. (1980). *Neuroethology*. Berlin: Springer-Verlag. One of the first textbooks treating neuroethology as a distinct area of study, it remains useful for its expert treatment of prey recognition in toads.

Ewert, J.-P. (1985). Concepts in vertebrate neuroethology. *Anim Behav* **33**, 1–29.

This brief essay clearly explains the ideas about neural filtering that have emerged from research on prey recognition in toads, using both ethological and neurophysiological methods.

The International Society for Neuroethology provides a Web site with many links to interesting aspects of this branch of biology: <http://www.neurobio.arizona.edu/isn/>