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Peter J. Simmons and David Young
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Organisation of animal behaviour and of brains: feeding in star-nosed moles and courtship in fruit flies

What is special about animal behaviour? Many people like watching animals behave, and an understanding of animal behaviour has been vital throughout human history, enabling people to hunt, to farm, and to understand something about themselves. More recently, understanding how the brains of animals work has given important information about how the human brain works, and why it sometimes malfunctions. But although animal behaviour can be complex and even sometimes seems mysterious, it can be understood and appreciated by the same scientific approaches that are used to study other aspects of the structure and function of living organisms. It is shaped by evolution in the same way as anatomical characters, and natural selection acts on animal behaviour by shaping the ways in which nervous systems work.

The ways in which the internal workings of brains control behaviour is the subject of this book and we shall illustrate them by using examples drawn from many different animal groups. There are several reasons for this catholic approach, but two are particularly important. First, some animals have nervous systems that are especially favourable for study. For example, nervous systems of invertebrates usually contain smaller numbers of nerve cells than those of mammals, so it is much more possible to trace the flow of signals from cell to cell within these simpler nervous systems. In some cases, there are particularly large nerve cells that are especially easy to study, such as the giant neurons involved in escape responses described in Chapters 3 and 4. Second, animals that specialise in particular behaviours often have parts of their brains that reflect that specialisation, making it feasible to relate the function of those brain parts to particular identifiable behaviours. We describe two different examples of specialisations for

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particular behaviours in this chapter, but there are many more examples in the book including echolocation by bats (Chapter 7) and bird song (Chapter 9). The two examples for this chapter are hunting by the star-nosed mole, in which specialisation of brain areas is associated with their extraordinary nose; and courtship by fruit flies, in which expression of a particular gene labels some neurons with the specialisation of playing a role in that behaviour.

The scientific study of natural behaviour in animals is called **ethology**. Many of the fundamental approaches to studying ethology arose from pioneering observations by Konrad Lorenz and experimental work by Niko Tinbergen that started in about 1930 (Tinbergen, 1951; Bolhuis and Verhulst, 2008). Tinbergen (1963) described four principal questions about a particular behavioural trait that still form the basis of a structured approach to the study of animal behaviour. Our book is mainly concerned with one of these, about the nervous mechanisms that control it; the others are about its function, its development, and its evolution. **Neuroethology** describes the field of science that is concerned with the way that nervous systems control animal behaviour.

Elements of behaviour

A study in which Lorenz and Tinbergen (1938) collaborated provides an excellent introduction to the way we can analyse behaviour into basic elements. The study was on egg retrieval behaviour in greylag geese, *Anser anser*, but various other birds perform it too. These birds nest on the ground, and while an adult is incubating its eggs it is common for an egg to roll away from the nest. The adult goose extends its long neck to the egg and then retrieves it, drawing the head towards its body and using the bill to gently roll the egg (Fig. 1.1). To identify the stimuli that trigger this response, Tinbergen made models, each of which had some of the features of an egg. One of the models was a cardboard Easter egg; others included cardboard boxes of various shapes, and model eggs of different sizes and colours. A stimulus is described as **releasing** a behaviour if it usually triggers that response by the animal, and by comparing the effectiveness of different model eggs in triggering retrieval behaviour, Lorenz and Tinbergen could compare the releasing values of different stimulus features. The most important feature that enables a goose to recognise an egg as an egg is its shape, but colour and pattern also matter. Larger eggs than normal are particularly

Fig. 1.1 Egg retrieval behaviour by a goose, *Anser*. To retrieve an egg, a goose extends its head to the egg, and then rolls it towards its nest guiding the rolling movements of the egg with side-to-side movements of its beak. (Redrawn from Lorenz and Tinbergen, 1938.)

attractive for retrieval – they are supernormal stimuli. A natural stimulus that releases a particular behaviour is termed the **sign stimulus** for that behaviour. An essential step in discovering how a nervous system controls a behaviour is to identify the mechanisms in sensory pathways that recognise the sign stimulus. The process of recognition is often referred to as **sensory filtering**: the nervous system selectively filters out and retains some features of the original stimulus, but ignores and discards others. An excellent example that has been analysed in some detail is the way toads recognise worm-like objects as potential food, described in Chapter 3.

Within the nervous system, there needs to be a link between the processes of stimulus recognition and of triggering the muscle activity responsible for the behaviour. Tinbergen and Lorenz coined the phrase '**innate releasing mechanism**' for this link. It can be likened to a lock. When the correct sign stimuli are filtered, they act as a key in the lock, to release the appropriate behavioural response. In some cases, single nerve cells play this role – for example, giant neurons of crayfish that trigger startle responses (Chapter 4) – but the exact cells involved in innate releasing mechanisms are usually very hard to pinpoint. The word 'innate' was important to Lorenz and Tinbergen because they were particularly interested in the heritability of patterns of behaviour. However, there is no reason why some releasing mechanisms should not be learned by an animal – for example, the sight of Konrad Lorenz walking would release following behaviour by geese that he reared as hatchlings.

It is hard to roll an egg with a beak or a pencil because the egg often escapes sideways. When a goose is retrieving an egg and it escapes, the goose does not immediately re-extend its head towards the egg, but instead it first retracts the head to the nest before re-extending the neck. The movement of flexing the neck towards the body is always completed before the next behaviour pattern starts – the goose completes the action pattern of neck extension and retraction. Such a sequence of movements that goes to completion once initiated is called a **fixed action pattern**, but the word 'fixed' does not mean that the behaviour pattern is completely stereotyped in form – a goose does steer an egg by side-to-side movements of the beak while trying to retrieve it, for example. The observation that some sequences of movements tend to be completed rather than interrupted mid-flow is significant because it implies that central nervous systems generate sequences of instructions, a bit like computer programmes, that specify the order in which different muscles should be used. An alternative would be that sequences of movements are broken down into small elements arranged in a chain, so completion of one element triggers the next. Mechanisms within a nervous system that generate sequences of actions are called **pattern generators** (Chapter 7). Some action patterns can be learned – for example, bird song and human music often include very fast sequences of movements that are almost certainly laid down as kinds of programmes within the central nervous system.

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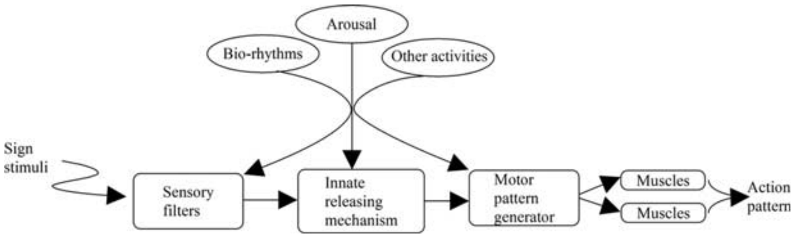

Fig. 1.2 Schematic diagram to show the steps involved in producing a behavioural response to a sign stimulus.

The idea of programmes for behaviour was important in the thinking of Tinbergen and Lorenz, and is still significant today, although terms such as fixed action pattern or innate releasing mechanisms are not much used. The idea provides impetus for neuroethologists to search for networks of particular neurons in the animal nervous system that create the programmes. In terms of the life history of an animal the idea of programmes is important, too. It is normal for an animal to encounter specific kinds of stimuli at particular times in its lifetime, which enables the brain to be programmed according to environmental needs as the animal develops.

The relationship between basic concepts about the mechanisms for the control of behaviour is illustrated in Fig. 1.2. Thinking in this way about how behaviour is organised enables neuroethologists to frame experiments designed to determine how nervous systems control behaviour. Although putting names inside boxes might indicate that there are identifiable regions of a brain that correspond to sensory filters, innate releasing mechanisms or motor programme generators, this is unlikely to be the reality. Neurons involved in a particular operation are often scattered in different regions, and some neurons fulfil more than one job. As indicated in the diagram, behaviour is subject to many factors that act within the nervous system to influence its performance, including daily patterns of wakefulness and sleep or yearly reproductive cycles.

Nerve cells and networks

Neurons, or nerve cells, are thickly interwoven within a nervous system. Distinguishing one neuron from its neighbours is very much like trying to make out the detail of a single tree in a dense wood. During the last part of the nineteenth century, however, a histological method was discovered that enabled the intricate detail of single neurons to be traced using the light microscope. In this method, silver is deposited onto individual neurons; but the method is very selective in that only a small proportion of the neurons in a block of nervous tissue are stained. The silver staining method is sometimes called Golgi staining, after its discoverer, and it was used to great effect by the Spanish doctor Santiago Ramon y Cajal. One of Ramon y Cajal's drawings (Fig. 1.3*a*) illustrates one of the main types of neuron in the mammal brain, a pyramidal neuron. The name pyramidal neuron is given for the shape of the shape of the **cell**

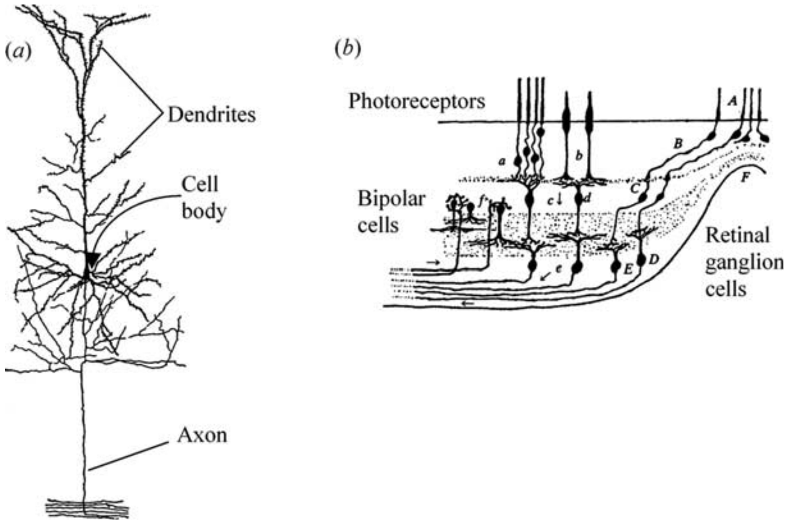

Fig. 1.3 Drawings of silver-stained neurons in mammalian nervous systems. (*a*) A single pyramidal cell from the brain. The cell body, about 20 μm (0.02 mm) across, gives rise to two different kinds of processes: dendrites, and an axon. At the bottom of the figure, the axon is shown joining a bundle of axons from similar cells. (*b*) Some of the types of neurons in the primate retina, including sensory neurons (rods and cones, *a*, *b*, *B*, *A*), bipolar cells (*c*, *D*, *C*) and the retinal ganglion cells (*e*, *E*, *D*). *F* indicates the fovea, where bipolar and retinal ganglion cells are displaced from their receptors. Arrows indicate pathways through which Ramon y Cajal thought that signals passed. (From Ramon y Cajal, 1911.)

body, the region of cytoplasm that contains the cell nucleus. Ramon y Cajal thought that neurons are dynamically polarised, by which he meant that some parts have the function of collecting signals and other parts pass signals onwards. Although the experimental techniques were not available to him to test his ideas, and Golgi vehemently disagreed with them, this view of a functional separation between different parts of a neuron is fundamental to a modern understanding of how they work. In the case of the pyramidal neuron, the **dendrites** collect signals from other neurons, and the **axon** carries signals on to target cells. The way in which information is received, processed and transmitted by individual neurons will be explained in Chapter 2.

Ramon y Cajal also had the insight to propose that individual neurons connect with each other to form networks that process information in specific ways. One of his drawings proposing interactions between neurons in a vertebrate retina is shown in Fig. 1.3*b*, which also illustrates some of the great diversity of form between different neurons. For example, in the retina neurons of the innermost layers called ganglion cells have long axons that convey signals into the brain, whereas the photoreceptors and bipolar cells are involved in much more local operations and lack long axons. In studies of neuroethology, considerable effort goes into attempts to trace the routes by which information flows between different neurons, and into understanding how it is collected, transformed and transmitted to control animal behaviour. These routes are sometimes referred to as ‘circuits’, although the pathways rarely form a complete loop around which the signals travel.

Nervous systems

Jellyfish, sea anemones and starfish have relatively simple nervous systems in which neurons are connected into a nerve net. In this

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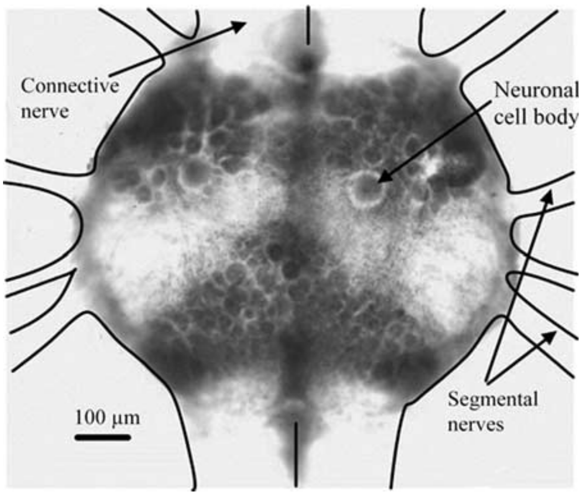

A ganglion that controls the forewings and middle pair of legs in a cockroach thorax. The ganglion was stained with a dye called toluidine blue that sticks to nucleic acids, so the cell bodies and nuclei of neurons stain darkly. The outline of the ganglion and some of the major nerves, which do not stain with this dye, have been drawn in. (Photograph by Peter Simmons.)

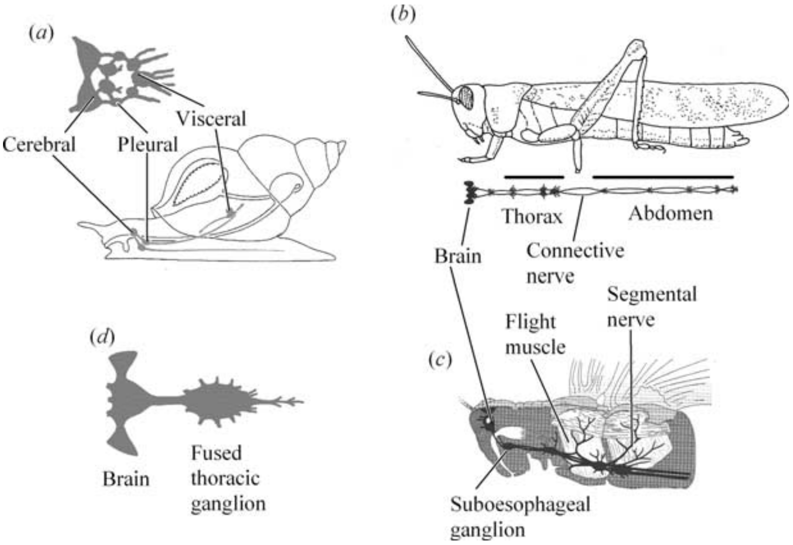

Fig. 1.4 Invertebrate central nervous systems. (*a*) A snail such as the pond snail, *Lymnaea*. Above is a dorsal view of the major ganglia; below, a diagram of a snail from the side, showing positions of ganglia and connective nerves. Three of the ganglia are labelled. (*b*) A locust, *Schistocerca*, with its central nervous system below. (*c*) Cut-away view of the head and thorax of a locust showing the segmental nerves innervating some of the large flight muscles. (*d*) A fly such as the blow fly (*Calliphora*) or *Drosophila*. Note that the thoracic ganglia are fused into one. (Part (*a*) redrawn from Kandel, 1979, and Bullock and Horridge, 1965; (*b*) based on Burrows, 1996; (*c*) redrawn from Wilson, 1968; (*d*) redrawn from Bullock and Horridge, 1965.)

net, there are no or relatively few centralised points for collecting information, so that if one of these animals is prodded the resulting signal spreads out in rather a diffuse manner. Most animals are more highly organised for action, with bilateral symmetry, appendages for locomotion and a clear head end that carries special sensory structures. In most invertebrates, the central nervous system is composed of discrete **ganglia** connected with sensory structures and with muscles by nerves. Usually, each ganglion serves a particular area of the body. For example, in a snail, different individual ganglia are associated with the muscular foot, with the feeding muscles and other body parts (Fig. 1.4*a*). In clearly segmented animals such as crayfish and insects, there is usually one ganglion associated with each body segment (Fig. 1.4*b*, *c*) but complex segments, such as the hind two thoracic segments that bear wings and legs in most adult insects, tend to have ganglia that are larger and contain more neurons than those of more simple segments. Nerves called **connectives** run between different ganglia, although fusion between ganglia occurs in several arthropods such as flies (Fig. 1.4*d*), bees, moths and crabs.

The brain, which originated by fusion of different ganglia, is located above the gut, and includes several specialised areas dedicated to particular functions such as senses of sight or smell. One area of the insect brain, called the mushroom body, is important for learning and memory, and organisation of complex behaviour patterns. The invertebrate central nervous system is solid and, apart from the brain, is located near the ventral surface of the body. Nerves are essentially bundles of axons, which function to transmit signals over some distance. Each ganglion contains the cell bodies and dendrites of neurons and tracts of axons. In areas of **neuropile**, dendrites and axon branches form a tangled network, and in these areas neurons communicate with each other and process information. Often the cell bodies are clustered in areas distinct from the neuropile.

In vertebrates, the central nervous system includes the spinal cord and brain, which are hollow and dorsally located. Muscles and sense organs are connected with the spinal cord by segmental nerves (31 pairs in humans) and with the brain by cranial nerves. The ancestral segmentation of the brain is still apparent in some of the brain stem structures that connect the brain with the spinal cord, especially reticulospinal neurons (Chapter 4).

The vertebrate brain can be divided into three major structural areas: the hindbrain, midbrain and forebrain. Figure 1.5 shows brains

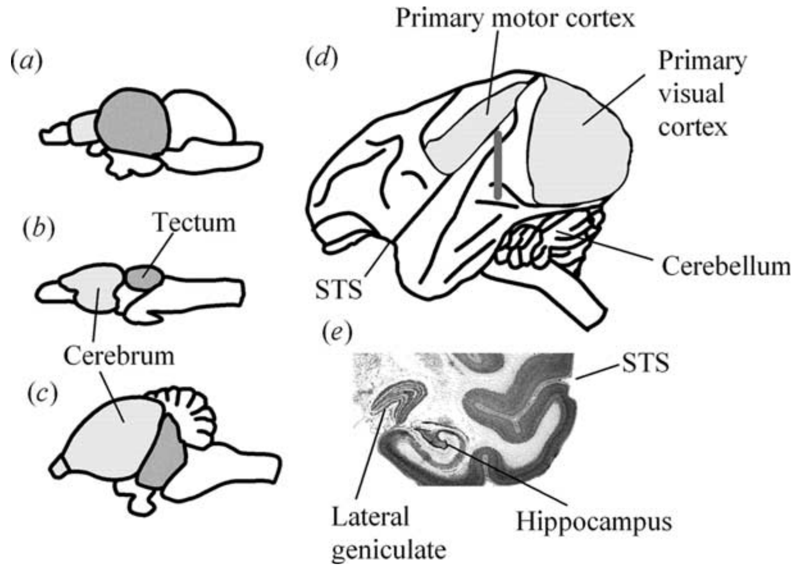

Fig. 1.5 Vertebrate brains. Side views of brains of (*a*) teleost fish, (*b*) frog, (*c*) pigeon, (*d*) macaque monkey. (*e*) A section through a macaque brain in the region indicated by the vertical grey bar in (*d*). This shows the dark grey, folded cortex, which contains six layers of cell bodies, dendrites and axons. The paler white matter beneath it contains mainly axons. Structures in this section that are deeper in the brain include the lateral geniculate body, which receives information from the optic nerves and distributes it to the visual cortex; and the hippocampus, which is involved in spatial memory. STS in (*d*) and (*e*) is the superior temporal sulcus. (Part (e) drawn from www.brainmaps.org (accessed 2 September 2009).)

of various different vertebrate classes. In fish the hindbrain is most significant and in mammals the forebrain has become greatly enlarged, including the cerebral cortex. The midbrain also has a different proportion relative to other brain regions in different classes. It includes the tectum (indicated in the diagram of an amphibian brain, Fig. 1.5*b*), which is where visual neurons described in Chapter 3 are found. Birds have a much smaller cerebral cortex than mammals, but these two groups of animal are recognised as having similar cognitive abilities, with many birds able to learn complex spatial relationships or songs (Chapter 9). During evolution, birds have followed an alternative pathway of brain sophistication to that followed by mammals.

In terms of function, the mammalian cortex is divided into various sensory regions, motor regions and associative regions (Fig. 1.5*d*). To reach the sensory regions, signals from sense organs are processed in a series of brain regions, each dedicated to particular aspects of sensory stimuli. Most sensory information first passes through a region called the thalamus from where different aspects are parcelled into separate pathways that act in parallel, before signals from the different pathways reconverge at higher levels. Similarly, motor areas of the cortex control muscle actions by relaying information through a series of processing stations. Areas of white matter are distinguishable from areas of grey matter in both the brain and spinal cord: white matter is composed of bundles of neuronal axons, and grey matter contains cell bodies and dendrites, so is where neurons communicate with each other and process signals. Many areas of the brain are covered with distinct layers of grey matter. In fish that are considered related to ancestral vertebrates, there are three layers; some parts of the mammalian cortex have six or seven layers. The area of grey matter in these areas is sometimes greatly increased by folds in the surface, such as those that are a familiar feature of the human cerebral cortex. These folds on the surface of the cerebral cortex of a macaque monkey are shown in Fig. 1.5*d*. A slice through part of the macaque brain is shown in Fig. 1.5*e* (the region is indicated by the vertical grey line in Fig. 1.5*d*; notice that the superior temporal sulcus occurs in both parts). The slice shows the layered nature of the grey matter of the outer cortex, and indicates how the folds increase the number of nerve cells that can be accommodated in the grey matter. A human brain is estimated to contain 10^{12} neurons, each potentially connecting with thousands of others. Despite this complexity, many regions of the cortex are arranged as repeating modular columns, each of which is thought to process information in essentially the same manner. Deeper regions of the brain have significant impacts on behaviour – for example, the hippocampus (Fig. 1.5*e*; Chapter 8) is important in some types of learning; and the amygdala is responsible for processing emotional aspects, such as fear.

In the rest of this chapter, we explore two different approaches to discovering which neurons are involved in particular behaviours. The first approach is to study an animal with clear anatomical and behavioural specialisations, which are often reflected in obvious adaptations of parts of the nervous system. The second is to use genetic mutants to correlate changes in behaviour with neurons or parts of the nervous system.

An animal with a specialised nervous system: the star-nosed mole

A spectacular specialisation is the star-shaped nose of a species of mole, *Condylura cristata*, that lives in wetlands in the eastern parts of USA and Canada. Its nostrils are surrounded by 22 fleshy and mobile appendages or rays, a star-shaped structure that gives the mole its name. Although the rays are part of the nose and look a bit like fingers of a hand, the structure is actually a highly specialised touch-sensitive organ. It plays a vital role enabling the star-nosed mole to detect and catch food. This mole needs to sustain a high rate of energy input, and lives in an environment where there are large numbers of relatively small prey, including small worms, and this mole is an expert at eating large numbers of small food items rather than relying on finding larger single bites to eat (Catania and Remple, 2005). It can identify and take into its mouth up to ten pieces of earthworm within 2.3 seconds, making it the fastest mammal at food handling. Like other moles, this species spends most of its time

The nose of the star-nosed mole, *Condylura cristata*, is a specialised sensory structure that enables the mole to detect and identify worms and other food very quickly. Its surface is represented by three separate maps in the animal's brain. Inset is a scanning electron micrograph of part of the surface of the nose, showing individual touch-sensitive dome-shaped Eimer's organs, each about 40 μm across. (Photographs provided by Kenneth Catania, Vanderbilt University.)

in underground burrows and has poor eyesight. Investigation of the nose by Ken Catania and various colleagues led to an appreciation that it is a unique sensory structure, served by specialised regions of the cerebral cortex. The mole identifies the worm as food and distinguishes it from inedible objects using touch-sensitive structures on its star-shaped nose, although it is not yet known exactly how an edible object feels different from an inedible one. The rays of the nose are covered by touch-sensitive structures called Eimer's organs. On the surface, each is a dome-shaped projection of skin about 40 μm across, and below the surface is an array of flat skin cells regularly arranged, a bit like an onion. A number of different nerve endings supply the organ, and these are exquisitely sensitive to touch over a very small area of the ray. All moles have Eimer's organs on their noses, but the star-nosed mole has many more than other species.

When a star-nosed mole is feeding, it explores the ground with the rays of its nose, rapidly applying rays to a patch of substrate and then moving them to another patch. Up to 13 different patches are sampled each second. If the mole misses a chunk of worm with its nose rays, even by a very small distance, it ignores it. But if one of the longer rays hits a worm, the mole immediately moves its nose to examine the worm in greater detail with the shortest nose ray, the one numbered 11 on each side. A mole hardly ever bites and swallows a piece of food it has not first inspected with ray 11. This behaviour, of first noticing a potentially interesting object and then using a specialised region of a sense organ to examine it, is familiar to humans in our sense of sight. While our eyes make us aware of objects anywhere within a wide area, particularly if they are moving, a relatively small part of a retina called the **fovea** is able to examine an object in detail. While reading, the eyes move so that the images of words under attention are directed to the fovea, but more peripheral parts of the retina have insufficient acuity to distinguish letters from each other. In a similar way, a star-nosed mole uses ray 11, and to a lesser extent ray 10, to examine the feel of potential food.

So what is special about ray 11? It is smaller than other rays; and has 900 Eimer's organs, compared with 1500 that larger rays have. But each of its Eimer's organs is innervated by more sensory axons: ray 11 on average has 7.1 sensory axons per Eimer's organ compared with 4 for rays 1–9 and 5.6 for ray 10. This greater number of axons probably increases the sensitivity of individual Eimer's organs in ray 11 compared with other rays. But it is in the brain that the most significant difference between ray 11 and the others was found by Catania and Kaas (1997). Using small electrodes, they recorded responses from individual neurons in the sensory cortex of anaesthetised moles to touches of the nose and other parts of the body. As in other mammals, the star-nosed mole has a somatosensory cortex, a region of cortex that is dedicated to receiving and processing touch to the body surface. A light touch anywhere on the body surface is registered somewhere within the somatosensory cortex. But the area of cortex in which Catania and Kaas recorded responses when