Sensory Processes

7

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Learning Objectives

By the end of this chapter you should appreciate that:

- psychologists have developed rigorous, objective methods for investigating sensory processes;
- processing of sensory information relies on transduction (or transformation) of energy by sensory receptors;
- information conveyed by light differs from that conveyed by sound;
- light travels very fast and in straight lines over large distances, gives highly precise directional information, and can tell us about properties of distant objects;
- different types of light radiation are perceived differently by different animal species;
- many tasks are made much easier for humans by the way in which we process colour information;
- sound travels in lines that are not straight, so we cannot use it to determine locations in space as well as we can with light;
- sound also travels less quickly than light, so its time-of-arrival information can tell us about the direction of the sound source and the locations of sound-reflecting surfaces around us;
- the analysis of speech is one of the most important tasks of the auditory system for humans;
- we have other important senses apart from vision and hearing; for example, the perception of pain has probably been very important for human survival.

INTRODUCTION

It seems clear that in order to survive and function well in the world, an animal needs to know what is in its environment. What kinds of things it needs to know will depend on the kind of animal it is.

For example, a hawk flying high above ground and looking for prey needs some system of detecting that prey at a great distance; it seems equally obvious that it would be in the prey's interests to be able to see the hawk and take evasive action. In another situation, a dog may need to know whether another dog has been present in its territory, and therefore needs some way of detecting faint chemical traces left by the other dog. Sensing those traces will tell it that there is an intruder who needs to be persuaded to leave.

This chapter is about 'sensation' – the process of 'sensing' information about our environment. We can see from the hawk and dog examples that there are two major aspects to the process, and therefore the study, of sensation:

1. Understanding what is 'out there' to be sensed: what types of information are available that could, in principle, be used to tell us what lies around us? This first area involves thinking about the physical properties of the world.

2. How this information may be utilized by a biological system.

It is no good having information all around us if we have no means of sensing it. So a major part of this chapter will be about the sense organs and the type of information they send to the brain. This process is often placed within the domain of physiology, which is the study of the detailed functioning of biological systems in terms of their 'hardware'. We will make the link into psychology by asking how psychological techniques can be used to study the process of sensation in humans. Historically, this area is one of the first in which psychological techniques were perfected, long before the word 'psychology' was coined. This chapter shows you how these techniques allow us to study the function of mechanisms without requiring a person to describe his or her sense experiences in detail.

But first we will be moving within the realms of physical science, which might feel a little strange to students of psychology. From here, we move through physiology towards psychology.

Hopefully, what will emerge is an appreciation of the amazing cleverness of the sense organs, and the intricate nature of the information that they send for further processing by the brain.

HOW DO WE GATHER INFORMATION?

Our world is a complex place. Right now, I am sitting at a desk. I see the computer screen, and beyond that a window through which I see a garden and then a pine forest. I hear the faint whirring noise of the fan in the computer and the buzz of cicadas outside. I can smell the jasmine and pine sap from the garden – these smells become more potent if I concentrate on them. I can taste the coffee, which I recently sipped. My skin feels pleasantly warm in the summer heat, but my knee hurts where I grazed it a few days ago. I also feel the itching from some mosquito bites.

How does all this information reach me? Examining the above description in more detail, especially the physical sources of information, will help to explain what is going on when we receive information from the world.

LIGHT

Arguably our most important perceptual ability is vision. We know that vision depends on light: when there is no light, we cannot see. What are the important characteristics of light, and how do these affect the kind of information it conveys to us?

Light is a form of electromagnetic radiation. 'Visible' light forms just a small part of the full spectrum of this radiation (see figure 7.1). The sun emits radiation over a much larger part of the spectrum than the chunk of it that we can see. Why might this be so?

To answer this question, it may help to consider why we do not see the two parts of the spectrum that border on the visible part.

Ultra-violet radiation

There is plenty of ultra-violet (UV) radiation about, especially as you get nearer to the equator and at high altitude. You will have heard about your skin being at risk of sunburn when there is a lot of UV radiation around you. Sunburn is the first stage of the process of the skin dying as a result of damage.

So we know that UV radiation is damaging to skin, and presumably other biological tissue too. This is the most likely explanation for our eyes having an in-built filter to remove UV radiation. To put it simply, if we were able to see UV rays, they would be likely to damage our eyes.

Some animals do possess UV vision, especially insects and birds. It is thought that they are less vulnerable to this hazardous radiation because they live a shorter timespan than humans. Our eyes must function throughout a long lifetime.

Other forms of short-wavelength information, such as X-rays and gamma rays, are even more damaging to tissue, but these are filtered out by the earth's atmosphere.

Infra-red radiation

Why are we unable to see infra-red (IR) radiation? Would it be helpful if we could? The answer to the second question is certainly 'yes'. IR radiation is given off in proportion to an object's temperature. This is why it is used in night-vision devices, which can locate a warm object, such as a living body, even in the absence of light. This information could be extremely useful to us. So why do we not see it?

Precisely because we are warm creatures ourselves. Imagine trying to see while holding a strong light just below your eyes. The glare from the light prevents you from seeing other objects. In the same way, we would suffer from glare if we could see IR radiation. It would be like having light-bulbs inside your own eyes.

Again, some animals do see IR radiation, but these are cold-blooded creatures, such as pit vipers, which do not suffer from this glare problem. The IR information is very useful in helping them to locate warm objects, such as the small mammals they hunt for food.

Humans build devices that transform IR into visible light – useful for armies (and the psychopath in the movie *Silence of the Lambs*) needing to 'see' warm objects at night, such as vehicles

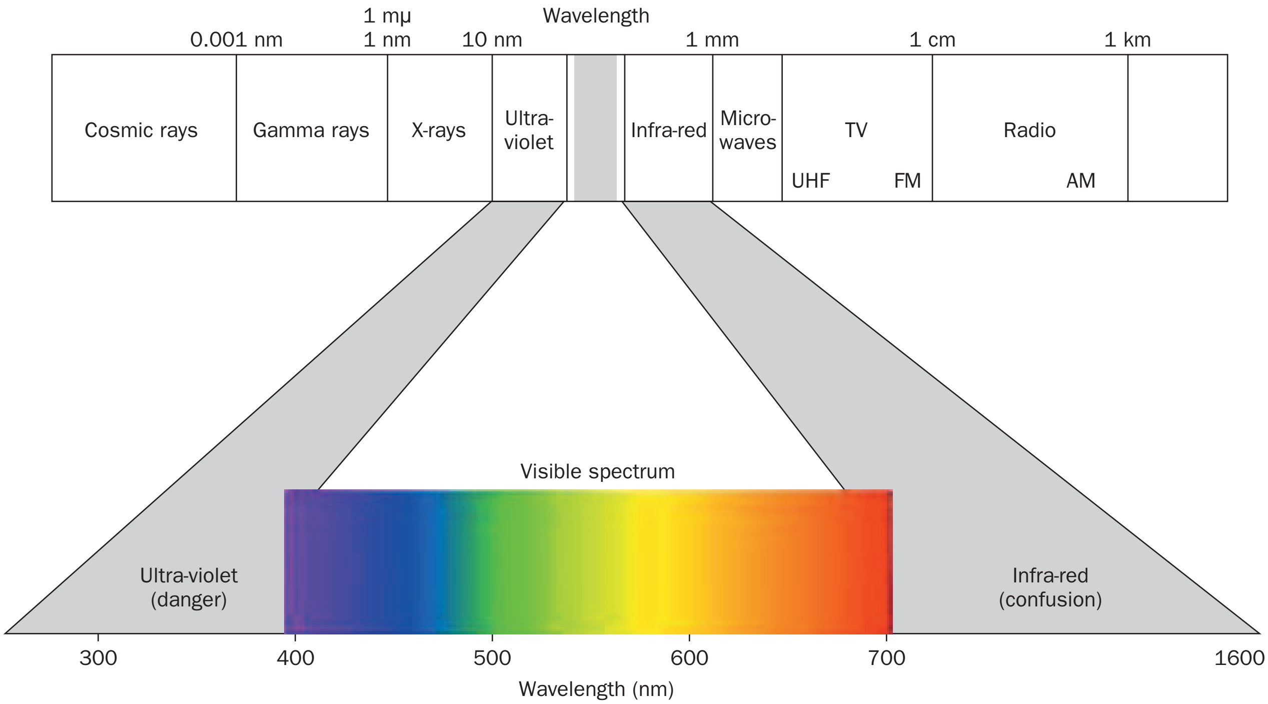


Figure 7.1

The range of electromagnetic radiation. Note the small range of this spectrum (wavelengths from about 400 nm to 700 nm, where 1 nm is 10^{-9} metres) which gives rise to visual sensation.

with hot engines and living humans. More humane uses of this technology include looking for living earthquake victims. Figure 7.2 shows an example of an IR terrain image. A Landrover is clearly visible from its engine's heat. A normal photo of this scene would simply look black.

Figure 7.2

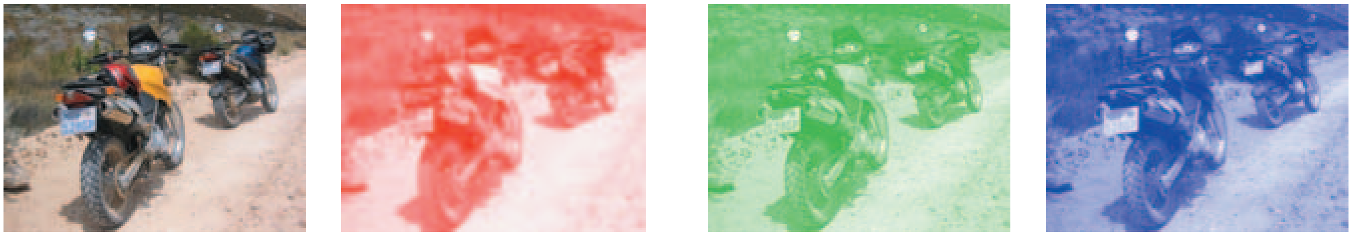
A terrain image of a scene at night in the infra-red range (approximately 1000 to 1500 nanometres). Visually, this image would be completely dark. However, because infra-red radiation is emitted by hot objects, the engine of the vehicle shows up clearly. The military use this kind of imaging device to enable night vision of such objects.

Visible light – speed and spatial precision

Light travels extremely quickly, at a rate of about 300,000 km per second. In effect, this means that light transmission is instantaneous. So we cannot determine where light is coming from by perceiving differences in arrival time. No biological system exists that could respond quickly enough to signal such tiny time intervals.

One of the fastest neural systems in humans is the auditory pathway, which can sense differences in the time of arrival of sound waves at each side of the head. Such differences are of the order 1 ms, or one-thousandth of a second (see Moore, 2003, pp. 233–67). As light travels so much faster, the equivalent difference in time-of-arrival we would need to detect would be one millionth of a millisecond. This is impossible for neurons to resolve.

Fortunately, the other major property of light means that we do not need time-of-arrival information to know where the light is coming from. In transparent media such as air, light rays travel in straight lines, enabling it to convey information with high spatial precision. This means that two rays of light coming to me from adjacent leaves on the tree outside the window, or adjacent letters on this page, fall on different parts of the retina – the part of the eye that translates optical image information into neural signals. As a result of this simple property (travelling in straight lines), we can resolve these separate details. In other



Colour image Red Green Blue

Figure 7.3

A coloured scene and its decomposition into three primary-colour maps (red, green and blue). Adding these three pictures together generates the full-colour scene. The fact that three primary colours are sufficient to yield a full-colour scene is a consequence of us having three different cone types in the retina, each responding to a different range of wavelengths.

directional sensitivity similar to acuity

acuity the finest detail that the visual (or other) system can distinguish

words, we have a high degree of *directional sensitivity*, or a high *acuity*.

Without this property, the light from adjacent letters on this page would become irretrievably jumbled and we would not be able to resolve the letters.

The benefits of colour

reflectance the relative proportion of each wavelength reflected by a surface: the higher the reflectance, the lighter the object will look

When light hits a solid object, it can either be reflected or absorbed. An object that absorbs all the light hitting it will look black. One that reflects all light will look white. Intermediate levels of *reflectance* (the term given to the ratio of incident to reflected light) will elicit shades between black and white. Also, objects reflect different amounts of light at different wavelengths. Figure 7.3 shows how different objects in an image reflect different amounts of red, green and blue light.

So the ability to distinguish between the amounts of different wavelengths of light reaching us from a given surface can convey a lot of information about the composition of the surface, without us having to come close to it. This is the basis of colour vision. It is possible to tell whether a fruit is ripe or not, or whether meat is safe to eat or putrid, using the colour information from the surface of the fruit or meat. Equally, it is possible to break camouflage.

Figure 7.4 compares a monochrome and a coloured display of a scene. The ripe fruit is virtually invisible in the monochrome version because its *luminance* (the amount of light that comes to us from it) is not sufficiently different from the canopy of leaves that surround it, the canopy serving

luminance the intensity of light corrected for the degree to which the visual system responds to different wavelengths

Figure 7.4

A colour and monochrome version of the same scene – a red fruit among leaves. The fruit is very hard to find in the monochrome version, and is easily seen in the colour version. Recent theories of the evolution of colour vision suggest that, in primates, it developed partly to enable detection of fruit in leafy canopies.

as camouflage because it contains large random fluctuations in luminance. As soon as colour is added, we can see the fruit clearly.

It has been argued (Osorio & Vorobyev, 1996; Sumner & Mollon, 2000) that the need to find fruit is the main reason for primates' trichromatic colour vision. 'Trichromatic' simply means that there are three types of cone cells in the retina (see figure 7.3). Curiously, though, other mammals have only dichromatic colour vision, which means they only have two cone types – one corresponding to medium-to-long wavelengths and another responding to short wavelengths. As a result, they cannot discriminate between objects that look green or red to us. So a red rag does not look particularly vivid to a bull! Interestingly, most animals (i.e. all birds and insects) have four cone types, one responding to UV radiation.

SOUND

Those cicadas are still chirping outside the window, and the computer is whirring. These sensations are clearly conveyed to me by sound. But what is sound?

The mechanical nature of sound

Like light, sound is also a form of physical energy, but this type of energy is mechanical. Sources of sound cause the air molecules next to them to vibrate with certain frequencies; these vibrations are transmitted to neighbouring molecules and cause waves of vibration to spread outwards from the source, just like waves spread on a calm pond if you throw a pebble into it.

In this way, sound can travel around corners, unlike light. So sound conveys a very different form of information than light. Since it is not constrained to travel in straight lines, it can tell us about things that are out of sight – but at a price. The price is that sound cannot tell us about spatial location with as much precision as light can; this is a consequence of its physical properties, and nothing to do with our ears.

As sound travels through the air, the air pressure at a given point will change according to the *frequency* of the sound. We are sensitive to a range of frequencies from about 30 Hz (Hertz in full, which means cycles per second) to about 12 kHz (or kiloHertz, meaning thousands of cycles per second). Figure 7.5 shows the patterns of waves reaching us from objects vibrating at a given frequency.

frequency the rate at which a periodic signal repeats, often measured in cycles per second or Hertz (Hz); the higher the frequency, the higher the perceived pitch

Using sound to locate objects

As we have already seen, sound also travels much more slowly than light, with a speed of about 300 metres per second. Even though this is still pretty fast, it is slow enough for our brains to process time-of-arrival information. It takes sound just under one millisecond to travel from one side of the head to the other. This information can be encoded by neurons (Moore 2003; see also chapter 3), giving information about what direction the sound is coming from.

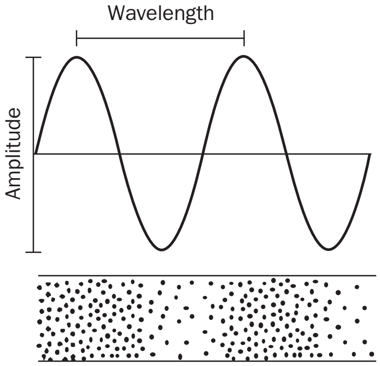


Figure 7.5

Sound waves and how they vary in wavelength and amplitude. Each wave can be measured as the pressure of air at a point in space, and the lower part of the figure depicts the density of air molecules, i.e. the pressure at each point of the wave. The frequency of a wave is the number of wavelengths passing a given point per second.

Sound also gets reflected or absorbed by surfaces. Think about echoes in a cave. These are extreme examples of a process that happens less spectacularly, but more usefully, in everyday life. Subtle echoes give us clues about the location of large objects, even in the absence of vision. Blind people tend to develop this skill to a higher level, using sticks to tap the ground and listen for new echoes. Bats use echolocation to fly at night (see figure 7.6).

Communication

Dolphins use a similar echolocation mechanism, both for finding their way and for communication.

In general, communication is the other main use for sound, since it is generally easier for animals to produce sound than light. Speech production and recognition in humans is a spectacularly impressive process, which is crucial to our success as a species. The fact that sound can travel around corners is an added bonus – the person you are talking with does not need to be in a direct line of sight.

THE CHEMICAL SENSES

Light travels virtually infinitely fast; sound travels more slowly but is still unable to linger in one spot for any length of time. In our efforts to gather useful information about the world out there, we really could use a source of information that sticks around for much longer.

This is where the chemical senses – smell and taste – prove useful. Biological systems have developed an ability to detect certain types of molecule that convey information about sources of food,

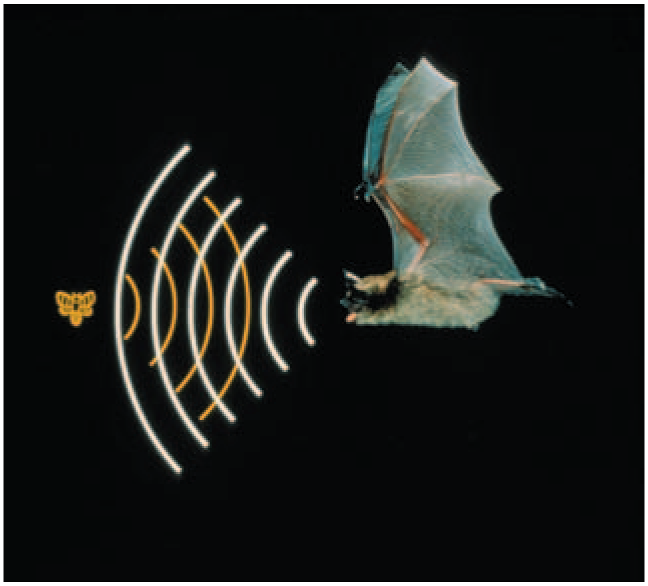


Figure 7.6

A bat uses echolocation to detect sound waves reflected off another object – in this case, a fly. The bat emits high-frequency sound waves and senses their reflection from other objects and surfaces nearby. That way, it can locate such things without light. Blind people do a similar trick when tapping their white cane – they listen to the reflected echo from nearby objects.

other animals and possible hazards and poisons. To appreciate this information, just watch a dog sniffing for a buried bone – or tracking the path taken by another dog. Here we have a source of information that comes with a level of persistence, a spatial memory of previous events.

In humans, the sense of smell seems to be less developed than in other animals. But we do have a well-developed sense of taste, which tells us about the chemical composition of the food we eat and warns us (together with smell) of toxins, for example in food that is putrid.

Clearly this is a very different type of information from that provided by light and sound. It requires physical contact or at least close proximity, but the information persists for much longer.

THE SOMATOSENSES

There are senses which we use to explore the world immediately around us – just outside our bodies and also on or within our bodies. *Somatosenses* respond to:

- pressure
- temperature
- vibration
- information signalling dangers to our bodies (e.g. cuts and abrasions, corrosive chemicals, extreme heat, electrical discharges)
- possible problems inside our bodies

Exploring through touch

Our skin contains nerve endings which can detect sources of energy. Some parts of our bodies, such as our fingers, have a higher density of nerve endings than other parts, and so fingers and hands are used in active exploration of the world immediately around us. Mostly, this is to corroborate information that is also provided by other senses, such as vision; but of course we can still touch things without seeing them.

I recently played a game with some friends in New York, where there is a park with small statues of weird objects. We closed our eyes, were led to a statue, and had to tell what it was. Through active exploration lasting many minutes, we were able to give a pretty precise description of the object, but it was still a big surprise to actually see it when we opened our eyes.

This experiment shows that the sense of touch can be used to give a pretty good image of what an object is, but the information takes time to build up. Also, for the process to work efficiently, we need a memory for things that we have experienced before – in this case, a tactile memory.

Sensing pain and discomfort

The same nerve endings that respond to mechanical pressure and allow this kind of tactile exploration also respond to temperature and any substances or events that cause damage to the skin, such as cuts, abrasions, corrosive chemicals or electric shock. The sensation of pain associated with such events usually initiates a response of rapid withdrawal from the thing causing the pain.

There are similar nerve endings inside our bodies, which enable us to sense various kinds of 'warning signals' from within. An example of this is that dreadful 'morning-after' syndrome, comprising headache, stomach ache and all the other cues that try to persuade us to change our lifestyle before we damage ourselves too much!

SENSE ORGANS

The role of our sense organs is to 'capture' the various forms of energy that convey information about the external world, and to change it into a form that the brain can handle. This process is called *transduction*.

transduction the process of transforming one type of energy (e.g. sound waves, which are mechanical in nature) into another kind of energy – usually the electrical energy of neurons

As a transducer, a sense organ captures energy of a particular kind (e.g. light) and transforms it into energy of another kind – action potentials, the neural system's code for information. Action potentials are electrical energy derived from the exchange of electrically charged ions, which inhabit both sides of the barrier between the neuron and its surroundings (see chapter 3). So our eyes transduce electromagnetic radiation (light) into action potentials, our ears transduce the mechanical energy of sound, and so on.

Transduction is a general term, which does not apply only to sense organs. A microphone is a transducer, which (rather like the ear) transduces mechanical sound energy to electrical potentials –

but in a wire, not in a neuron. There are many other examples of transduction in everyday equipment.

As we gradually move away from physics and into psychology, we pass through an area of physiology – how biological transducers work.

How do we see?

We know that light travels in straight lines. It therefore makes sense for a biological transducer of light to preserve information about the direction from which a particular ray of light has come. In fact, this consideration alone accounts for a large swathe of visual evolution.

As creatures have become larger and therefore begun to travel further, they have developed an ever greater need to know about things that are far away – so eyes have developed an increasing ability to preserve spatial information from incident light. Where is each ray coming from?

To achieve this, there must be some means of letting the light strike a particular *photoreceptor*. This is the name given to the smallest unit that transduces light. If a given photoreceptor always receives light coming from a given direction, then the directional information inherent in light can be preserved.

photoreceptor a cell (rod or cone) in the retina that transforms light energy into action potentials

Pinhole cameras and the need for a lens

The simplest way to illustrate light transduction is to make a pinhole camera – a box with a small hole in it (see figure 7.7). From

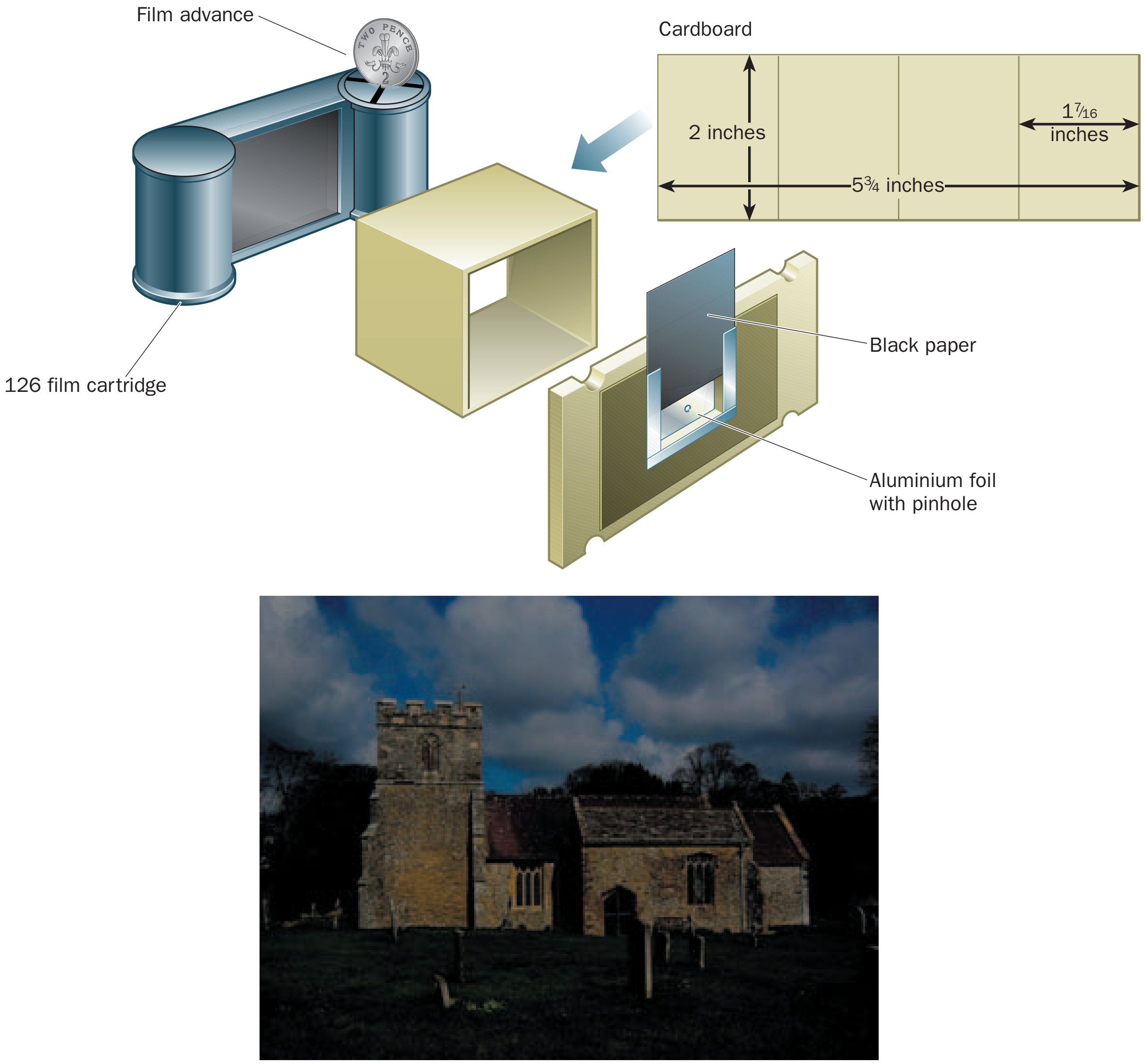


Figure 7.7

Above, a pinhole camera, which is quite simple to construct, and requires no lenses or mirrors. Below, a picture taken with this camera.

Figure 7.8

An image taken through a larger pinhole. Note that the image is brighter than that in figure 7.7, but also more blurred.

the geometry of rays travelling in straight lines, it is possible to see that a given place on the rear surface of the pinhole camera will only receive light from one direction. Of course, this is only true until you move the camera. But even then, the relative positional information is usually preserved – if something is next to something else out there, its ray will be next to its neighbour's ray on the back surface of the camera.

One of the drawbacks with a pinhole camera is that the image (the collection of points of light on the back of the box) is very dim, and can only be seen in very bright, sunny conditions. If you make the pinhole bigger to let more light through, the image becomes fuzzy, or blurred, because more than one direction of incident light can land on a given point on the back surface (figure 7.8). With this fuzziness we begin to lose the ability to encode direction.

The solution is to place a lens over the now-enlarged hole. The lens refracts (bends) the light so that the sharpness of the image is preserved even if the pinhole is large. Add film and you have a normal camera. The same construction in your head is called an eye.

Nature evolved lenses millions of years ago. We then reinvented them in Renaissance Italy in about the 16th century. Possibly the earliest description of the human eye as containing a lens was given by Arab scholar Abu-'Ali Al-Hasan Ibn Al-Haytham, often abbreviated to Al Hazen, in the eleventh century AD. Al-Haytham was born in Basra – now an Iraqi town, which has had a sadly turbulent history recently.

Pioneer

Abu-'Ali Al-Hasan Ibn Al-Haytham (965–1040) often abbreviated to Al Hazen, was born in Basra, Iraq. He studied the properties of the eye and light at a time when European science was singularly lacking in progress. He is remembered for the discovery that the eye has a lens which forms an image of the visual world on the retina at the back of the eyeball.

Looking at the eye in detail

In human vision, there are two types of photoreceptors, called *rods* and *cones*. Rods are cells that only work at low levels of illumination, at night; cones are cells that give us our vision in normal daylight levels of illumination. There is only one kind of rod, but three different kinds of cone, each responding preferentially to a different range of wavelengths of light – the basis of colour vision.

rods cells in the retina that transform light energy into action potentials and are only active at low light levels (e.g. at night)

cones cells in the retina that transform light energy into action potentials, different kinds responding preferentially to different wavelengths

Figure 7.9 shows how light travels through the cornea, pupil and lens, eventually falling on the retina, which is illustrated in more detail in figure 7.10.

When a ray of light hits a photoreceptor (a rod or a cone), it sets up a photochemical reaction, which alters the electrical potential inside the photoreceptor. This, in turn, produces a change in the firing rate of the neuron connected to that photoreceptor. There are four types of neuron in the retina (see figure 7.9) – horizontal, bipolar, amacrine and ganglion cells.

Now we meet with a problem: there are about 100 million photoreceptors but only about one million neurons in the *optic nerve*. Nobody really knows why, but the most persuasive argument is that if you made the optic nerve thick, then the eye could not move! How can all the important information be squeezed into these few neurons? The only way is to discard a lot of redundant information. Think about how you would give instructions for someone to find your home. It is usually a waste of time to describe exactly how long they need to walk in a straight line. Instead, you might say, 'turn left, then right, then second left'. What you are doing is noting the points of change in the route information.

optic nerve conveys information from the retina to the visual cortex

The retina does pretty much the same thing. It signals the points of change in the image – i.e. the places where intensity or colour alter – and ignores regions where no changes occur, such as a blank uniform surface.

receptive field a region of the visual world where a change in the intensity of light results in changes in production of action potentials in a neuron

Figure 7.11 shows how each retinal ganglion cell has a *receptive field* – a particular part of the visual world. If you change the amount of light in this field, you will produce a change in the cell's activity. A neuron only changes its firing rate when there is an abrupt change in the amount of light falling on

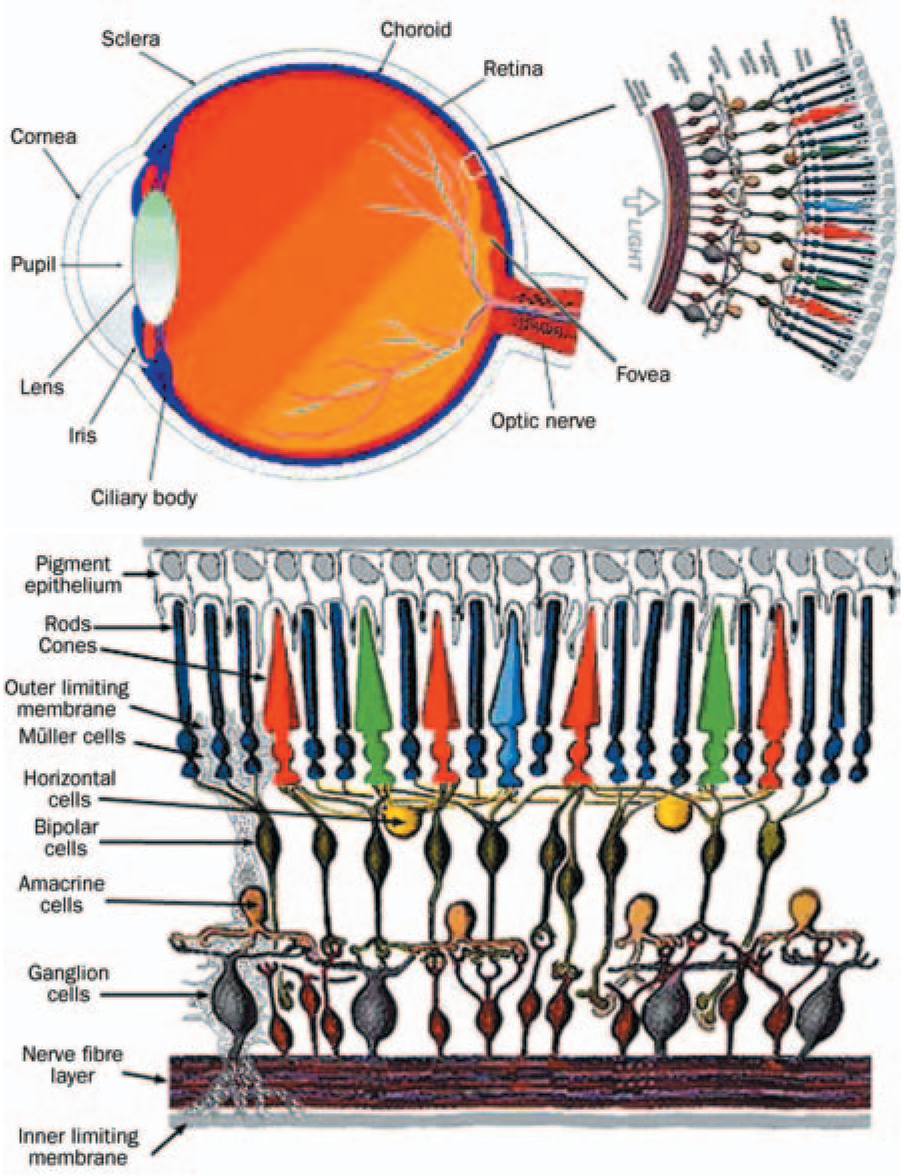


Figure 7.9

A section through the human eye which shows how light reaches the retina, which is shown in expanded section in the lower part of the figure. Note that the retina is the only piece of brain that we can observe directly in a living human. We can look into the eye with a device called an ophthalmoscope, and take pictures of the retina in a similar way. Figure 7.10 shows such images – a healthy retina, and one which is afflicted by a common illness called age-related macular degeneration. An ophthalmologist is trained to spot the onset of retinal pathology. Source: http://webvision.med.utah.edu/sretina.html

the receptive field – for example the boundary between a white object and a dark background.

The retina contains many such receptive fields in any one location, so there is a large degree of overlap between them. They are smallest in the area called the *fovea*, the high-acuity part of which occupies approximately the central one degree of the visual field. This is the part of the retina that receives light rays from the direction you are looking in. Since a receptive field cannot distinguish between different locations within it, the smaller the receptive field is, the finer the spatial detail that can be resolved. So the fovea is able to resolve the finest detail.

fovea the central five degrees or so of human vision, particularly the central, high-acuity part of this area (about one degree in diameter)

To convince yourself of this, try looking at the opposite page out of the corner of your eye and then try to read it. If you

Pioneer

Thomas Young (1773–1829) was a physicist who postulated that there are only three different kinds of photoreceptors in the retina, even though we can distinguish thousands of different colours. The basis of this argument was that, to have thousands of different photoreceptors would compromise the acuity of the eye, since the acuity is determined by the distance to the nearest neighbour of the same type. Later, Hermann von Helmholtz added the physiological basis of this argument. Thomas Young also studied the mechanical properties of materials, defining a number later known as Young's Modulus to describe how stretchable a material is. In Young's days, there was no distinction between the subjects which we now call physics, psychology and physiology.

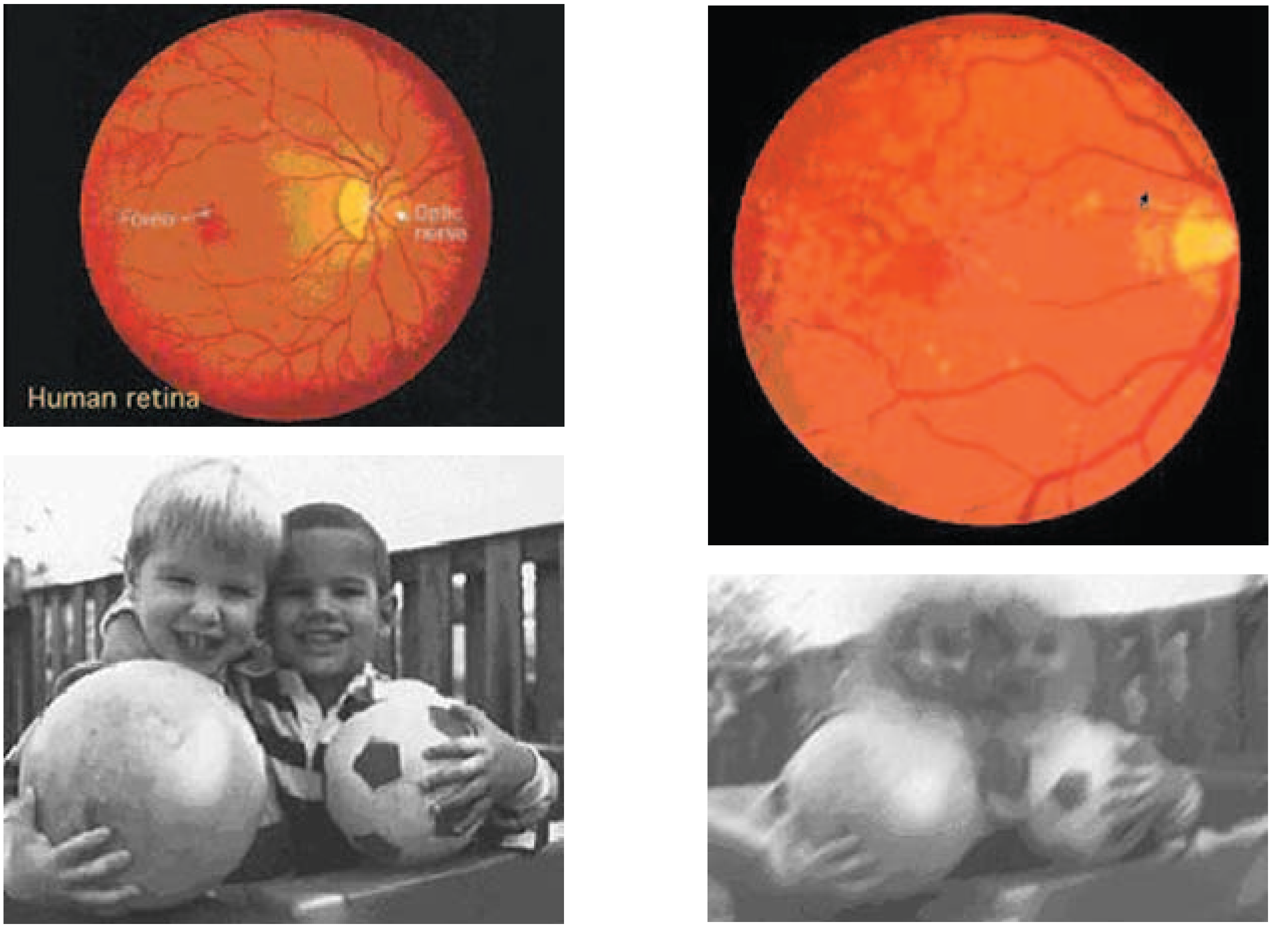


Figure 7.10

A view of a normal human retina (on the left). Note the fovea, which is the area which gives high-acuity vision with densely packed photoreceptors and no retinal blood vessels. On the right is a retina of a patient with age-related macular degeneration, a common retinal condition affecting elderly people. Note the 'splodgy' abnormal structure of the retina in the area near the fovea. Such a patient would be unable to use their central, high-acuity vision and would probably be registered blind. The images at the bottom attempt to demonstrate the vision as seen by people with normal vision and by those with age-related macular degeneration. Source: http://webvision.med.utah.edu/sretina.tml

cannot do so, it is because the receptive fields in the periphery of your retina are larger and incapable of resolving the small print.

Vision as an active process

Of course, our eyes are able to move in their sockets, and this allows the visual system to choose new parts of the image to look at. These rapid eye movements, called *saccades*, occur several times per second. We are mostly unaware of them and, during a saccade, vision is largely 'switched off' so that we do not see the world moving rapidly in the opposite direction to the saccade (see also p. 255).

saccades rapid eye movements in which the fovea is directed at a new point in the visual world

Figure 7.12 presents the results of two studies. One is a classic study by the Russian psychologist Yarbus (1967), which shows how we move our eyes when looking at a visual object. The other is a study by Gilchrist, Brown, and Findlay (1997), which investigated similar scan patterns by a young woman (a female university undergraduate aged 21) who had no ability to move her eyes due to a condition called extraocular muscular fibrosis. Instead, she moved her whole head using the neck muscles. There are strong similarities between the two sets of scan patterns, indicating that, even if the eye cannot move, the image scan sequence needs to be broadly similar.

All of this raises the question of exactly why the eye needs to be moved to so many locations. Presumably it is to resolve fine detail by using the fovea with its small receptive fields. Moving the eyes in this manner is usually associated with a shift of attention.

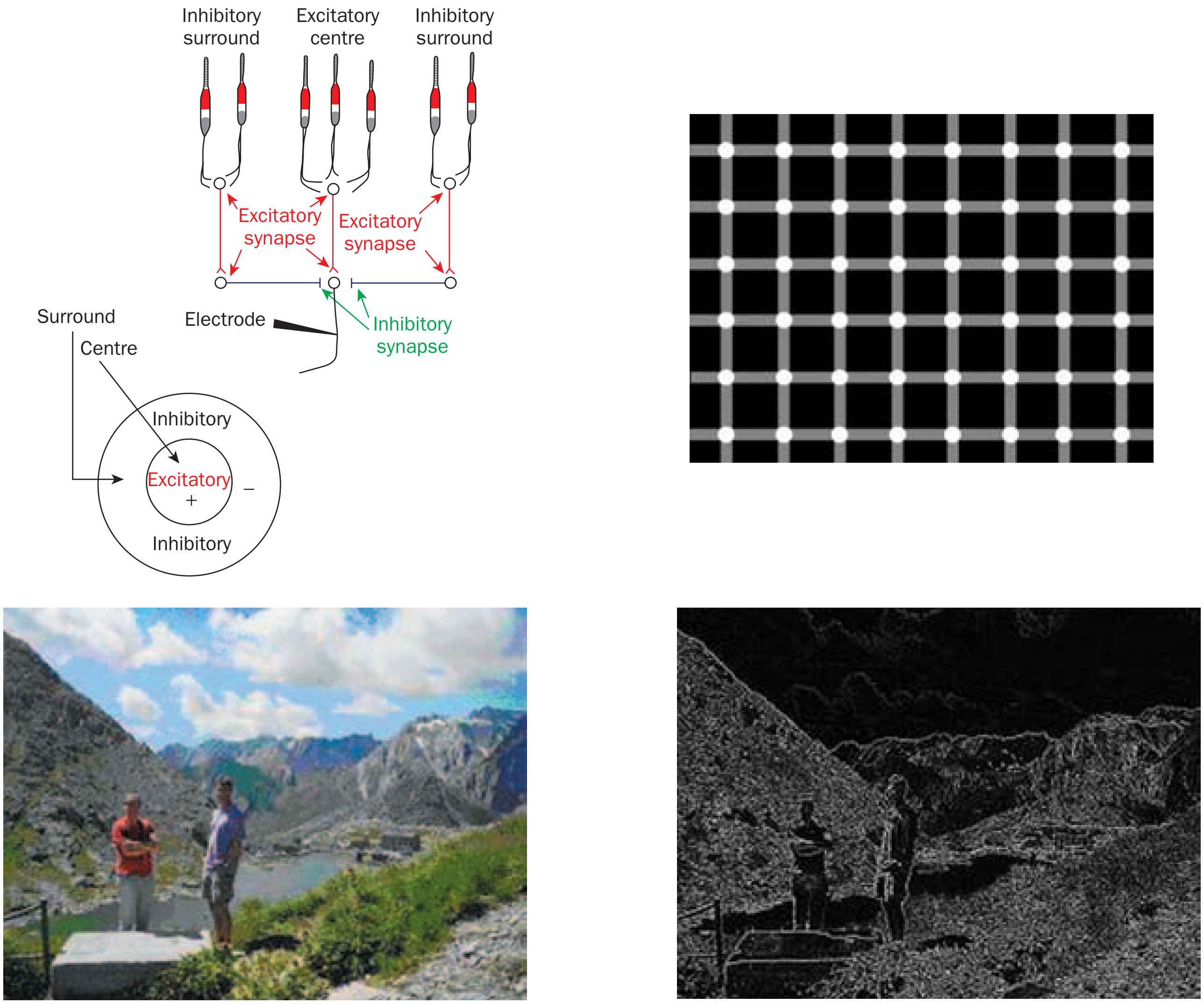


Figure 7.11

The basis of receptive fields in the retina. The diagram shows how retinal signals from different photoreceptors are combined and organized into ‘excitatory’ and ‘inhibitory’ regions, which can be mapped by placing an electrode in the ganglion cell neuron and waving a light around in different regions of the visual field. Those regions where light produces more neuronal firing are called excitatory, and those where light stimulation results in less neuronal firing are called inhibitory. The panel shows a variant of the Hermann Grid illusion, in which illusory grey spots are seen at the intersections of the light crosses. The traditional explanation for these illusory grey spots is from the action of centre/surround receptive fields. Finally, we show a natural scene and the ‘edges’ that are output by centre/surround receptive fields. These edges occur where there is a sudden change in intensity on the retina, which often corresponds to edges of real objects in the image, e.g. the people.

When we move our eye to a given location, we are more likely to be processing the information from that location in greater detail than information from elsewhere. This is the concept of selective attention (see chapter 8). The process is intimately related to physical action, in this case movement of the eyes (or head). This implies that vision is not just a passive process, but an active one. In fact, there appear to be two streams of visual information in the cortex – *ventral* and *dorsal*. The former processes information about the nature of objects; the latter allows you to interact with ‘stuff out there’ – i.e. to plan actions – without a detailed representation of objects (see Milner & Goodale, 1995).

Seeing in colour

So far, we have looked at how the retina responds to rapid spatial changes in illumination. But it also selectively signals temporal changes, such as occur when there is a flash of lightning or (more usefully) when a tiger suddenly jumps out from behind a tree

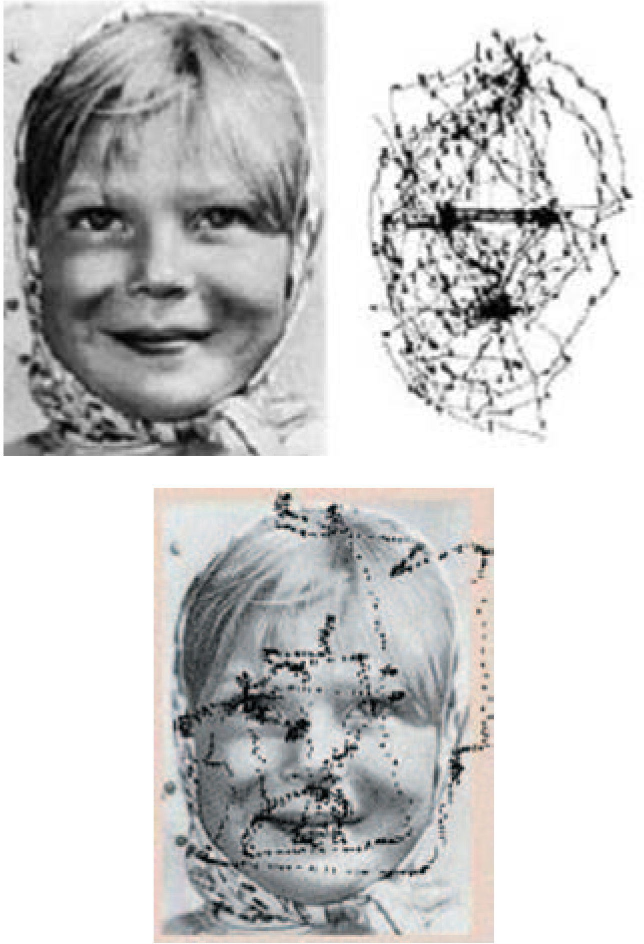


Figure 7.12

At the top, a photograph of a girl used as a stimulus by Yarbus (1967) in a study designed to measure rapid eye movements (saccades) made by the observer. The panel next to the photograph shows the locations of these eye movements, which go to regions of interest in the image and allow them to be resolved by the high-acuity fovea. At the bottom, a scan pattern measured by Gilchrist, Brown and Findlay (1997) in an observer who had no eye movements due to a failure of the ocular muscles, and instead moved her whole head with her neck muscles to scan the same image. Sources: top, Yarbus (1967); bottom, Gilchrist et al. (1997).

or moves against a background of long grass, so breaking its camouflage.

There are various mechanisms involved in processes of adaptation to static scenes (see chapter 8). Perhaps the best-known form of adaptation occurs when we enter a dark room on a sunny day. At first we cannot see anything, but after a few minutes we begin to notice objects in the room, visible in the faint light there. This phenomenon occurs because our receptors become more sensitive when they are not stimulated for a while, and also because there is a change from cone vision to rod vision.

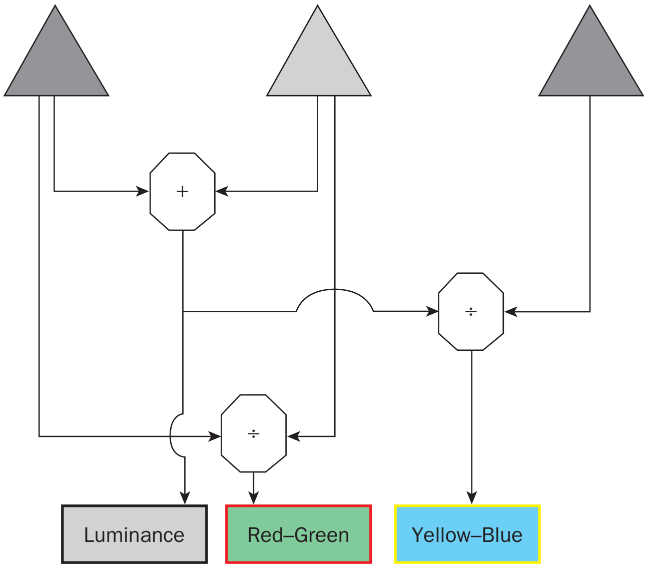


Figure 7.13

A combination of colour information from the three types of retinal cone resulting in three ‘opponent’ channels signalling luminance (intensity), the red–green dimension of colour, and the yellow–blue dimension of colour.

You may have noticed that in a faint light all objects appear to have no colour, quite unlike our daylight vision. This is because there is only one type of rod but three different types of cone, and the cones have a dual function: they encode the amount of light present, but they also encode colour, since they are maximally sensitive to different wavelengths in the visible spectrum.

Figure 7.13 shows how the outputs of the cones are compared. It is important to realize that they must be compared, since the output of a single cone cannot unambiguously encode wavelength.

Suppose you have a cone maximally sensitive to light which has a wavelength of 565 nm. By using an electrode to measure the output of this cone (do not try this at home!), suppose you find that the cone is producing a ‘medium’ level of output. Can you deduce that the cone is being stimulated by a ‘medium’ amount of light whose wavelength is 565 nm? No – because precisely the same response would arise from stimulation by a larger quantity of light of a slightly different wavelength – say 600 nm. This is because cones do not respond in an ‘all or none’ manner to rays of light of a given frequency. Instead, they show a graded response profile.

We have three different types of cone in the retina. They are sometimes called ‘red’, ‘green’ and ‘blue’ cones. More strictly, we refer to these cones as ‘L’, ‘M’ and ‘S’ cones, which refers to the fact that the L cones respond most to long-wavelength light, M cones to medium-wavelength light, and of course S to short-wavelength light.

So the output of a single cone is fundamentally ambiguous, and for a meaningful colour sensation to arise, we must know how much one cone type responds compared to another

Research close-up 1

How do we know when things are moving?

The research issue

Motion blindness, also known as akinetopsia, is very rare. It is usually the result of trauma or other lesions to the parieto-temporal area of the cerebral cortex. As with many other neuropsychological conditions, it helps us to understand not only impaired functioning, but also the functional characteristics of the non-damaged system.

Zihl, von Cramon and Mai (1983) identified a patient with bilateral posterior brain damage to an area considered to be similar to the monkey brain area MT (also called V5), which is believed to be responsible for motion perception. The findings of this study indicate that the patient (M.P.) experienced disturbance of movement vision in a rather pure form.

Design and procedure

The specificity of the deficit in M.P.'s movement perception was systematically investigated. Tests included those for the perception of: colour, form, depth, movement, after-effects as well as acoustic and tactile perception. Where relevant, visual perception in both the central and peripheral regions of the visual field was evaluated.

Results and implications

Both colour perception and form perception were found to be within the normal range. But M.P. apparently had no impression of movement in depth, and she could only discriminate between a stationary and a moving target in the periphery of her otherwise intact visual fields. It was apparent that M.P. had some movement vision in the central part of her visual fields, but this was observed reliably only if the target velocity did not exceed 10 degrees of arc per second. M.P. also failed to demonstrate perceptual signs such as visual movement after-effects (see chapter 8) or apparent visual movement phenomena. Visually guided eye and finger movements were impaired too.

In contrast to the disturbance of movement perception in the visual modality, movement perception elicited by acoustic and tactile stimuli was not impaired in M.P. This suggests there was selectivity of her lesion with respect to (a) the sensory modality of vision and (b) movement perception within this modality.

On the basis of the localization of M.P.'s cerebral damage (as evaluated via brain scanning as well as the kind of neuropsychological testing just described), it was concluded that selective impairment in movement perception is due to bilateral cerebral lesions affecting the parieto-temporal cortex and the underlying white matter in this region of the brain.

The selectivity of the visual disturbance in M.P. supports the idea that movement vision is a separate visual function, depending on distinctive neural mechanisms.

Subsequently, other similar clinical cases have been reported. Other areas of research which are relevant to address the questions raised by patient M.P. include electrophysiological studies, lesion-based methodologies and functional magnetic resonance imaging (fMRI) recordings of brain activity in awake non-brain-damaged humans while they are viewing moving stimuli.

Taken together, these findings support the idea that there are bilateral regions of the parietotemporal cortex that are selectively involved in the processing and perception of motion.

Zihl, J., von Cramon, D., & Mai, N., 1983, 'Selective disturbance of movement vision after bilateral brain damage', *Brain*, 106, 313–40.

chromatic opponency a system of encoding colour information originating in retinal ganglion cells into red–green, yellow–blue and luminance signals; so, for example, a red–green neuron will increase its firing rate if stimulated by a red light, and decrease it if stimulated by a green light

cone type. This is achieved through *chromatic opponency*, a process that also explains why we can see four 'pure' colours – red, yellow, green and blue – even though there are only three kinds of cone. The 'yellow' sensation arises when L and M cones receive equal stimulation. Their combined output is then compared to that of the S cones. If L+M is much greater than S, we see yellow, and if less, we see blue. If L+M is about the same as S, we see white.

Figure 7.14 shows how these opponent processes encode detail in natural scenes. This effect was achieved using a special kind of camera, first constructed by Parraga, Troscianko and Tolhurst (2002), which produces different cone responses for each point in the scene (or pixel in the image). Parraga et al. found that the red–green system is suited to encoding not just the colour properties of images of red fruit on green leaves, but also the spatial properties of such images for a foraging primate.

We know that the receptive fields for colour are different from the receptive fields for luminance. Specifically, they lack the 'centre-surround' structure that makes the centre effectively as big as the whole receptive field. As a result, we are less sensitive to fine detail in colour than in luminance.

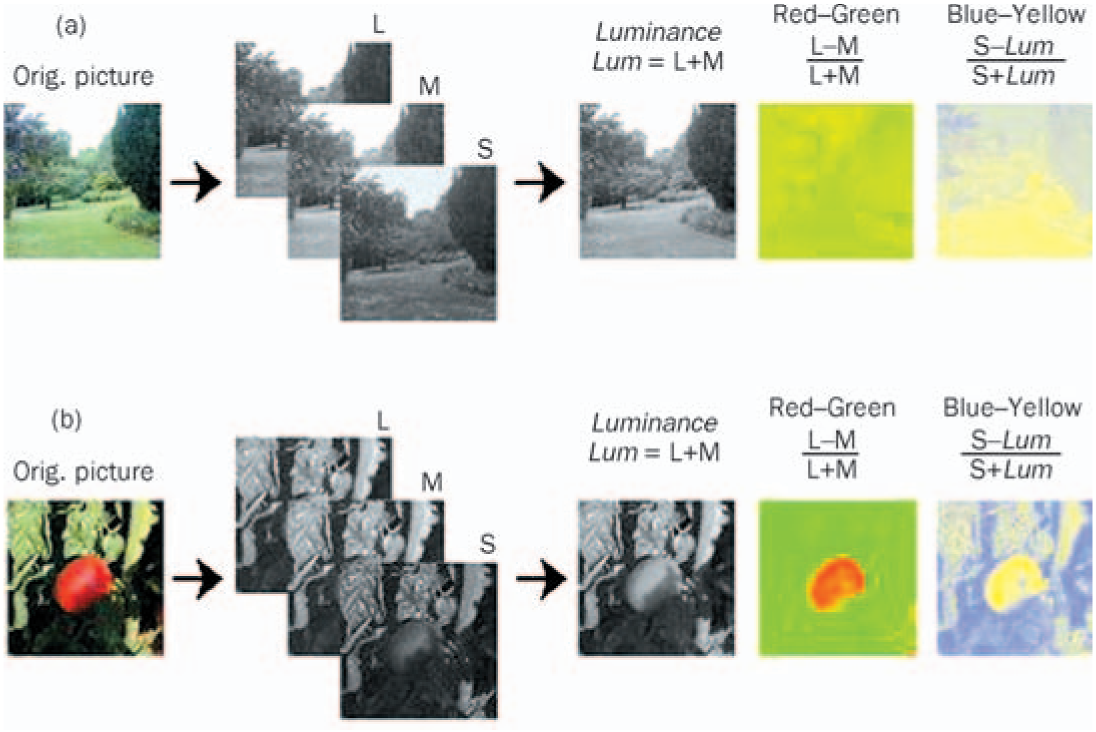


Figure 7.14

Two images encoded via the cones and opponent processes. On the left are the two images. Next, we show the L, M, and S cone responses to these images. Finally, we show the three opponent responses to these two scenes. Note that the red–green mechanism removes shadows from an image of red fruit on green leaves, and therefore allows the visual system to see a 'clean' image of the fruit and its background.

Figure 7.15 shows an early attempt to capitalize on this. Early photographs were only in black and white, but the technique of using watercolours to paint the various objects (e.g. blue sky) on top of the photograph became quite popular. The interesting point is that the paint only needed to be added in approximately the right areas – some creeping across object boundaries did not seem to matter.

About fifty years later, the inventors of colour TV rediscovered this fact. The trick is to find a way of transmitting as little information as possible. So only a sharp luminance image is transmitted. The two chrominance (colour) images are transmitted in blurred form, which means that less information needs to be transmitted without a perceived loss of picture quality (Troscianko, 1987). The main consequence of this 'labour-saving' trick in the brain is that the optic nerve can contain relatively few neurons.

The optic nerve conveys the action potentials generated by the retina to other parts of the brain, principally the *primary visual cortex*, also known as Area V1, where the

primary visual cortex a region at the back of the visual cortex to which the optic nerves project, and which carries out an initial analysis of the information conveyed by the optic nerves

Figure 7.15

A postcard of the Thames Embankment from 1904, with the colour information added by hand-tinting. Close inspection reveals that the colour tint has been added in an imprecise manner. Modern colour TV uses the same principle, based on the idea that the human visual system processes colour information at a coarser scale than intensity information.

Pioneer

John Lythgoe (1937–92), a biologist at Bristol University, studied the relationship between the sense organs and visual apparatus of an animal, and between its surroundings and the tasks it has to perform within these surroundings. Lythgoe's main research was on fish living at different depths of water, since the depth of water affects the wavelength composition of daylight reaching that point. He found a marked relationship between where the fish lived and what their cones were like. His research founded a flourishing new research discipline called 'ecology of vision' with the publication of his book in 1979 (*The Ecology of Vision*).

information is then analysed and distributed further to other visual areas (see chapter 8).

How do we hear?

Since sound does not travel in straight lines, it is not important to have a particular sound receptor pointing in a unique direction in space in the way that photoreceptors do. This considerably simplifies the design of an ear (figure 7.16).

The outer part of the ear – the *pinna* – routes the sound waves in towards the passage leading to the *eardrum*. The incoming sound waves then set up mechanical vibrations of the eardrum, which is connected via a system of tiny bones to the oval window of an organ called the *cochlea*. These bones function like a gear-box, transforming the *amplitude* of the vibration to one which is useable by the cochlea.

The cochlea (so called because its structure resembles a snail's shell), shown in figure 7.16, contains a membrane stretched along its length. This is the basilar membrane, and all parts of it are attached to very delicate elongated cells, called *hair cells*. When a given part of the basilar membrane vibrates, a deformation occurs in the group of hair cells that are attached there. This deformation is the stimulus for the production of action potentials in the neuron attached to the hair cell. The neurons are bundled together and become part of the *acoustic nerve*, which transmits information to the *auditory cortex*.

pinna the structure made of skin and cartilage on the outer part of the ear

eardrum a membrane between the outer and middle ear that vibrates when sound waves reach it

cochlea coiled structure in the inner ear responsible for transforming mechanical vibration (sound energy) into action potentials in the acoustic nerve

amplitude the difference between the peaks and troughs of a waveform

hair cells long, thin cells in the cochlea and the vestibular system, which, when bent, produce an action potential

acoustic nerve conveys information from the cochlea to the auditory cortex

auditory cortex a region of the cortex devoted to processing information from the ears

Volume, pitch and timbre

Vibrations reaching the ear can differ in amplitude and frequency. Different frequencies cause the basilar membrane to vibrate in different places, stimulating different sub-populations of hair cells. For low frequencies, the site of maximal vibration lies further from the oval window of the cochlea than for high frequencies.

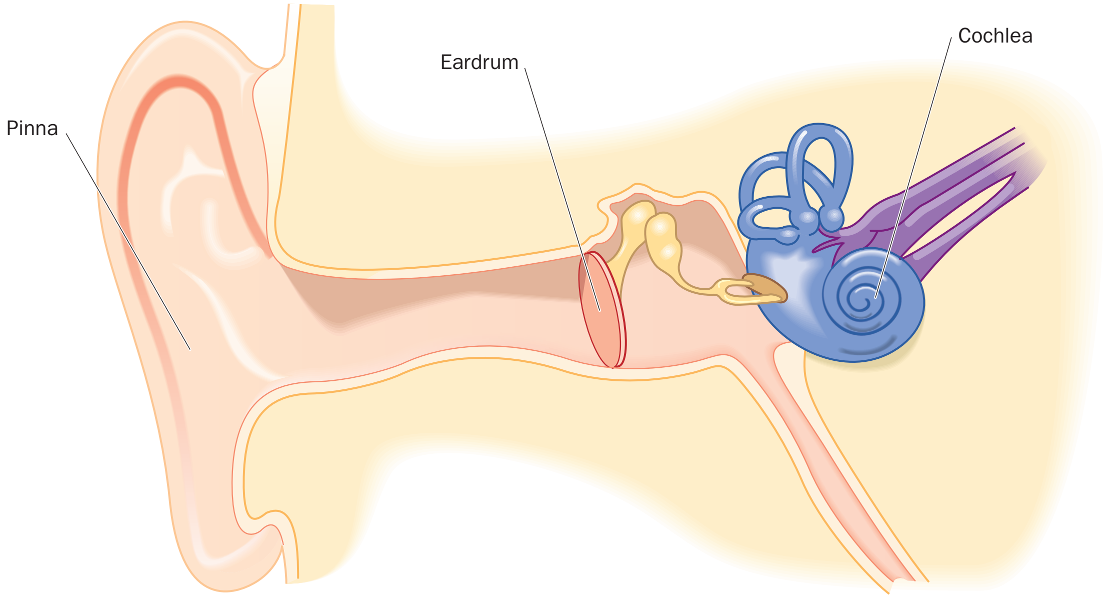


Figure 7.16

A diagram of the three parts of the ear. Source: www.iurc.montp.inserm.fr/cric/audition/english/ear/fear.htm

Everyday Psychology

Development, diagnosis and treatment of visual defects among infants

Imagine that you have recently become a proud parent. But a few months later you notice that your child is squinting in order to see. What can be done? Can psychology help?

Binocularity, the mechanism by which signals from two eyes interact, is a key feature of cortical organization. Binocular function among infants first appears between 12 and 17 weeks. Studies show that from this age onwards recordings of electrical brain activity can help us to understand the nature of the problem (see Braddick & Atkinson, 1983, for a review). When non-corresponding random dot patterns seen by the two eyes suddenly come into exact correspondence, an electrical signal can be detected from the surface of the scalp (an *evoked potential*; see chapter 3), indicating a brain response to a sensory event. These findings imply a form of selectivity: it appears that there are neurons that require a correlated input from both eyes for optimal activation to occur. In circumstances where binocularity does not develop properly, however, two abnormal conditions may arise: *amblyopia* and *strabismus.*

Amblyopia is a functional loss of visual performance, usually in one eye. Physiological studies in cats and monkeys (see Blakemore, 1978, for a review) demonstrate that if an animal has one eye covered in early life, or its image grossly blurred, that eye loses almost all connections to the visual cortex. Similarly, in humans, it appears that having a dense cataract clouding one eye produces the strongest form of human amblyopia. This might be explained in terms of a key adaptive function of the brain: nerve fibres carrying signals from the two eyes effectively compete for access to cortical neurons, the brain becoming more responsive to significant inputs at the expense of inactive ones. Essentially, if one eye is not frequently stimulated by visual input, it may become functionally disconnected from the brain.

Strabismus (squint) is a condition in which the two eyes become permanently misaligned. While both eyes retain their input to the visual cortex, the cortex lacks neurons that combine inputs from the two eyes. This suggests that to establish and maintain cortical connections requires not just activity but correlated activity that occurs when the two eyes are receiving the same stimulus (Atkinson & Braddick, 1989). If children with strabismus lack cortical neurons with binocular input, we would expect impairment in functions such as *stereopsis*. This has been confirmed in clinical and experimental studies.

stereopsis the ability to see objects three-dimensionally based on having two eyes that give us two slightly different views of those objects and their relative locations in space

But why does strabismus develop? Infants with the condition may intrinsically lack cortical neurons with binocular input. Most, however, initially have normal cortical binocularity. One explanation for why infants go on to develop strabismus is linked to hypermetropia (or hyperopia). This is a form of refractive error in which the eye, when relaxed, is focused beyond infinity, resulting in the blurring of objects at all distances. Children suffering from this disorder need to accommodate more rigorously than normal even for distant objects, but if the child has difficulty focusing with both eyes on one point, neurons that respond to binocular input may become inactive.

Fortunately, research on perception can be used to minimize abnormal visual conditions of this kind if there is early screening for vision. Hypermetropia in infancy has been found to have a high correlation with pre-school onset of both strabismus and amblyopia, and once hypermetropia is detected in infants they can be given prescription spectacles to reduce accommodation and thus prevent the development of strabismus in later childhood. Atkinson (1989) undertook a randomized controlled trial in which half the infants (aged between six and nine months) diagnosed with hypermetropia were offered a spectacle correction that brought their refraction close to the norm for their age group. Compared to a control group of uncorrected infants, the correction led to significantly better vision at three and a half years compared to the control group.

Atkinson, J., 1989, ‘New tests of vision screening and assessment in infants and young children’ in J.H. French, S. Harel and P. Casare (eds), *Child Neurology and Developmental Disabilities*. Baltimore: Brookes Publishing.

Pioneer

Georg von Bekesy (1899–1972) was a Hungarian physiologist working on hearing at Harvard University whose most famous discovery was that different parts of the basilar membrane in the cochlea are stimulated by different frequencies of sound. He won the Nobel Prize for medicine in 1961 for this type of work.

This is how the cochlea achieves *frequency selectivity*. Differences in the physical variable we refer to as sound frequency give rise to differences in the psychological attribute we refer to as *pitch*.

The physical amplitude of the incoming wave translates into the sensation of loudness.

frequency selectivity the degree to which a system (e.g. a neuron) responds more to one frequency than another

pitch auditory sensation associated with changes in frequency of the sound wave

This is encoded by a combination of (a) increased firing rate in auditory neurons and (b) a greater number of neurons firing. Finally, acoustic signals can vary in their complexity. The same note played on a piano and violin sound different, even though their fundamental frequencies are the same. This difference in sound quality gives rise to the sensation of *timbre*.

timbre the complexity of a sound wave, especially one emitted by a musical instrument, allowing us to distinguish the same note played on, say, a piano and a guitar

Of course, our auditory system did not evolve to hear musical instruments. More likely, it is there to make sense of complex signals occurring naturally in nature. Figure 7.17 shows how different sources of sound produce a different pattern of amplitude and frequency over time. These different patterns are recognized as different sounds – in the case of speech, as different *phonemes*. A phoneme is a speech sound, such as the ‘sh’ in ‘rush’. The English language contains around 40 phonemes (Moore, 2003, p. 301). We can look more closely at the sounds in a word by plotting the relationship between the amplitude and frequency of the sound over time in a *spectrogram* – so called because it displays the spectrum of sound (figure 7.18).

phonemes basic building blocks of speech: English contains around 40 different phonemes

spectrogram a way of plotting the amplitude and frequency of a speech sound-wave as we speak individual phonemes

Deducing sound direction

Although sound is less directional than light, information about direction can be deduced from sound. The role of the pinna

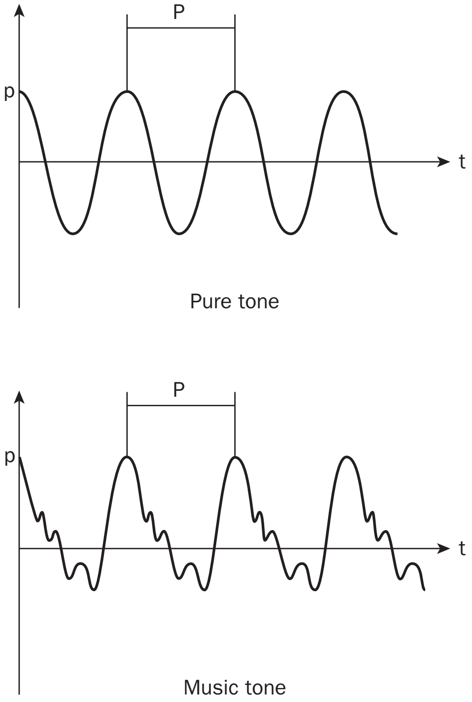


Figure 7.17

The upper diagram represents the waveform of a pure tone with period P (wavelength), which gives the pitch of the tone. p = air pressure at eardrum. The lower diagram shows the waveform produced by playing the same note (pitch) on a musical instrument – in this case, a violin. The period (wavelength) of the waveform is the same, hence the similarity in pitch. The extra complexity in the waveform gives the sound its timbre, which is what distinguishes the same note played on (say) a violin and a trumpet.

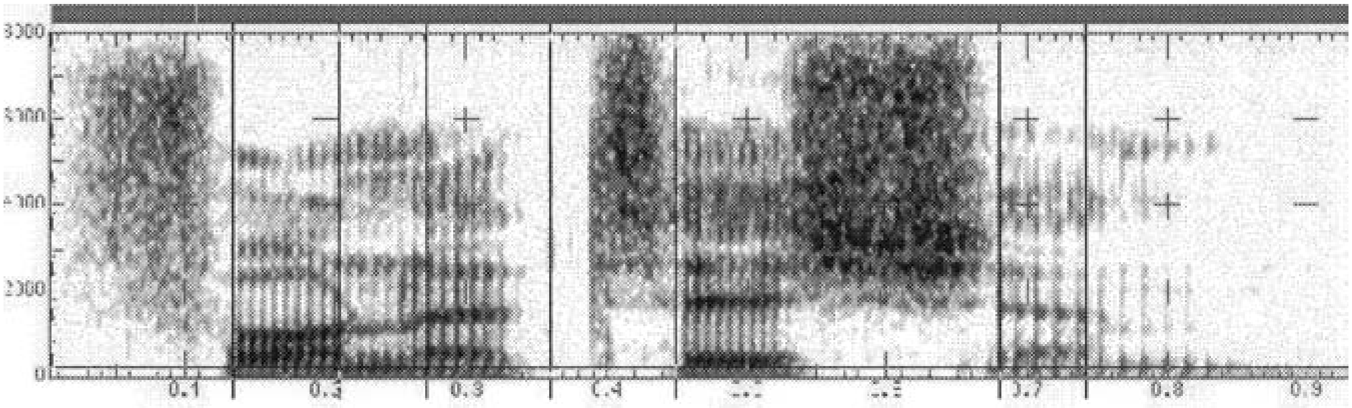


Figure 7.18

The spectrogram of the word ‘phonetician’, showing the individual phonemes along the x-axis and the frequencies in Hz along the y-axis. The darker the blob, the more of the frequency is present. So, for example, the ‘f’ sound has a much broader spectrum of frequencies than the ‘o’ sound – which is why the ‘f’ sound is more like the sound of a waterfall (noise which contains all frequencies is called ‘white noise’). Each phoneme has a different frequency composition, and also varies across time. Source: www.ling.lu.se/research/speechtutorial/tutorial.html seems to be to route the sound towards the eardrum, but they also produce small echoes, which allow us to distinguish something that is high up above us from something that is below us.

Horizontal information is given by comparing signals from the two ears. For low frequencies (up to about 1000 Hz) the time of arrival of each peak of the sound vibration contains this information. A sound wave coming from the right will reach our right ear about 1 ms before it reaches our left ear, and this 1 ms difference is detected by the auditory system. For higher frequencies, where there are too many wave crests per second for a 1 ms difference to be meaningful, it is the amplitude of the sound that matters. A source to our right will project a higher amplitude to the right ear than to the left ear, since the head attenuates sound (in other words, sound reduces in amplitude as it passes through the head by being partially absorbed). This, too, provides directional information.

TASTING AND SMELLING

We know that information travels to our chemical senses (taste and smell) much more slowly and lingers after the stimulus has gone. Simple logic will therefore suggest that the time-course of the transduction is less critical than for hearing and vision.

A matter of taste

Gustation (taste) is relatively simple in that it encodes only five dimensions of the stimulus: sourness, sweetness, saltiness, bitterness, and 'umami', which is a taste similar to monosodium glutamate. The receptors for taste – our taste buds – are on the surface of the tongue.

Figure 7.19 shows a microscope image of mammalian taste buds. Different types of chemical molecules interact differently with the taste buds specialized for the five different taste sensations. Salty sensations arise from molecules that ionize (separate into charged ions) when they dissolve in the saliva. Bitter and sweet sensations arise from large non-ionizing molecules. Sour tastes are produced by acids, which ionize to give a positively charged hydrogen ion. The umami taste is produced by specific salts such as monosodium glutamate.

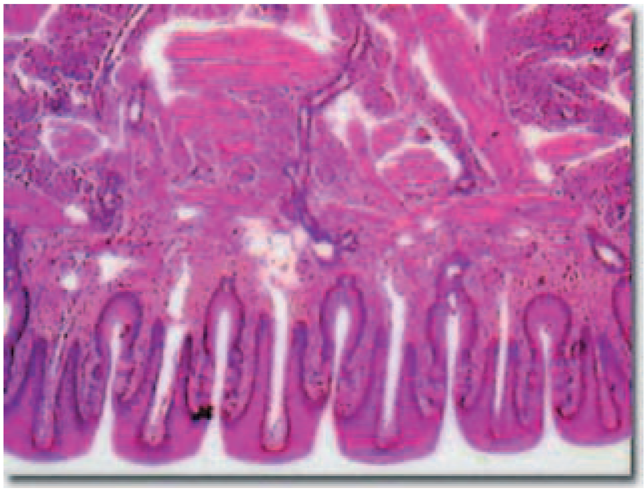


Figure 7.19

Taste buds on the mammalian tongue.

The mystery of smell

Olfaction (smell), on the other hand, is shrouded in mystery (figure 7.20 shows the olfactory system). We do not understand much about how the receptors in the nose respond to different trigger molecules carried in the air that we breathe. It seems a fair assumption that these airborne molecules interact with specific receptors to elicit certain sensations. Unlike the other senses, there is a vast array of receptor types, possibly up to 1000 (see Axel, 1995).

Subjectively, it seems that smell elicits certain memories and is notoriously hard to describe verbally. The flavour of a food

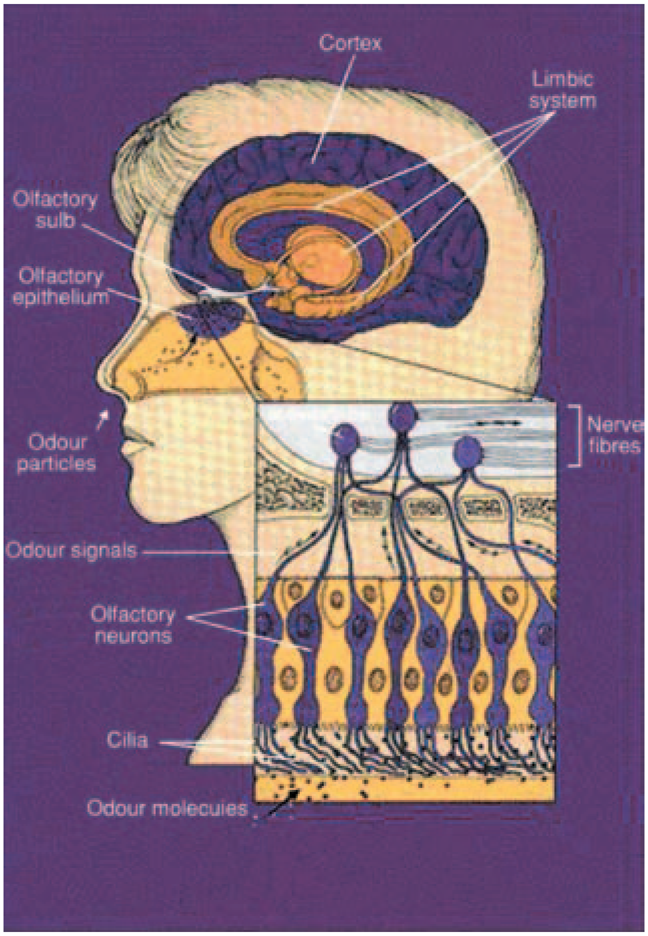


Figure 7.20

The human olfactory system. Molecules containing those chemical substances that produce the sense of odour interact with cilia in the olfactory epithelium. Source: www.sfn.org/content/Publications/BrainBriefings/smell.html is conveyed by a combination of its smell and taste. Flavours are described by a complex set of references to substances that possess elements of these flavours. For example, wine experts talk about the 'nose' of a wine, meaning its smell; the early taste sensation is the 'palate', and the late taste sensation is the 'finish'. The tasting terminology is esoteric and has a poetic quality, with words like 'angular', 'lush', and 'rustic'.

INVISIBLE FORCES AND PHANTOM LIMBS

The somatosenses, which detect things like pressure, vibration and temperature, are normally grouped into the skin senses, the internal senses and the vestibular senses. It is important for us to know which way up we are, and how we are moving (especially how we are accelerating). This is achieved by a part of the inner ear called the semicircular canals, which contain small lumps immersed in a viscous fluid. When we move, these lumps move within the fluid. The lumps are in contact with hair cells (like those in the cochlea), and the motion of the lumps in the fluid bends the hair cells and results in neural messages, which are relayed to the vestibular nuclei in the brainstem (see chapter 3).

This type of sense is referred to as the *vestibular system*, and without it we could not walk without staggering. You can see impairment of this system in someone who has consumed too much alcohol. Motion sickness and dizziness are associated with unusual output from the vestibular system.

vestibular system located in the inner ear, this responds to acceleration and allows us to maintain body posture

In the skin senses, the transducers are nerve endings located around the surface of the body. There are also inner senses that tell us, for example, about muscle tension and joint position, which have detectors distributed in all the muscles and joints of the body. These work together with our vestibular system to coordinate our movements and maintain balance and posture.

Many people who have had limb amputations report that they still feel that they have the amputated limb, and often say that this 'phantom limb' is causing them great pain. Research by Ramachandran and Blakesee (1999) on patients who have such feelings shows that the representation of touch by neurons in the brain can be changed, resulting in a remapping of the body's tactile representation of itself. So, for example, touching the cheek of a patient elicited an apparent sensation in the phantom thumb.

The 'motor homunculus' (see chapter 3) shows the sensory representations of different parts of the body in the cortex. The proximity of the representations of the different parts of the body in this mapping, and the remapping of neurons within this after a limb amputation, is the probable reason for these remarkable effects.

Research close-up 2

Are faces special?

The research issue

Prosopagnosia is the inability to identify familiar faces. This disorder occurs rarely as an isolated deficit, but when it does it can help us to understand whether there is a specific region of the brain devoted to the processing and identification of familiar faces.

Prosopagnosia has previously been associated with damage to the medial occipito-temporal region of the brain, especially on the right. But in brain-damaged patients it is almost impossible to locate the precise site of damage accurately. There is also a question mark over whether we can necessarily infer the functioning of any part of a complex system from the effects of damaging or removing (i.e. in surgical cases) that part. (This last point is very important conceptually and applies to the types of inferences that we can validly make in any case of brain injury; for example, it also applies to patient M.P. referred to in *Research close-up 1*.)

Fortunately, in recent years it has been possible to investigate the brain regions involved in prosopagnosia in another way: by using functional brain imaging (see chapter 3) to study neural activity in the brains of prosopagnosic patients when they are shown familiar faces and are asked to identify them. We can also compare how the brains of prosopagnosic patients become activated relative to the brains of non-prosopagnosic individuals who are given the same familiar face identification task.

Using this approach, functional imaging has revealed a focal region in the right fusiform gyrus activated specifically during face perception.

Because no investigative technique is perfect, and we want to be absolutely certain that we have identified the correct brain region, we can give similar tasks to patients with brain damage in the fusiform gyrus.

Design and procedure

This study attempted to determine whether lesions of the fusiform gyrus are associated with deficits in face perception in patients with prosopagnosia.

Five patients with prosopagnosia due to acquired brain injury were tested. The patients were asked to discriminate faces in which the spatial configuration of the facial features had been altered. Face stimuli in the study differed quantitatively with respect to vertical mouth position and distance between the eyes.

Results and implications

The findings of the study revealed:

1. that all four patients whose lesions included the right fusiform face area were severely impaired in discriminating changes in the spatial position of facial features;
2. the fifth patient who manifested more anterior bilateral lesions was normal in this perceptual ability; and
3. when participants knew that only changes in mouth position would be shown, face processing performance improved markedly in two of the four patients who were impaired in the initial test.

Finding (1) indicates that perception of facial configuration is impaired in patients with prosopagnosia whose lesions involve the right fusiform gyrus. Finding (2) indicates that this impairment does not occur with more anterior bilateral lesions, while finding (3) indicates that this impairment is especially manifested when attention has to be distributed across numerous facial elements.

The researchers concluded that the loss of ability to perceive this type of facial configuration may contribute to the identification deficits that occur in some forms of prosopagnosia. It might also be possible for the findings to be employed in developing techniques for prosopagnosic patients to identify faces more efficiently, for example by encouraging them to focus their attention on individual facial features.

Note also that the findings of this study are consistent with a study conducted by Hadjikhani and de Gelder (2003). They found, using functional neuroimaging techniques, that patients suffering from prosopagnosia showed no activation of the fusiform gyrus when viewing faces compared to normal controls.

Barton, J.J.S., Press, D.Z., Keenan, J.P., & O'Connor, M., 2002, 'Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia', *Neurology*, 58, 71–8.

FINAL THOUGHTS

We have explored the nature of the information in the outside world, and the methods by which this can be transduced to neural messages by sense organs.

It remains to ask precisely what 'sensation' is and how it differs from 'perception'. In this chapter, there has been no talk of object recognition, of knowing how far away something is, or of knowing what shape it is. These are all examples of perception, which will be dealt with in the next chapter. Sensation refers to a process that occurs earlier in the stream of processing and works out general descriptions of stimuli in terms of features such as brightness, colour, loudness, smell, and so on. These features have nothing to do with a particular object, but can be used to describe any object. This seems to be the goal of early sensory processing – to reduce the incoming stream of information to a code, a set of descriptors or features, which can describe any stimulus in a way that can then drive higher-level processes such as recognition.

Summary

- There are different types of physical energy, which convey various types of information about the external and the internal world. Different forms of energy require different types of apparatus to detect them.
- Light information is instantaneous, works over large distances, gives highly precise directional information, and can tell us about properties of distant objects.
- There are good reasons why certain animals have vision that responds in the ultra-violet and infra-red light.
- Information from retinal cones in humans is processed in a manner that describes each point in the scene in terms of its colour and relative intensity.
- Sound information travels in lines that are not straight, so we cannot use it to determine locations in space as well as we can with light.
- Sound travels less quickly than light, so its time-of-arrival information can tell us about the direction of the sound source and also the locations of reflecting surfaces around us.
- We can produce sound both by tapping the ground with sticks and, even more importantly, by using our in-built speech production system. This makes sound the medium of choice for complex interpersonal communication.
- Sound information is analysed, at the moment of transduction, into frequency and amplitude components, and these give rise to the sensations of pitch and loudness. More complex sounds are analysed on this scheme as well, allowing the possibility of analysing speech and other complex signals.

REVISION QUESTIONS

1. Why do you think there are problems with asking people to describe their subjective experiences? Might it be difficult to interpret such data?
2. How does information conveyed by light differ from that conveyed by sound? For which tasks are these different kinds of information useful?
3. Why are humans unable to see infra-red and ultra-violet radiation? What animals respond to these types of radiation?
4. How does the sensation of colour arise from the cone responses to light of a given wavelength composition? What tasks are made much easier by having colour vision?
5. How does the human auditory system transpose sound energy into an internal representation? How does speech get analysed by this system?
6. Why do we have senses other than vision and hearing? What are their properties, and what happens when these senses malfunction?

FURTHER READING

Bruce, V., Green, P.R., & Georgeson, M. (2003). *Visual Perception: Physiology, Psychology and Ecology*. 4th edn. Hove: Psychology Press.
A detailed and up-to-date account of research on visual perception, with an emphasis on the functional context of vision.

Gazzaniga, M., Ivry, R.B., & Mangun, G.R. (2002). *Cognitive Neuroscience: The Biology of the Mind*. 2nd edn. New York: Norton.
Excellent textbook dealing with the material covered here in greater detail.

Gregory, R.L. (1997). *Eye and Brain: The Psychology of Seeing*. 5th edn. Oxford: Oxford University Press.
A very readable account of visual perception.

Moore, B.C.J. (2003). *An Introduction to the Psychology of Hearing*. 5th edn. London: Academic Press.
An excellent textbook on hearing.

Sekuler, R., & Blake, R. (2001). *Perception*. 4th edn. New York: McGraw-Hill.
A textbook which deals with all the senses covered in this chapter.

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