R.L. Gregory
Eye and Brain
the psychology of seeing
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May I take this opportunity to thank the publishers for producing in the first place, and now revising, *Eye and Brain*. Appearing in 1966, it was the first volume of the World University Library. This was the imaginative conception of Lord Weidenfeld. Production could be made quite lavish, with many colour pictures, by printing in several countries and as many languages simultaneously. The more financially successful books of the series supported the more specialised, which could not be expected to command economic sales with the production standards of this conception. The series was originally edited by Colin Haycraft, who has remained a close and valued friend.

Research on eyes and brains – on how our predecessors and ourselves on the incredible ladder of life see and understand – has made exciting advances during the ten years since this book was first written. I can only hope that some of this has been captured and encapsulated in this edition. I have also taken this opportunity to rephrase passages which seemed less than happy.

May I thank particularly John Curtis. He was responsible for editing – and made immense contributions to – *The Intelligent Eye*, which appeared in 1970. With his usual care and imaginative judgment, he has now produced this new edition of *Eye and Brain*.

R.L.G.
1 Seeing

We are so familiar with seeing, that it takes a leap of imagination to realise that there are problems to be solved. But consider it. We are given tiny distorted upside-down images in the eyes, and we see separate solid objects in surrounding space. From the patterns of stimulation on the retinas we perceive the world of objects, and this is nothing short of a miracle.

The eye is often described as like a camera, but it is the quite uncamera-like features of perception which are most interesting. How is information from the eyes coded into neural terms, into the language of the brain, and reconstituted into experience of surrounding objects? The task of eye and brain is quite different from either a photographic or a television camera converting objects merely into images. There is a temptation, which must be avoided, to say that the eyes produce pictures in the brain. A picture in the brain suggests the need of some kind of internal eye to see it – but this would need a further eye to see its picture... and so on in an endless regress of eyes and pictures. This is absurd. What the eyes do is to feed the brain with information coded into neural activity – chains of electrical impulses – which by their code and the patterns of brain activity, represent objects. We may take an analogy from written language: the letters and words on this page have certain meanings, to those who know the language. They affect the reader's brain appropriately, but they are not pictures. When we look at something, the pattern of neural activity represents the object and to the brain is the object. No internal picture is involved.

Gestalt writers did tend to say that there are pictures inside the brain. They thought of perception in terms of modifications of electrical fields of the brain, these fields copying the form of perceived objects. This doctrine, known as isomorphism, has had unfortunate effects on thinking about perception. Ever since, there has been a tendency to postulate properties to these hypothetical brain fields such that visual distortions, and other phenomena, are 'explained'.
But it is all too easy to postulate things having just the right properties. There is no independent evidence for such brain fields, and no independent way of discovering their properties. If there is no evidence for them, and no way of discovering their properties, then they are highly suspect. Useful explanations relate observables.

The Gestalt psychologists did however point to several important phenomena. They also saw very clearly that there is a problem in how the mosaic of retinal stimulation gives rise to perception of objects. They particularly stressed the tendency for the perceptual system to group things into simple units. This is seen in an array of dots (figure 1.1). Here the dots are in fact equally spaced, but there is a tendency to see, to ‘organise’, the columns and rows as though they are separate objects. This is worth pondering, for in this example we have the essential problem of perception. We can see in ourselves the groping towards organising the sensory data into objects. If the brain were not continually on the look-out for objects, the cartoonist would have a hard time. But, in fact, all he has to do is present a few lines to the eye and we see a face, complete with an expression. The few lines are all that is required for the eye – the brain does the rest: seeking objects and finding them whenever possible. Sometimes we see objects which are not there: faces-in-the-fire, or the Man in the Moon.

Figure 1.2 is a joke figure which brings out the point clearly. Just a set of meaningless lines? No – it is a washer-woman with her bucket! Now look again: the lines are subtly different, almost solid – they represent objects.

The seeing of objects involves many sources of information beyond those meeting the eye when we look at an object. It generally involves knowledge of the object derived from previous experience, and this experience is not limited to vision but may include the other senses; touch, taste, smell, hearing and perhaps also temperature or pain. Objects are far more than patterns of stimulation: objects have pasts and futures; when we know its past or can guess its future, an object transcends experience and becomes an embodiment of knowledge and expectation without which life beyond the simplest is not possible.

Although we are concerned with how we see the world of objects, it is important to consider the sensory processes giving perception –
1.1 This array of equally spaced dots is seen as continually changing patterns of rows and squares. We see something of the active organising power of the visual system while looking at this figure.
1.2 A joke figure – what is it?
When you see it as an object, not merely meaningless lines, it will suddenly appear almost solid – an object, not a pattern.

what they are, how they work and when they fail to work properly. It is by coming to understand these underlying processes that we can understand how we perceive objects.

There are many familiar so-called ‘ambiguous figures’, which illustrate very clearly how the same pattern of stimulation at the eye can give rise to different perceptions, and how the perception of objects goes beyond sensation. The most common ambiguous figures are of two kinds: figures which alternate as ‘object’ or ‘ground’, and those which spontaneously change their position in depth. Figure 1.3 shows a figure which alternates in figure and ground – sometimes the black part appears as a face, the white being neutral background, and at others the black is insignificant and the white surround dominates and seems to represent an object. The well-known Necker cube (figure 1.4) shows a figure alternating in depth. Sometimes the face
This figure alternates spontaneously, so that sometimes it is seen as a pair of faces, sometimes as a white urn bounded by meaningless black areas – the faces. The perceptual 'decision' of what is figure (or object) and what ground, is similar to the engineer's distinction between 'signal' and 'noise'. It is basic to any system which handles information.

marked with the ‘o’ lies in front, sometimes at the back – it jumps suddenly from the one position to the other. Perception is not determined simply by the stimulus patterns; rather it is a dynamic searching for the best interpretation of the available data. The data are sensory signals, and also knowledge of the many other characteristics of objects. Just how far experience affects perception, how far we have to learn to see, is a difficult question to answer; it is one which will concern us in this book. But it seems clear that perception involves going beyond the immediately given evidence of the senses: this evidence is assessed on many grounds and generally we make the best bet, and see things more or less correctly. But the senses do not give us a picture of the world directly; rather they provide evidence for the checking of hypotheses about what lies before us. Indeed, we may say that the perception of an object is an hypothesis, suggested
This figure alternates in depth: the face of the cube marked by the small circle sometimes appearing as the front, sometimes as the back face. We can think of these ways of seeing the figure as perceptual 'hypotheses'. The visual system entertains alternative hypotheses, and never settles for one solution. This process goes on throughout normal perception, but generally there is a unique solution.

The Necker cube is a pattern which contains no clue as to which of two alternative hypotheses is correct: the perceptual system entertains first one then the other hypothesis, and never comes to a conclusion, for there is no best answer. Sometimes the eye and brain come to wrong conclusions, and then we suffer hallucinations or illusions. When a perceptual hypothesis - a perception - is wrong we are misled, as we are misled in science when we see the world distorted by a false theory. Perceiving and thinking are not independent: 'I see what you mean' is not a puerile pun, but indicates a connection which is very real.
To see, we need light. This may seem too obvious to mention but it has not always been so obvious – Plato thought of vision as being due not to light entering, but rather to particles shot out of the eyes, spraying surrounding objects. It is difficult to imagine now why Plato did not try to settle the matter with a few simple experiments. Although to philosophers the problem of how we see has always been a favourite topic of speculation and theory, it is only in the last hundred years that it has formed the object of systematic experiments; which is odd, because all scientific observations depend upon the human senses – most particularly upon sight.

For the last three hundred years there have been two rival theories of the nature of light. Isaac Newton (1642–1727) argued that light must be a train of particles, while Christiaan Huygens (1629–93) argued that it must be pulses travelling through an all-pervading medium – the *aether* – which he thought of as small elastic balls in contact with each other. Any disturbance, he suggested, would be carried in all directions through the packed spheres as a wave, and this wave is light.

The controversy over the nature of light is one of the most exciting and interesting in the history of science. A crucial question in the early stages of the discussion was whether light travelled at a finite speed, or whether it arrived instantaneously. This was answered in a quite unexpected way by a Danish astronomer Olaus Roemer (1644–1710). He was engaged in recording eclipses of the four bright satellites orbiting round Jupiter, and found that the times he observed were not regular, but depended upon the distance of Jupiter from the earth.

He came to the conclusion, in 1675, that this was due to the time light took to reach him from the satellites of Jupiter, the time increasing when the distance increased, because of the finite velocity of light. In fact, the distance of Jupiter varies by about 300,000,000 km. (twice the distance of the sun), and the greatest time-
difference he observed was 16 minutes 36 seconds earlier or later than the calculated time of the eclipses of the satellites. From his somewhat faulty estimate of the distance of the sun he calculated the speed of light as 309,000 km. per second. With our modern knowledge of the diameter of the earth’s orbit, we correct this to a velocity of about 300,000 km. per second, or $3 \times 10^{10}$ cm/sec. The speed of light has since been measured very accurately over short distances on earth, and it is now regarded as one of the basic constants of the Universe.

Because of the finite velocity of light, and the delay in nervous messages reaching the brain, we always sense the past. Our perception of the sun is over eight minutes late: all we know of the furthest object visible to the unaided eye (the Andromeda nebula) is so out of date that we see it as it was a million years before men appeared on Earth.

The value of $3 \times 10^{10}$ cm/sec for the speed of light strictly holds only for a perfect vacuum. When light travels through glass or water, or any other transparent substance, it is slowed down to a velocity which depends upon the refractive index (roughly the density) of the medium through which it is travelling. This slowing down of light is extremely important, for it is this which causes prisms to bend light, and lenses to form images. The principle of refraction (the bending of light by changes of refractive index) was first understood by Snell, a Professor of Mathematics at Leyden, in 1621. Snell died at thirty-five, leaving his results unpublished. René Descartes (1596–1650) published the Law of Refraction eleven years later. The Law of Refraction (The ‘Sine Law’) is:

When light passes from a medium A into a medium B the sine of the angle of incidence bears to the sine of the angle of refraction a constant ratio.

We can see what happens with a simple diagram (figure 2.3): if AB is a ray passing from a dense medium (glass) into a vacuum (or air) the ray will emerge into the air at some angle i along BD.
2.2 Sir Isaac Newton (1642–1727) by Charles Jervas. On the whole, Newton held that light consists of particles, but he was aware of many of the difficulties, anticipating the modern theory that light has the dual properties of particles and waves. He devised the first experiments to show that white light is a mixture of the spectral colours, and paved the way to an understanding of colour vision by elucidating the physical characteristics of light.

The Law states that \( \frac{\sin i}{\sin r} = \mu \). The constant \( \mu \) is the refractive index of the glass or other refracting substance.

Newton thought of his corpuscles of light as being attracted to the surface of the denser medium, while Huygens thought that the bending was due to the light travelling more slowly in the denser medium. It was many years before the French physicist Foucault showed by direct measurement that light does indeed travel more slowly in a denser medium. It seemed for a time that Newton’s corpuscle theory of light was entirely wrong – that light is purely a series of waves radiating through a medium, the aether – but at the beginning of the present century it was dramatically shown that the wave theory does not explain all the phenomena of light. It now seems that light is both corpuscles and waves.

Light consists of packets of energy – quanta – these combining the characteristics of corpuscles and waves. Light of short wavelength has more waves in each bundle than light of longer wavelength. This is expressed by saying that the energy of a single quantum is a function of frequency, such that \( E = h \nu \) where \( E \) is the energy in ergs, \( h \) is a small constant (Planck’s constant) and \( \nu \) is the frequency of the radiation.

When light is bent by a prism, each frequency is deviated through a slightly different angle, so that the emergent beam comes out of the prism as a fan of light, giving all the spectral colours. Newton discovered that white light is a compound of all the spectral colours, by splitting a beam of sunlight into a spectrum in this way and then finding that he could re-combine the colours back into white light by passing the spectrum through a second similar prism, held the other way up. Newton named seven colours for his spectrum – red, orange, yellow, green, blue, indigo, violet. One does not really see indigo as a separate colour, and orange is a bit doubtful. What happened is that Newton liked the number seven and added the names orange and indigo to make the magic number!
2.3 Light is bent (refracted) by a dense transparent medium. The ratio of the sines of the angles of the rays entering and leaving the dense medium are constant for a given refractive index of the medium. This is the basis of image formation by lenses. (The angle of deviation of light is also a function of the wavelength of light, so that a beam is split into the spectral colours by a prism.) The lettering is explained in the text.

![Diagram of light bending through a dense medium](image)

We know now, though Newton did not, that each spectral colour, or hue, is light of a different frequency. We also know that all so-called electromagnetic radiation is essentially the same. The physical difference between radio waves, infra-red, light, ultraviolet and X-rays is their frequency. Only a very narrow band of these frequencies, less than an octave in width, stimulates the eye to give vision and colour. The diagram (figure 2.5) shows how this narrow window fits into the physical picture. Looked at in this way, we are almost blind.

If we know the speed of light and its frequency, it is a simple matter to calculate its wavelength, but in fact its frequency is difficult to measure directly. It is easier to measure the wavelength of light than its frequency; though this is not so for the low frequency radio waves. The wavelength of light is measured by splitting it up not with a prism, but with a grating of finely ruled lines, which also produces the colours of the spectrum. (This can be seen by holding an L.P. record at an oblique angle to a source of light, when the reflection will be made up of brilliant colours.) Given the spacing of the lines of a grating, which are specially ruled, and the angle producing light of a given colour, wavelength may be determined very accurately. It turns out that the blue light has a wavelength of about $4 \times 10^{-5}$ cm. ($\frac{1}{70,000}$ inch), while the wavelength of red light is about $7 \times 10^{-5}$ cm. ($\frac{1}{40,000}$ inch). The range of wavelengths adopted by eyes is important for it
2.4 A freehand sketch by Newton of one of his experiments on colour. He first split light into a spectrum (with the large prism), then allowed light of a single colour to pass through a hole in a screen to a second prism. This did not produce more colours. He also found that a second prism placed in the spectrum would recombine the colours into white. Thus white light is made up of all the colours of the spectrum.

sets the limit to their resolution, just as for optical instruments such as cameras, and it is adapted to accept the wavelengths of maximum energy of sunlight as it is filtered by the atmosphere.

We cannot with the unaided eye see individual quanta of light, but the receptors in the retina are so sensitive that they can be stimulated by a single quantum, though several (five to eight) are required to give the experience of a flash of light. The individual receptors of the retina are as sensitive as it is possible for any light detector to be, since a quantum is the smallest amount of radiant energy which can exist. It is rather sad that the transparent media of the eye do not quite match this development to perfection. Only about ten per cent of the light reaching the eye gets to the receptors, the rest being lost by absorption and scattering within the eye before the retina is reached. In spite of
this loss, it would be possible under ideal conditions to see a single candle placed seventeen miles away.

The quantal nature of light has an important implication for vision, which has inspired some particularly elegant experiments bridging the physics of light and its detection by the eye and brain. The first experiment on the effect of light being packaged into quanta was undertaken by three physiologists, Hecht, Schlaer, and Pirenne, in 1942. Their paper is now a classic. Realising that the eye must be almost if not quite as sensitive as theoretically possible, they devised a most ingenious experiment for discovering how many quanta actually accepted by the receptors are required to see a flash of light. The argument is based on a statistical function known as the Poisson distribution. This gives the expected distribution of hits on a target. The idea is that part at least of the moment-to-moment variation in the effective sensitivity of the eye is not due to anything in the eye or the nervous system, but to the variation in moment-to-moment energy of weak light sources. Imagine a desultory rain of bullets: they will not arrive at a constant rate, but will fluctuate; similarly there is fluctuation in the number of light quanta that arrive. A given flash may contain a small or large number of quanta, and is more likely to be detected if there happen to be more than the average number of quanta in the flash. For bright lights, this effect is unimportant, but since the eye is sensitive to but a few quanta, the fluctuation is sufficient for estimating the number of quanta required for detection.

The quantal nature of light is also important in considering the ability of the eye to detect fine detail. One of the reasons why it is possible to read only the largest newspaper headlines by moonlight, is that there are insufficient quanta falling onto the retina to build up a complete image within the time-span over which they eye can integrate energy – about a tenth of a second. In fact this is not by any means the whole story; but the purely physical factor of the quantal nature of light contributes to a well known visual phenomenon – loss of acuity in dim light – which until recently has been treated purely as though it were a property of the eye. Indeed, it is often quite difficult to establish whether a visual effect should be regarded as belonging to psychology, physiology or physics. They get pretty well mixed up.

How are images produced? The simplest way an image can be formed is by a pin hole. Figure 2.6 shows how this comes about. A ray
2.5 Light is but a narrow region of the total electromagnetic spectrum, which includes radio waves, infra red, ultra violet and X-rays. The physical difference is purely the wavelength of the radiation, but the effects are very different. Within the octave to which the eye is sensitive, different wavelengths give different colours. Beyond light these are very different properties when radiation interacts with matter.

How are images produced? The simplest way an image can be formed is by a pin hole. Figure 2.6 shows how this comes about. A ray from a part of the object (x) can only reach one part of the screen (y) – the part lying along the straight line passing through the pin-hole. Each part of the object illuminates a corresponding part of the screen, so an upside-down picture of the object is formed on the screen. The pin-hole image will be rather dim, for
2.6 Forming an image with a pinhole. A ray from a given region of the source reaches only a single region of the screen – the ray passing through the hole. Thus an (inverted) image is built up from the rays lying in the path of the hole. The image is free from distortion, but is dim and not very sharp. A very small hole introduces blurring through diffraction effects, due to the wave nature of light.

from a part of the object (x) can only reach one part of the screen (y) – the part lying along the straight line passing through the pin hole. Each part of the object illuminates a corresponding part of the screen, so an upside-down picture of the object is formed on the screen. The pin hole image will be rather dim, for the hole must be small if the image is to be sharp. (Though if it is too small it will be blurred because the wave structure of the light is upset).

A lens is really a pair of prisms (figure 2.7). It directs a lot of light from each point of the object to a corresponding point on the screen, thus giving a bright image. Lenses only work well when they are suitable, and adjusted correctly. The lens of the eye can be unsuitable to the eye in which it finds itself, and it can be adjusted wrongly. The lens may focus the image in front of or behind the retina, instead of on it, giving ‘short’ or ‘long’ sight. The lens may not be truly spherical in its surface, giving distortion and, in some directions, blurring of the
A lens can be thought of as a pair of converging prisms, forming an image from a bundle of rays. The image is far brighter than from a pinhole, but it is generally distorted in some degree, and the depth of focus is limited. [This figure should not be taken too literally – image-forming lenses have curved surfaces.]

image. The cornea may be irregular, or pitted (perhaps due to abrasion from metal filings in industry, or grit from riding a motor cycle without protective goggles). Most optical defects can be corrected by adding artificial lenses – spectacles. Spectacles correct for errors in accommodation by changing the power of the lens of the eye; they correct for astigmatism by adding a non-spherical component. Ordinary spectacles cannot correct for damage to the surface of the cornea but corneal lenses, fitted to the eye itself, serve to give a fresh surface to the cornea.

Spectacles lengthen our effective lives. With their aid we can see to read and to perform skilled tasks into old age: before their invention scholars and craftsmen were made helpless by lack of sight, though they still had the power of their minds.
3.1 Various primitive eyes. All of the ones here have the same basic plan: a lens forming an image on a mosaic of light-sensitive receptors.
Almost every living thing is sensitive to light. Plants accept the energy of light, some moving to follow the sun almost as though flowers were eyes to see it. Animals make use of light, shadows, and images to avoid danger and to seek their prey.

The first simple eyes responded only to light, and changing intensity of light. Perception of form and colour waited upon more complicated eyes capable of forming images, and brains sufficiently elaborate to interpret the neural signals from optical images on the retinas.

The later image-forming eyes developed from light-sensitive spots on the surface of simpler animals. How this occurred is largely mysterious, but we know some of the characters in the story. Some can be seen as fossils; some are inferred from comparative studies of living species; others appear fleetingly during the development of embryo eyes.

The problem of how eyes have developed has presented a major challenge to the Darwinian theory of evolution by Natural Selection. We can make many entirely useless experimental models when designing a new instrument, but this was impossible for Natural Selection, for each step must confer some advantage upon its owner, to be selected and transmitted through the generations. But what use is a half-made lens? What use is a lens giving an image, if there is no nervous system to interpret the information? How could a visual nervous system come about before there was an eye to give it information? In evolution there can be no master plan, no looking ahead to form structures which, though useless now, will come to have importance when other structures are sufficiently developed. And yet the human eye and brain have come about through slow painful trial and error.

Response to light is found even in one-celled animals. In higher forms, we find specially adapted cells to serve as receptors sensitive to light. These cells may be scattered over the skin (as in the earth worm)
The fossil eye of a species of trilobite. This is the earliest kind of eye preserved as a fossil. The facets are the corneal lenses, essentially the same as a modern insect eye. Some trilobites could see all round, but none above.
or they may be arranged in groups, most often lining a depression or pit, which is the beginning of a true image-forming eye.

It seems likely that photoreceptors became recessed in pits because there they lay protected from the surrounding glare, which reduced their ability to detect moving shadows heralding the approach of danger. Millions of years later but for the same reason Greek astronomers, it is said (though this has been questioned), dug pits in the ground from which they observed stars in the daytime.

The primitive eye pits were open to the danger of becoming blocked by foreign particles lodging within them, shutting out the light. A transparent protective membrane developed over the eye pits, serving to protect them. When, by chance mutations, this membrane became thicker in its centre, it became a crude lens. The first lenses served merely to increase intensity, but later they came to form useful images. An ancient pit type of eye is still to be seen in the limpet. One living creature, _Nautilus_, has an eye still more primitive – there is no lens, but a pin hole to form the image. The inside of the eye of _Nautilus_ is washed by the sea in which it lives, while eyes with lenses are filled with specially manufactured fluids to replace the sea. Human tears are a re-creation of the primordial ocean, which bathed the first eyes (figure 3.1).

We are concerned in this book with human eyes, and how we see the world. Our eyes are typical vertebrate eyes, and are not among the most complex or highly developed, though the human brain is the most elaborate of all brains. Complicated eyes often go with simple brains – we find eyes of incredible complexity in pre-vertebrates serving tiny brains. The compound eyes of arthropods (including insects) consist not of a single lens with a retina of many thousands or millions of receptors, but rather of many lenses with a set of about seven receptors, for each lens. The earlier known fossil eye belongs to the trilobites, which lived 500,000,000 years ago. In many species of trilobite, the eyes were highly developed. The external structure of these most ancient eyes may be seen perfectly preserved (figure 3.2). Some of the internal structure can be seen in the fossils with X-rays. They were compound eyes, rather like those of a modern insect: some had over a thousand facets.

Figure 3.3 shows an insect eye. Behind each lens facet ('corneal lens') lies a second lens ('lens cylinder') through which light passes to
the light-sensitive element, this usually consisting of seven cells grouped in a minute flowerlike cluster. Each complete unit of a compound eye is known as an ‘ommatidium’. It used to be thought that each ommatidium is a separate eye – so that insects must see thousands of worlds – but how this came to be believed is strange, for there is no separate retina in each ommatidium, and but a single nerve fibre from each little group of receptors. How then could each one signal a complete image? The fact is that each ommatidium signals the presence of light from a direction immediately in front of it, and the combined signals represent effectively a single image.

Insect eyes have a remarkable mechanism to give dark or light adaptation. The ommatidia are isolated from each other by black cones of pigment: with reduced light (or in response to signals from the brain) the pigment migrates back towards the receptors so that light can then pass through the side of each ommatidium to neighbouring receptors. This increases the sensitivity of the eye, but at a cost to its acuity – a trade balance found also in vertebrate eyes, though for somewhat different reasons, and by very different mechanisms.

The lens cylinder of the compound eye does not function by virtue of the shape of its optical surfaces, as in a normal lens, so much as by change of its refractive index, which is greater near its centre than at its edge. Light is funnelled through it, in a way quite different from a normal lens. Compound eyes are principally detectors of movement, and can be incredibly efficient, as we known from watching a dragon fly catching its prey on the wing.

Among the most curious eyes in the whole of nature is that of a creature the size of a pin’s head – a little known copepod – *Copilia*. She (the males are dull by comparison) has a pair of image-forming eyes, which function neither like vertebrate nor like compound eyes, but something like a television camera. Each eye contains two lenses, and the photoreceptor system is similar to the insect eye; but in *Copilia* there is an enormous distance between the corneal lens and the lens cylinder. Most of the eye lies deep within the body of the animal, which is extraordinarily transparent. She is shown in figure 3.4. The secret of this eye is to be found by looking at the living animal. Exner, in 1891, reported that the receptor (and attached lens cylinder) make a ‘continuous lively motion.’ They oscillate across the
The parts of a compound eye. The primitive trilobite eye was probably similar, though the internal structure is not preserved. We see this in arthropods, including insects, e.g. bees and dragon flies. Each corneal lens provides a separate image to a single functional receptor (made up often of seven light-sensitive cells), but there is no reason to think that the creature sees a mosaic. The compound eye is especially good at detecting movement.
3.4 A living female specimen of a microscopic copepod, *Copilia quadrata*. Each eye has two lenses: a large anterior lens and a second smaller lens deep in the body, with an attached photoreceptor and single optic nerve fibre to the central brain. The second lens and photoreceptor are in continual movement, across the image plane of the first lens. This seems to be a scanning eye: a mechanical television camera.
3.5 The posterior lens of *Copilia*, and attached photoreceptor (in red) during a single scan. The rate can be as high as 5 scans per second.
mid line of the animal, and evidently scan across the focal plane of the
front corneal lens. It seems that the pattern of dark and light of the
image is not given simultaneously by many receptors, as in other eyes,
but in a time-series down the optic nerve, as in the single channel of a
television camera. It is possible that many small compound eyes (e.g. *Daphnia*) also go in for scanning to improve the resolution and
channel capacity of their few elements. Is *Copilia*'s eye ancestral to
the compound eye? Is scanning generally abandoned, because a
single neural link could not transmit sufficient information? Is it a
simplification of the compound eye found in the earliest fossils? Or is
it perhaps an aberrant experiment, unrelated to the main streams of
evolutionary development?

The scanning movement of the lens cylinder and the attached
photoreceptor is shown by the successive frames of a cine film in
figure 3.5. The receptors move precisely towards, then away from each
other – never independently. The speed of the scan varies from about
five per second to about one scan every two seconds. One would give a
lot to know why it exists, and whether it is the remaining example of a
very early kind of eye. If *Copilia* is an evolutionary failure she
deserves a prize for originality.
The brain is more complicated than a star and more mysterious. Looking, with imagination, back through the eyes to the brain mechanisms lying behind, we may there discover secrets as important as the nature of the external world, perceived by eye and brain.

It has not always been obvious that the brain is concerned with thinking, with memory, or with sensation. In the ancient world, including the great civilisations of Egypt and Mesopotamia, the brain was regarded as an unimportant organ. Thought and the emotions were attributed to the stomach, the liver and the gall bladder. Indeed, the echo lingers in modern speech, in such words as ‘phlegmatic’. When the Egyptians enbalmed their dead they did not trouble to keep the brain (which was extracted through the left nostril) though the other organs were separately preserved, in special Canopic jars placed beside the sarcophagus. In death the brain is almost bloodless, so perhaps it seemed ill-suited to be the receptacle of the Vital Spirit. The active pulsing heart seemed to be the seat of life, warmth and feeling – not the cold grey silent brain, locked privily in its box of bone.

The vital role of the brain in control of the limbs, in speech and thought, sensation and experience, gradually became clear from the effects of accidents in which the brain was damaged. Later the effects of small tumours and gun shot wounds gave information which has been followed up and studied in great detail. The results of these studies are of the greatest importance to brain surgeons: for while some regions are comparatively safe, others must not be disturbed or the patient will suffer grievous loss.

The brain has been described as ‘the only lump of matter we know from the inside.’ From the outside, it is a pink-grey object, about the size of two clenched fists. Some relevant parts are shown in figure 4.1. It is made up of the so-called ‘white’ and ‘grey’ matter, the white matter being association fibres, connecting the many kinds of cell bodies which form the grey matter.
4.1 The brain, showing the visual part – the *area striata* – at the back (occipital cortex). Stimulation of small regions produces flashes of light in corresponding parts of the visual field. Stimulation of surrounding regions (visual association areas) produces more elaborate visual experiences.

The brain has, in its evolution, grown up from the centre, which in man is concerned primarily with emotion. The surface – the *cortex* – is curiously convoluted. It is largely concerned with motor control of the limbs, and with the sense organs. It is possible to obtain maps relating regions of the cortex with groups of muscles; and also maps relating touch – giving bizarre ‘homunculi’ as in figure 4.2. The sense of sight has its own region of cortex, as we shall see in a moment.
4.2 A ‘homunculus’ – a graphic representation showing how much of the cortex is devoted to sensation from various regions of the body. Note the huge thumb. Different animals have very different ‘homunculi’, corresponding to the sensory importance of the various parts of the body.

The nerve cells in the brain consist of cell bodies each having a long thin process – or axon – conducting impulses from the cell. The axons may be very long, sometimes extending from the brain down the spinal cord. The cell bodies also have many finer and shorter fibres, the dendrites which conduct signals to the cell (figure 4.3). The cells, with their interconnecting dendrites and their axons, sometimes seem to be arranged randomly, but in some regions they form well ordered
4.3 A nerve cell. The cell body has a long axon, insulated by its myelin sheath, often sending control signals to muscle. The cell body accepts information from the many fine dendrites, some of which tend to make the cell fire, while others inhibit firing. The system is a simple computer element. The inter-connected elements serve to control activity and handle information for perception.
patterns, indicating ordered connections; in the visual cortex they are arranged in layers.

The neural signals are in the form of electrical pulses, which occur when there is an alteration in the ion permeability of the cell membrane (figure 4.4). At rest, the centre of the fibre is negative with respect to the surface; but when a disturbance occurs, as when a retinal receptor is stimulated by light, the centre of the fibre becomes positive, initiating a flow of current which continues down the nerve as a wave. It travels very much more slowly than does electricity along a wire: in large fibres it travels at about 100 metres per second, and in the smallest fibres at less than one metre per second. The thick high-speed fibres have a special fatty coating – the myelin sheath – which insulates the fibres from their neighbours and also serves to increase the rate of conduction of the action potential. The low rate of travel – first measured by Helmholtz in 1850 – was a great physiological surprise. It only accounts however for part of the human 'reaction-time' of nearly half a second; for there is also delay from the switching time of the synapses of the brain which route sensory and motor signals, to give perception and behaviour.

There are many sophisticated techniques for studying the nervous system. Electrical activity of individual cells or groups of cells may be recorded, and regions may be stimulated electrically to evoke not only responses but even – in patients undergoing brain operations – sensations. The effects of loss of regions of brain may be discovered, resulting behaviour changes being related to the regions of damage. The effects of drugs or chemicals applied directly to the surface of the brain may be investigated; this is becoming an important area of research, both to establish that new drugs do not have unpleasant psychological side effects and as another technique for changing the state of the brain to discover functions of its various regions.

These techniques, together with examination of the way regions are joined by bundles of fibres, have made it clear that different parts of the brain are engaged in very different functions. But when it comes to discovering the processes going on in each region, even the most refined techniques look rather crude.

It may seem that the most direct way to study the brain is to examine its structure, and stimulate it and record from it. But like electronic devices, it is not at all easy to see how it works from its
structure; and the results of stimulation, recording, and removal of parts are difficult to interpret in the absence of a general model of how it works. In order to establish the results of stimulating or ablating the brain it is essential to perform associated behaviour experiments. The results of recording from brain cells are also most interesting when there is some related behaviour, or reported experience. This means that animal and human psychology are very important, for it is essential to relate brain activity to behaviour, and this involves specially designed psychological experiments.

The brain is, of course, an immensely complicated arrangement of nerve cells but it is somewhat similar to man-made electronic devices, so general engineering considerations can be helpful. Like a computer, the brain accepts information, and makes decisions according to the available information; but it is not very similar to actual computers designed by engineers, if only because there are already plenty of brains at very reasonable cost (and they are easy to make by a well-proved method) so computers are designed to be different.

It is easier to make a machine to solve mathematical or logical problems – to handle symbols according to rules – than to see. The problem of making machines to recognise patterns has been solved in various ways for restricted ranges of patterns, but so far there is no neat solution, and no machine comes anywhere near the human perceptual system in range or speed. It is partly for this reason that detailed study of human perception is important. Finding out what we can of human perception is important not only for understanding ourselves; it may also suggest ways in which perception can be achieved by machines. This would be useful for many purposes – from reading documents to exploration of space by robots.

One of the difficulties in understanding the function of the brain is that it is like nothing so much as a lump of porridge. With mechanical systems, it is usually possible to make a good guess at function by considering the structure of the parts, and this is true of much of the body. The bones of the limbs are seen to be levers. The position of attachment of the muscles clearly determines their function.

Mechanical and optical systems have parts whose shapes are closely related to their function, which makes it possible to deduce, or at least guess, their function from their shape. It was possible for
4.4 Mechanism of electrical conduction in nerve. Hodgkin, Huxley and Katz have discovered that sodium ions pass to the inside of the fibre, converting its standing negative charge to positive. Potassium ions leak out, restoring the resting potential. This can happen up to a thousand times a second transmitting spikes of potential which run along nerve as signals – by which we know the world through perception and command behaviour.
Kepler in the seventeenth century to guess that a structure in the eye (called at that time the 'crystalline') is in fact a lens from its shape. But unfortunately the brain presents a far more difficult problem, if only because the physical arrangement of its parts and their shapes is rather unimportant to their function. When function is not reflected in structure we cannot deduce function by simply looking. It may be necessary to invent an imaginary brain; or invent and perhaps construct a machine, or write a computer program to perform much as the biological system performs. In short, we may have to simulate to explain: but simulations are never complete or perfect. So far we have no machines which approach the brain in thinking or seeing. We have not yet invented anything adequate – so we cannot understand. Nevertheless, some principles may be suggested by engineering considerations. If the brain were strictly unique – impossible to reproduce with symbols or other materials – then we cannot hope to find general explanations. Its secrets would be locked in mysterious properties of protoplasm. But this is hard to believe. If this is not the case we should be able to 'mechanise' brain function; and understand at deep levels the nature of perceptual processes and, perhaps, even consciousness. Meanwhile, we may watch out for developments in machine perception and intelligence to illuminate the brain.

The visual regions

The neural system responsible for vision starts with the retinas. These, as we have seen, are essentially outgrowths of the brain, containing typical brain cells as well as specialised light-sensitive detectors. The retinas are effectively divided down the middle: the optic nerve fibres from the inner (nasal) halves crossing at the chiasma while fibres from the outer halves do not cross. The visual representation corresponds to the brain's representation of touch – in spite of the optical reversal of the eyes (figure 4.5). So touch and vision are closely related. This visual region of brain is known as the area striata, from its appearance, the cells being arranged in layers (frontispiece).

The brain as a whole is divided down the middle, forming two hemispheres, which are really more or less complete brains, joined by a massive bundle of fibres, the corpus callosum, and the smaller
4.5 The optic pathways of the brain. The optic nerve divides at the chiasma, the right half of each retina being represented on the right side of the occipital cortex, the left side on the left half. The lateral geniculate bodies are relay stations between the eyes and the visual cortex.

optic chiasma. On their way from the chiasma, the optic tracts pass through a relay station in each hemisphere, the lateral geniculate body.

The area striata is sometimes known as the ‘visual projection area’. When a small part is stimulated a human patient reports a flash of light. Upon a slight change of position of the stimulating electrode, a flash is seen in another part of the visual field. It thus seems there is a spatial representation of the retinas upon the visual cortex.
Hubel and Wiesel's discovery that selected single brain cells (in the cat) fire with movement of the eye in a certain direction. The arrows show various directions of movement of a bar of light presented to the eyes. The electrical record shows that this particular cell fires only for one direction of movement.

Stimulation of surrounding regions of the striate area also gives visual sensations, but instead of flashes of light the sensations are more elaborate. Brilliant coloured balloons may be seen floating up in an infinite sky. Further away, stimulation may elicit visual memories, even complete scenes coming vividly before the eyes.

It has recently been found that there is a second projection area – the *superior colliculus* – which gives cruder mapping, and provides command signals to move the eyes. This is evolutionarily more ancient: it seems that the sophisticated feature analysing of the *area* 46
Hubel and Wiesel’s records from single cells in the visual cortex of the cat. A line (shown on the left) was presented to the cat at various orientations. A single cell in the brain fires only at a certain orientation. This is shown by the spikes of the electrical records.

**striata** has been grafted on to the primitive but still useful – though not conscious – vision of the *colliculus*, as the cortex developed through the evolution of mammals, primates, to man.

Among the most exciting of recent discoveries, is the finding of two American physiologists, David Hubel and Torstien Wiesel, who recorded activity from single cells of the *area striata* of the cat’s brain, while presenting its eyes with simple visual shapes. These were generally bars of light, projected by a slide projector on a screen in front of the cat. Hubel and Wiesel found that some cells were only
active when the bar of light was presented to the cat at a certain angle. At that particular angle the brain cell would fire, with long bursts of impulses, while at other angles it was 'silent'. Different cells would respond to different angles. Cells deeper in the brain respond to more generalised characteristics, and would respond to these characteristics no matter which part of the retina was stimulated by the light. Other cells responded only to movement, and movement in only a single direction (figure 4.6). These findings are of the greatest importance, for they show that there are specific mechanisms in the brain selecting certain features of objects. Perceptions may be built up from combinations of these selected features.

We do have 'mental pictures', but this should not suggest that there are corresponding electrical pictures in the brain, for things can be represented in symbols – but symbols will generally be very different from the things represented. The notion of brain pictures is conceptually dangerous. It is apt to suggest that these supposed pictures are themselves seen with a kind of inner eye involving another picture, and another eye . . . and so on.

Retinal patterns are represented by coded combinations of activity. The visual cortex is organised not only in the clearly seen layers parallel to its surface, but also in functional 'columns' running through the layers of the striate region. An electrode pushed through the layers, at right angles to them, picks up cells all responding to the same orientation, with more and more general properties as it reaches first the 'simple', then the 'complex' and the 'hypercomplex' cells. If the electrode is inserted about half a millimetre away, then the critical orientation is different. Further away, the signalled orientations are still more different. Each block of (as Colin Blakemore puts it) 'like-minded' orientation detectors is called a 'column'. Various sizes of retinal image features, velocities, and (in monkey and probably man) colours are represented by cells of common orientation down each functional column. Most of the cells are 'binocular' – responding to corresponding points of the two retinas. Gradually the organisation of the 'visual cortex' is becoming clear, though just how this brain activity is related to contours, colours and the shapes of objects as we see them remains mysterious.
5 The eye

Each part of the eye is an extremely specialised structure (figure 5.1). The perfection of the eye as an optical instrument is a token of the importance of vision in the struggle for survival. Not only are the parts of the eye beautifully contrived, but even the tissues are specialised. The cornea is special in having no blood supply: blood vessels are avoided by obtaining nutriment from the aqueous humour. Because of this, the cornea is virtually isolated from the rest of the body. This is fortunate for it makes possible transplants from other individuals in cases of corneal opacity, since antibodies do not reach and destroy it as happens to other alien tissues.

This system of a crucial structure being isolated from the blood stream is not unique to the cornea. The same is true of the lens, and in either case blood vessels would ruin their optical properties. It is also true of a structure in the inner ear, though here the significance is entirely different. In the cochlea, where vibrations are converted into neural activity, there is a remarkable structure known as the organ of Corti, which consists of rows of very fine hairs joined to nerve cells that are stimulated by the vibration of the hairs. The organ of Corti has no blood supply, but receives its nutriment from the fluid filling the cochlea. If these very sensitive cells were not isolated from the pulse of the arteries, we would be deafened. The extreme sensitivity of the ear is only possible because the crucial parts are isolated from the blood stream, and the same is true of the eye though for a different reason.

The aqueous humour is continually secreted and absorbed, so that it is renewed about once every four hours. ‘Spots before the eyes’ can be due to floating impurities casting shadows on the retina, seen as hovering in space.

Each eyeball is equipped with six extrinsic muscles, which hold it in position in its orbit, and rotate it to follow moving objects or direct the gaze to chosen features. The eyes work together, so that normally they are directed to the same object, converging for near objects.
5.1 The human eye. The most important optical instrument. Here lies the focusing lens, giving a minute inverted image to an incredibly dense mosaic of light-sensitive receptors, which convert the patterns of light energy into the language the brain can read – chains of electrical impulses.
Besides the extrinsic eye muscles, there are also muscles within the eyeball. The iris is an annular muscle, forming the pupil through which light passes to the lens lying immediately behind. This muscle contracts to reduce the aperture of the lens in bright light, and also when the eyes converge to view near objects. Another muscle controls the focusing of the lens. We may look in more detail at the mechanism and function of the lens and the iris. Both have their surprises.

The crystalline lens. It is often thought that the lens serves to bend the incoming rays of light to form the image. This is rather far from the truth in the case of the human eye, though it is true for fishes. The region where light is bent most in the human eye, though it is true for fishes. The region where light is bent most in the human eye to form the image is not the lens, but the front surface of the cornea. The reason for this is that the power of a lens to bend light depends on the difference between the refractive index of the surrounding medium and the lens material. The refractive index of the surrounding medium – air – is low, while that of the aqueous humour immediately behind the cornea is nearly as high as that of the lens. In the case of fish, the cornea is immersed in water, and so light is hardly bent at all when it enters the eye. Fish have a very dense rigid lens, which is spherical and moves backwards and forwards within the eyeball to accommodate to distant and near objects. Although the lens is rather unimportant for forming the image in the human eye, it is important for accommodation. This is done not by changing the position of the lens (as in a fish, or a camera) but by changing its shape. The radius of curvature of the lens is reduced for near vision, the lens becoming increasingly powerful and so adding more to the primary bending accomplished by the cornea. The lens is built up of thin layers, like an onion, and is suspended by a membrane, the zonula, which holds it under tension. Accommodation works in a most curious manner. For near vision tension is reduced on the zonula, allowing the lens to spring to a more convex form, the tension being released by contraction of the ciliary muscle. It becomes more convex for near vision, by the muscle tightening and not relaxing, which is a surprising system.

The embryological and later developments of the lens are of particular interest, and have dire consequences in middle life. The
lens is built up from its centre, cells being added all through life, though growth gradually slows down. The centre is thus the oldest part, and there the cells become more and more separated from the blood system giving oxygen and nutrient, so that they die. When they die they harden, so that the lens becomes too stiff to change its shape for accommodation to different distances.

We see this all too clearly in figure 5.2 which shows how accommodation falls off with age, as the starved cells inside the lens die, and we see through their corpses.

It is possible to see the changes in shape of someone else’s lens as he accommodates to different distances. This requires no apparatus beyond a small source of light, such as a flashlight. If the light is held in a suitable position it can of course be seen reflected from the eye, but there is not just one reflection—there are three. The light is reflected not only from the cornea, but also from the front and the back surfaces of the lens. As the lens changes its shape, these images change in size. The front surface gives a large and rather dim image, which is the right way up, while the back surface gives a small bright image which is upside down. The principle can be demonstrated with an ordinary spoon. Reflected from the back convex surface you will see large right-way-up images, but the inside concave surface gives small upside-down images. The size of the images will be different for a large (table) spoon and a small (tea) spoon, corresponding to the curvatures of the lens of the eye for distant and near vision. These images seen in the eye are known as Purkinje images, and are very useful for studying accommodation experimentally.

The iris. This is pigmented, and is found in a wide range of colours. Hence the ‘colour of a person’s eyes’—which is a matter of some interest to poets, geneticists and lovers, but less so to those concerned with the function of the eye. It hardly matters what colour the iris is, but it must be reasonably opaque so that it is an effective aperture stop for the lens. Eyes where pigment is missing (albinism) are seriously defective.

It is sometimes thought that the changes in pupil size are important in allowing the eye to work efficiently over a wide range of light intensities. This could hardly be its primary function however, for its area only changes over a ratio of about 16:1, while the eye works
efficiently over a range of intensity greater than 1,000,000:1. It seems that the pupil contracts to limit the rays of light to the central and optically best part of the lens except when the full aperture is needed for maximum sensitivity. It also closes for near vision, and this increases the depth of field for near objects.

To an engineer, any system which corrects for an external change (in this case light intensity) suggests a ‘servo-mechanism’. These are very familiar in the form of the thermostats in central heating, which switch on the heat automatically when the temperature drops below some pre-set value, and then switch it off again when the temperature rises. (An early example of a man-made servo-mechanism is the windmill which aims into the wind and follows its changing direction by means of a fantail sail, which rotates the top of the mill through gearing. A more elaborate example is the automatic pilot which keeps a plane on correct course and height by sensing errors and sending correcting signals to the control surfaces of the machine.)

To go back to the thermostat sensing temperature changes in a central heating system: imagine that the difference between the setting of the lower temperature for switching on the heat is very close to the upper temperature for switching it off. No sooner is it switched on than temperature will rise enough to switch it off again, and so the heating system will be switched on and off rapidly until perhaps something breaks. Now by noting how frequently it is switched on and off, and noting also the amplitude of the temperature variation, an engineer could deduce a great deal about the system. With this in mind, some subtle experiments have been performed on just how the iris servo-control system works.

The iris can be made to go into violent oscillation, by directing a narrow beam of light into the eye, so that it passes the edge of the iris (figure 5.4). When the iris closes a little the beam is partly cut off, and so the retina gets less light. But this gives the iris a signal to open. As soon as it opens the retina gets more light – and then the iris starts to close, until it gets another signal to open. Thus it oscillates in and out. By measuring the frequency and amplitude of oscillation of the iris a good deal can be learned about the neural servo-system controlling it.

*The pupil.* This is not, of course, a structure. It is the hole formed by the iris through which light passes to the lens and on to the retina as
5.2 (Top) Loss of accommodation of the lens of the eye with ageing. The lens gradually becomes rigid and cannot change its form. Bifocal spectacles serve to give effective change of focus when accommodation is lost.

5.3 (Bottom) Eye a cannot see into eye b. One’s own eye always gets in the way, preventing light reaching the only part of the retina which could form an image.
5.4 Making the iris oscillate with a beam of light. When the iris opens a little, more light reaches the retina, which then signals the retina to close. But when it closes less light reaches the retina, which signals the iris to open. Thus it oscillates. From the frequency and amplitude of oscillation the iris control system can be described in terms of servo-theory.
5.5 (right) How eyes look when we can see into them.
This photograph is taken with an ophthalmoscope.
It shows the yellow spot over the fovea, the retinal
blood vessels through which we see the world, and the blind
region where the vessels and nerves leave the eyeball.

an image. Although the human pupil is circular, there is a great
variety of shapes, the circular form being rather unusual in nature.
The pupil looks black, and we cannot see through it into another
person’s eye. This requires some explanation, for the retina is not
black, but pink: indeed it is a most curious fact that although we see
out of our pupils, we cannot see into someone else’s! The reason is
that the lens in the other person’s eye focuses light from any given
position on to a certain region of the retina, so the observing eye
always gets in the way of the light which would shine on to the part of
the retina he should be seeing (figure 5.3). Helmholtz (anticipated by
Charles Babbage) invented a device for looking into another person’s
eye, the trick being to direct a beam of light along the path the
observer is looking (figure 5.6). With this device the pupil no longer
looks black, and the detailed structure of the living retina may be
seen, inside the eye, the blood vessels on its surface appearing as a
great red tree of many branches.

Eye movements
Each eye is moved by six muscles (figure 5.7). The remarkable
arrangement of the superior oblique can be seen in the illustration.
The tendon passes through a ‘pulley’ in the skull, in front of the
suspension of the eyeball. The eyes are in continuous movement, and
they move in various ways. When the eyes are moved around,
searching for an object, they move quite differently from the way they
move when a moving object is being followed with the eyes. When
searching, they move in a series of small rapid jerks, but when
following they move smoothly. The jerks are known as saccades (after
an old French word meaning ‘the flick of a sail’) Apart from these
two main types of movement, there is also a continuous small high-
frequency tremor.

Eye movements can be recorded in various ways: they can be
5.6 The ophthalmoscope, invented by Charles Babbage and Helmholtz. Light reaches the observed eye by reflection *from* a half-silvered mirror, *through* which the observer sees inside the illuminated eye. (In practice he may look above the illuminated ray to avoid losses of the half-silvered mirror).
The muscles which move the eye. The eyeball is maintained in position in the orbit by six muscles, which move it to direct the gaze to any position and give convergence of the two eyes for depth perception. They are under continuous tension and form a delicately balanced system, which when upset can give illusions of movement.

filmed with a cine camera, detected by small voltage changes around the eyes, or most accurately by attaching a mirror to a contact lens placed on the cornea, when a beam of light may be reflected off the mirror and photographed on continuously moving film.

It turns out that the saccadic movements of the eyes are essential to vision. It is possible to fix the image on the retina so that wherever the eye moves, the images move with it and so remain fixed on the retina. When the image is optically stabilised (figure 5.8) vision fades after a few seconds, and so it seems that part of the function of eye...
5.8 A simple way of optically stabilising the retinal image. The object (a small photographic transparency), is carried on the eye on a contact lens, and moves exactly with it. After a few seconds the eye becomes blind to the stabilised image, some parts fading before others. This method was devised by R. Pritchard.

movements is to sweep the image over the receptors so that they do not adapt and so cease to signal to the brain the presence of the image in the eye. But there is a curious problem: when we look at a sheet of white paper, the edges of the image of the paper will move around on the retina, and so stimulation will be renewed; but consider now the centre of the image. Here the small movements of the eyes can have no effect, for a region of given brightness is substituted for another region of exactly the same brightness, and so no change in stimulation takes place with the small eye movements. Yet the middle of the paper
does not fade away. This suggests that borders and outlines are very important in perception. Large areas of constant intensity provide no information. They seem to be ‘inferred’ from the signalled borders: the central visual system makes up the missing signals.

Blinking is often assumed to be a reflex, initiated by the cornea becoming dry. But for normal blinking this is not so; though blinking can be initiated by irritation of the cornea, or by sudden changes in illumination. Normal blinking occurs with no external stimulus: it is initiated by signals from the brain. The frequency of blinking increases under stress, and with expectation of a difficult task. It falls below average during periods of concentrated mental activity. Blink rate can even be used as an index of attention and concentration on tasks of various kinds and difficulties.

The retina
The name retina is derived from an early word meaning ‘net’ or ‘cobweb tunic’, from the appearance of its blood vessels.

The retina is a thin sheet of interconnected nerve cells, including the light-sensitive rod and cone cells which convert light into electrical pulses – the language of the nervous system. It was not always obvious that the retina is the first stage of visual sensation. The Greeks thought of the retina as providing nutrient to the vitreous. The source of sensation was supposed by Galen (c. 130–201 A.D.) and by much later writers, to be the crystalline lens. The Arabs of the ‘dark’ ages – who did much to develop optics – thought of the retina as conducting the vital spirit, the ‘pneuma’.

It was the astronomer Kepler who, in 1604, first realised the true function of the retina – that it is the screen on which an image from the lens is formed. This hypothesis was tested experimentally by Scheiner, in 1625. He cut away the outer coating (the sclera and the choriod) from the back of an ox’s eye, leaving the retina revealed as a semi-transparent film – to see an upside-down image on the retina of the ox’s eye.

The discovery of the photoreceptors had to wait upon the development of the microscope. It was not until about 1835 that they were first described, and then none too accurately, by Treviranus. It seems that his observation was biased by what he expected to see, for
he reported that the photoreceptors face the light. Strangely, they do not: in mammals and in nearly all vertebrates – though not in cephalopods – the receptors are placed at the back of the retina, behind the blood vessels. This means that light has to go through the web of blood vessels and the fine network of nerve fibres – including three layers of cell bodies and a host of supporting cells – before it reaches the receptors. Optically, the retina is inside out, like a camera film put in the wrong way round (figure 5.9). Given the original ‘mistake’ however (which seems to result from the embryological development of the retina from the surface of the brain), the situation is largely saved by the nerve fibres from the periphery of the retina skirting around and avoiding the crucial central region giving best vision.

The retina has been described as ‘an outgrowth of the brain’. It is a specialised part of the surface of the brain which has budded out and become sensitive to light, while it retains typical brain cells functionally between the receptors and the optic nerve (but situated in the front layers of the retina) which greatly modify the electrical activity from the receptors themselves. Some of the data processing for perception takes place in the eye, which is thus an integral part of the brain.

There are two kinds of light-receptor cells – the rods and the cones – named after their appearance as viewed with a microscope. In the peripheral regions of the retina they are clearly distinguishable, but in the central region – the fovea – the receptors are packed exceedingly close together, and look like the rods.

The cones function in daylight conditions, and give colour vision. The rods function under low illumination, and give vision only of shades of grey. Daylight vision, using the cones of the retina, is referred to as photopic while the grey world given by the rods in dim light is called scotopic.

It might be asked how we know that only the cones mediate colour vision. This is deduced partly from studies of various animal eyes, by relating retinal structure to their ability to discriminate colours as determined by behaviour experiments; and also from the finding that in the human retina there are very few cones near the edge of the retina, where there is no colour vision. It is interesting that although the central foveal region, packed tightly with functional cones, gives
The retina. Light travels through the layers of blood vessels, nerve fibres and supporting cells to the sensitive receptors ('rods' and 'cones'). These lie at the back of the retina, which is thus functionally inside-out. The optic nerve is not, in vertebrate eyes, joined directly to the receptors, but is connected via three layers of cells, which form part of the brain externalised in the eyeball.
the best visual detail and colour, it is less sensitive than the more primitive rod-regions of the retina. (Astronomers 'look off' the fovea when they wish to detect very faint stars so that the image falls on a region of the retina rich in sensitive rods).

It might be said that by moving from the centre of the human retina to its periphery we travel back in evolutionary time; from the most highly organised structure to a primitive eye, which does little more than detect movements of shadows. The very edge of the human retina does not even give a sensation when stimulated by movement. It gives primitive unconscious vision; and directs the highly developed foveal region to where it is likely to be needed for its high acuity.

The size of the receptors and their density become important when we consider the ability of the eye to distinguish fine detail. We shall quote directly from Polyak's great book *The Retina*:

The central territory where the cones are almost uniformly thick measures approximately 100 μ (microns, or millionths of a metre) across, corresponding to 20', or one-third of a degree of arc. It contains approximately fifty cones in a line. This area seems to be not exactly circular but elliptical, with the long axis horizontal, and may contain altogether 2,000 cones... the size of each of the 2,000 receptor-conductor units measures, on the average, 24" of arc. The size of the units even in this territory varies, however, the central most measuring scarcely more than 20" of arc or even less. Of these – the most reduced cones, and therefore the smallest functional receptor units – there are only a few, perhaps not more than one or two dozen. The size of the units given includes the intervening insulating sheaths separating the adjoining cones from one another.

It is worth trying to imagine the size of the receptors. The smallest is one micron, only about two wavelengths of red light in size. One could not ask for much better than that. Even so, the visual acuity of the hawk is four times better than that of man.

The number of cones is about the same as the population of Greater New York. If the whole population of the United States of America were made to stand on a postage stamp, they would represent the rods on a single retina. As for the cells of the brain – if people were scaled down to their size, we could hold the population of the earth in our cupped hands; but there would not be enough people to make one brain.
The photopigments of the retina are bleached by bright light; it is this bleaching which – by some still mysterious process – stimulates the nerves, and it takes some time for the photochemical to return to normal. The retinal chemical cycle involved is now understood, primarily through the work of George Wald. While a region of photopigment is bleached, this region of the retina is less sensitive than the surrounding regions, and this gives rise to after-images. When the eye has been adapted to a bright light (e.g. a lamp bulb viewed with the eye held steady, or better a photographic flash) a dark shape, of the same form as the adapting light, is seen hovering in space. It is dark when seen against a lighted surface, but for the first few seconds it will look bright, especially when viewed in darkness. This is called a ‘positive’ after-image, and represents continuing firing of the retina and optic nerve after the stimulation. When dark, it is called a ‘negative’ after-image, and represents the relatively reduced sensitivity of the stimulated part of the retina due partly to bleaching of the photopigment.

Two eyes

Many of the organs of the body are duplicated, but the eyes and also the ears are unusual in working in close co-operation: for they share and compare information, so that together they perform feats impossible for the single eye or ear.

The images in the eyes lie on the curved surfaces of the retinas, but it is not misleading to call them two-dimensional. A remarkable thing about the visual system is its ability to synthesise the two somewhat different images into a single perception of solid objects lying in three-dimensional space.

In man the eyes face forwards, and share the same field of view; but this is rare among vertebrates, for generally the eyes are at the sides of the head and aim outwards in opposed directions. The gradual change from sideways to frontal looking eyes came about as precise judgment of distance became important, when mammals developed front limbs capable of holding and handling objects, and catching the branches of trees. For animals who live in forests and travel by leaping from branch to branch, rapid and precise judgment of distance of nearby objects is essential; and the use of two eyes, co-
5.10 The eyes converge on an object we examine, the images being brought to the foveas. In a we see the eyes converged to a near object, in b to one more distant. The angle of convergence is signalled to the brain as information of distance — serving as a range-finder.

operating to give stereo vision, is highly developed. Animals such as the cat have frontal eyes which function together, but the density of the receptors is nearly constant over the retina. There is no fovea unless precise depth perception is really important, as in birds and in the tree-living apes, when we find developed foveas and precise control of eye movements. Stereo vision for movement is also provided by the paired compound eyes of insects, and is highly developed in insects such as the dragon fly which catches its prey at high speeds on the wing. The compound eyes are fixed in the head, and the mechanism of their stereo vision is simpler than in apes and man where foveas are brought to bear on objects at different distances by convergence of the eyes.

Convergence, or range-finder, depth perception Figure 5.10 shows how the eyes pivot inwards for viewing near objects: distance is signalled to the brain by this angle of convergence. This, however, is by no means the whole story.

A simple experiment shows that the convergence angle is indeed
used to signal distance. Figure 5.11a shows what happens if a pair of prisms of suitable angle are introduced to bend the light entering the eyes, so that they have to converge to bring distant objects on to the centre of the foveas. If the prisms are placed to decrease the angle of convergence (figure 5.11b) objects will appear nearer and larger; with prisms arranged to increase convergence objects appear further and smaller.* Depth perception is given in part by the angle of convergence of the eyes indicating distance, just as in a range-finder.

Now there is a serious limitation to range-finders: they can only indicate the distance of one object at a time; namely, the object whose images are fused by the appropriate convergence angle. To find the distances of many objects at the same time it is necessary to adopt a very different system. The visual apparatus has developed such a system, but it involves some elaborate computation for the brain.

Disparity depth perception The eyes are horizontally separated (by about 6.3 cm) and so receive somewhat different views. This can be seen quite clearly if first one eye then the other is held open. Any near object will appear to shift sideways in relation to more distant objects,

* The size changes however are complicated, because the total depth scale is shrunk or expanded by convergence. Cf. page 73.
5.11 The angle of convergence for a given distance can be changed by interposing prisms. a shows increased, and b decreased, convergence. The effect is to change the apparent size and distance of objects viewed through the prisms. The change is not optical, but due to rescaling by the brain, its range-finder giving it the wrong information. This is a useful experimental trick for establishing the importance of convergence on perception of size and distance.

and to rotate when each eye receives its view. This slight difference between the images is known as ‘disparity’. It gives perception of depth by stereoscopic vision. This is employed in the stereoscope.

The stereoscope (invented by Sir Charles Wheatstone in about 1832) is a simple instrument for presenting any two pictures separately to the two eyes. Normally these pictures are stereo pairs, made with a pair of cameras separated by the distance between the eyes, to give the disparity which the brain uses to give stereo depth vision.

Stereo pictures may be presented reversed – the right eye receiving the left eye’s picture and vice versa – and then we may get reversal of perceived depth. Depth reversal always occurs with this pseudoscopic vision (as it is called) except when the reversed depth would be highly unlikely. People’s faces will not reverse in depth. Hollow faces are too improbable to be accepted. So stereopsis is but a cue to depth, which may be rejected (figure 5.12).

Stereo vision is only one of many ways in which we see depth, and it only functions for comparatively near objects, after which the difference between the images becomes too small: we are effectively one-eyed for distances greater than perhaps 100 metres.

The brain must ‘know’ which eye is which, for otherwise depth perception would be ambiguous. Also, reversal of the pictures in a stereoscope (or a pseudoscope) would have no effect. But oddly enough, when the light is cut off to one eye it is virtually impossible to say which eye is doing the seeing. Although the eyes are fairly well identified for the depth mechanism, this information is not available to consciousness.

If the pictures presented to the two eyes are very different (or if the difference between the viewing positions of an object is so great that the corresponding features fall outside the range for fusion) a curious and highly distinctive effect occurs. Parts of each eye’s picture are successively combined and rejected. This is known as ‘retinal rivalry’.

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5.12 Switching the eyes with mirrors. (Top) A *pseudoscope* – gives reversed depth, but only when depth is somewhat ambiguous. (Centre) A *telestereoscope* – effectively increases the separation of the eyes. (Bottom) An *iconoscope* – reduces the effective distance apart of the eyes. These arrangements are all useful for studying convergence and disparity in depth perception.
Rivalry also generally occurs if different colours are presented to two eyes, though fusion into mixture colours is possible, especially when contours are fused by the eyes.

A great deal has been discovered over the last few years of how the brain combines the images of the two eyes, using the minute 'disparity' differences to compute depth. We now know that most cells in the visual cortex respond to stimulation from corresponding points of the two retinas. These are called 'binocular cells'. Presumably corresponding retinal points, as related by disparity to distance, are indicated by the firing of these binocular cells.

Until recently it has been assumed that stereoscopic vision always functions by binocular comparison between the edges of objects. In what has turned out to be an unusually important technique, Bela Julesz, of the Bell Telephone Laboratories in America, has shown that lines or borders are not needed. Julesz generates pairs of random dot patterns with a computer, so arranged that for each dot in the pattern shown to one eye there is a corresponding dot for the other eye. When groups of corresponding dots are displaced horizontally, the displaced dots are fused with their corresponding dots of the other eye's field – and depth is seen. Regions of the random patterns stand out (or sink behind) the rest, and may be given complex three dimensional shapes. This shows that cross correlation of points even where there are no contours can give stereoscopic vision. This fits the 'binocular cells' discovered by micro-electrode recording in the brain. A pair of Julesz stereograms is shown in figure 5.13. These need to be fused with a stereoscope. Many beautiful examples will be found in Julesz' book *The Cyclopean Eye* (1971).

Is this all there is to stereo vision? As usual – there is more to it! In the first place it is not clear why some dots but not others are accepted as 'corresponding'. This needs some kind of global decision by the visual system. Further, we see illusory contours joining groups of dots standing out in depth from the random background. This is some kind of contour creation. We can also create illusory contours for each eye with patterns such as figure 5.14. Can we produce *stereopsis* with such illusory contours? The answer is, Yes. Figure 5.15 shows a pair of illusory contours having disparity, which when presented one to each eye in a stereoscope give stereoscopic depth – though there is no stimulation of binocular cells. This suggests that
5.13 These random patterns were computer-generated, with a lateral shift of each point in a central region of one of the patterns. When seen, one with each eye (using a stereoscope), this central region appears above the rest of the pattern — showing that the eyes perform a cross-correlation between the pair of patterns, to convert disparity (horizontal displacement) into perception of depth. Stereoscopic depth does not therefore depend upon contours, as had been thought before Julesz’s experiments.

Stereopsis can work not only from the physical points of stimulation at the sense organs — but also from inferred contours. On this (cognitive) explanation, illusory contours are postulated by the brain when gaps are unlikely — and are very probably due to masking by some nearer object hiding part of the figure. A nearer masking object is then postulated, from the evidence of the unlikely gaps. If this account is correct, we see that absence of stimulation can serve as data for perception. Similarly, the illusory letters seen in figure 10.17 seem to be postulated, or guessed, from the shadows. So even simple
perceptions, such as contours, may have subtle and 'cognitive' origins.

This account of illusory contours is not universally accepted. Some authorities suppose that these are contrast effects (cf. figure 6.1) or that they are given by neural interactive effects such as lateral inhibition. The issue is whether these illusory contours are produced indirectly, by data (surprising absence of stimulation) or more directly by (disturbed) signals, due to interactive effects early in the visual system. The first kind of theory is cognitive and the second is purely and simply physiological.
5.14 These broken ray figures (and there are many other examples) produce illusory contours, and whiter-than-white or blacker-than-black regions. It seems that they are 'postulated' as masking objects lying in front of improbable gaps. If so, to seek simple relations between physiological activity of, for example 'feature detectors' and experience of even simple features such as contours, is to be optimistic.

The issue is fundamental. On the cognitive account – that these illusory contours are inferred – we can hardly expect to find simple relations between neural activity (such as from the 'feature detectors' [pages 46–8]) and even elementary perceptions, such as contours.

Some people do not get depth from the Julesz dot figures, though they do from ordinary line or picture stereograms. Also, for normal observers, if there is no brightness contrast, but only colour contrast – then the dot figures do not give depth – though depth is still seen from lines. So there may be two brain mechanisms for stereo depth.
We end with a final feature of stereo depth perception. There is a clear linkage between two of the depth signalling mechanisms we have described—(1) the convergence of the eyes serving as a range finder, and (2) the difference between the two images giving disparity. The angle of convergence adjusts the scale of the disparity system. When the eyes fixate a distant object, disparities between the images are accepted as representing greater differences in depth than when the eyes are converged for near vision.

If this did not occur, distant objects would look closer together in
5.15 Shows a pair of figures which produce curved illusory contours. When presented to each eye - we observe stereoscopic depth from disparity of illusory contours (to be viewed horizontally with a stereoscope).
depth than near objects of the same depth separation, for the disparity is greater the nearer the objects. The linked mechanism compensating for this geometrical fact may be seen at work quite easily – by upsetting convergence while keeping the disparity the same. If the eyes are made to converge to infinity (with prisms) though near objects are being observed, they appear stretched out in depth. So we can see our convergence-disparity compensation system at work.

Is contour perception innate or learned? Recent experiments have attempted to decide whether the orientation feature detectors (as they are often though probably misleadingly called) are given innately or whether early experience affects them. Kittens have been reared in environments of vertical stripes, and have been tested for vision of vertical and for other orientations of stripes – and for corresponding feature detectors. It has been found, by Colin Blakemore and others, that kittens living in a world of only vertical stripes appear to be blind to horizontal stripes, and they lack horizontal feature detectors. Similarly, kittens denied horizontal stripes do not have the usual vertical feature detectors. Although some investigators have failed to repeat this result, it is now generally accepted. It suggests that not all the basic feature detectors are laid down at birth, but are developed by visual stimulation. Alternatively, such innate neural mechanisms may degenerate with lack of stimulation. In either case, the early visual environment of babies may be highly important for adult vision – so nursery wallpaper should be considered!

There are both practical and theoretical implications to this kind of research into the origins of neural connections and properties of brain mechanisms. How much detailed ‘wiring’ is laid down by genetic instructions? How flexible, how adaptable, is the nervous system? Can lost time be made up later in life? These are pioneer experiments relating physiology to knowledge gained from experience.
6.1 Simultaneous contrast. The part of the grey ring seen against the black appears somewhat lighter than the rest, seen against white. This effect is enhanced if a fine thread is placed across the ring along the black-white junction.