CHAPTER SIX

Physiology of the rétina

H. B. BARLOW

Much of the classical research on human visual performance was intended to elucidate physiological mechanisms of the retina, and in many cases indirect conclusions drawn from such research have been strikingly confirmed by more recent direct experimental investigations. But this direct approach has also revealed important new facts that were previously unsuspected, and the aim of this chapter is to give a brief description of retinal physiology emphasising these new aspects. Details that fit in well with previous knowledge will be found elsewhere, mainly in Chapter 2 for anatomy, Chapter 5 for biochemistry, and Chapters 7 to 9 where psychophysical measurements of performance are covered systematically.

6.1. DYNAMIC RANGE OF RETINAL INPUT AND OUTPUT

The retina is a thin sheet of photoreceptors and nerve cells lining the back of the eye where the image is formed (Figs. 2.2, 2.3, 2.4). It is obvious that its functional role is to encode the image falling on the retina as a pattern of nerve impulses in order to transmit the picture up the optic nerve to the brain, but a few words about the natural difficulties of this task may enable us to understand better the more detailed account that follows.

The total number of quanta that enter the pupil and form the retinal image varies from about 100 s^{-1} on a dark night where the light is just sufficient to help us orient ourselves, up to some 10^{14} s^{-1} on a sunny beach in summer when the light is uncomfortably strong. Nerve fibres are wretched channels to signal a quantity that varies over this range because their impulse frequency can only go from zero to about 1000 s^{-1}, so only a dozen or so distinguishable levels of activity are possible within the fraction of a second allowable if information is to be provided promptly. An electronic engineer uses differential inputs and zero offsets, or special devices such as automatic gain controls and contrast controls, to ensure that the meaningful aspects of the image are preserved in the electrical signal.

The very restricted dynamic range of nerve fibres compared with electrical transmission channels suggests strongly that equivalent functions are necessary in the retina. It is worthwhile bearing in mind the problem of matching the dynamic range of visual signals to the limited capacity of nerve fibres when reading about retinal physiology.

6.2. PHOTORECEPTORS: RODS AND CONES

The photoreceptor cells form the outermost layer of the retina, furthest from the vitreous and lens, and they are depicted in Figs. 2.3 and 2.4. Their outer segments, which contain the photosensitive pigment, have been discussed in Chapter 5.

Of the two main classes of receptor, rods are far more numerous in the human eye (over one hundred million in each) and also more sensitive; they are distributed widely over the retina but are absent in a region subtending about 1° in the centre of the fovea where powers of visual discrimination are greatest. They contain *rhodopsin* which is the photosensitive pigment that has been used for the vast majority of biochemical studies (see Chapter 5); its peak absorption occurs for blue-green light of wavelength 500 nm. Individual rods are linked electrically with their neighbours so that each of them signals the average illumination over a small region of the retina that overlaps the regions of its neighbours. Their response is relatively slow, which enables the results of quantum absorptions to accumulate for about 100 ms.

Rods are responsible for vision under conditions of poor illumination, roughly from bright moonlight downwards. The properties of *scotopic* vision, as it is called, result mainly from the facts about rods mentioned above. Cones do not respond at these low levels, so one is totally dependent upon the rods, but because of their interconnections they only provide poor spatial resolution compared to the cones, and because of their slow response they can only detect flicker up to about 12 Hz. All rods have the same spectral sensitivity, so there is no colour vision, and because they are absent from the central fovea and are most densely packed about 3 mm away from it, scotopic vision is actually best at 10°–20° eccentricity from the point of regard; at low light levels you can often see something better by looking slightly to one side of it, rather than directly at it.

There are far fewer cones, only about six million in each human eye, but they are much more important in ordinary daylight or good

artificial lighting. They are very tightly packed in the central fovea, where there are 150000 mm^{-2}, and in this region each cone probably has an individual ganglion cell and nerve fibre connecting it to the LGN and thence to the cortex. However it does not follow from this that there are no lateral connections through horizontal cells and amacrines giving the spatial and chromatic opponent aspects of the ganglion cell receptive fields described below. The time course of the cone response to a flash of light is quicker than for rods. There are three different types containing photosensitive pigments with different peak sensitivities; a red-sensitive one peaking at 560 nm, a green-sensitive one peaking at 530 nm, and a blue-sensitive one peaking at 420 nm. These blue-sensitive cones are curious in having substantially different properties from the other two types (see Chapter 9).

Vision using cones is called *photopic*, and the properties of such vision might be deduced from those of cone receptors. Spatial resolution is high, especially in the fovea, temporal resolution is improved by their quick response (see Fig. 8.12), and flicker can be seen up to about 55 Hz. Because their individual spectral sensitivities differ, colours as well as intensities can be signalled by the cone system.

The evidence for much that has been described so far comes from direct and rather simple observations. For instance the rod–cone 'duplicity' of retinal function was first enunciated by the German microscopist Max Schultze in 1866 on the basis of comparative studies of retinal histology in many animals; he found that the more nocturnal the species, the greater the preponderance of rods, and he concluded that rods were receptors specialised for vision at low luminances. The demonstration that psychophysical measurements of human visual functions usually show distinguishable scotopic and photopic regions corresponding to rod and cone functions was mainly accomplished by Selig Hecht in New York some 40 years ago; some measurements of this type will be found in the next section. The basic reason for the duplicity of the visual system is not altogether clear, but the hypothesis that cone pigments are less stable than rhodopsin, and therefore have a higher level of unavoidable intrinsic noise, would make sense of many of the structural and functional differences (see Chapter 7).

6.3. THE ACTION OF LIGHT ON PHOTORECEPTORS

In the last decade or so the biophysical mechanisms whereby the absorption of light activates the system have been intensively studied by measuring the flow of electrical currents around the receptors in light and darkness, and by measuring intracellular potential changes with very fine glass microelectrodes. Fig. 6.1 shows how the rods are thought to react to the absorption of light. It is found that, in darkness, a strong, steady current flows out of the inner segments of the rods towards their outer segments, and then in through the outer segment membranes to return to the inner segment intracellularly. The inner segment contains many mitochondria, and the resting current that flows in darkness is thought to result from a metabolically driven sodium ion pump similar to that of other cells. The expelled sodium ions are replaced by potassium ions to which the membranes are relatively freely permeable, and the excess internal concentration of potassium ions is accompanied by the well-known negative intracellular resting potential, which would be close to the electrochemical equilibrium potential for potassium ions if there was no resting current of sodium ions. However, unlike nerve cells, the membrane of the outer segment of rods in its unexcited state in darkness is quite freely permeable to sodium ions, so these pass down their large electrochemical gradient and cause the current shown flowing round the oval circuit in Fig. 6.1. This current short circuits the resting potential and reduces it from its usual value of more than -60 mV to about -25 to -30 mV. Now when light is absorbed this short-circuit current is found to be reduced, with the result that the negative intracellular potential increases towards the value typical for other neurons in their resting state. Records of intracellular responses to three different intensities of flash are shown in Fig. 6.1. Notice that most sensory receptors are *depolarised* when stimulated, whereas photoreceptors become *hyperpolarised* (their negative intracellular potential becomes more negative) when light is absorbed.

This hypothesis about the mechanism of rod activation was initially based on measurements of the potential difference between a pair of extracellular electrodes with their tips at slightly different depths in the retina. The flow of extracellular current was derived from these and has been confirmed by the much more sensitive method shown in Fig. 6.2: the outer segment of a rod is gently sucked into a glass micropipette so that all the current entering it can be

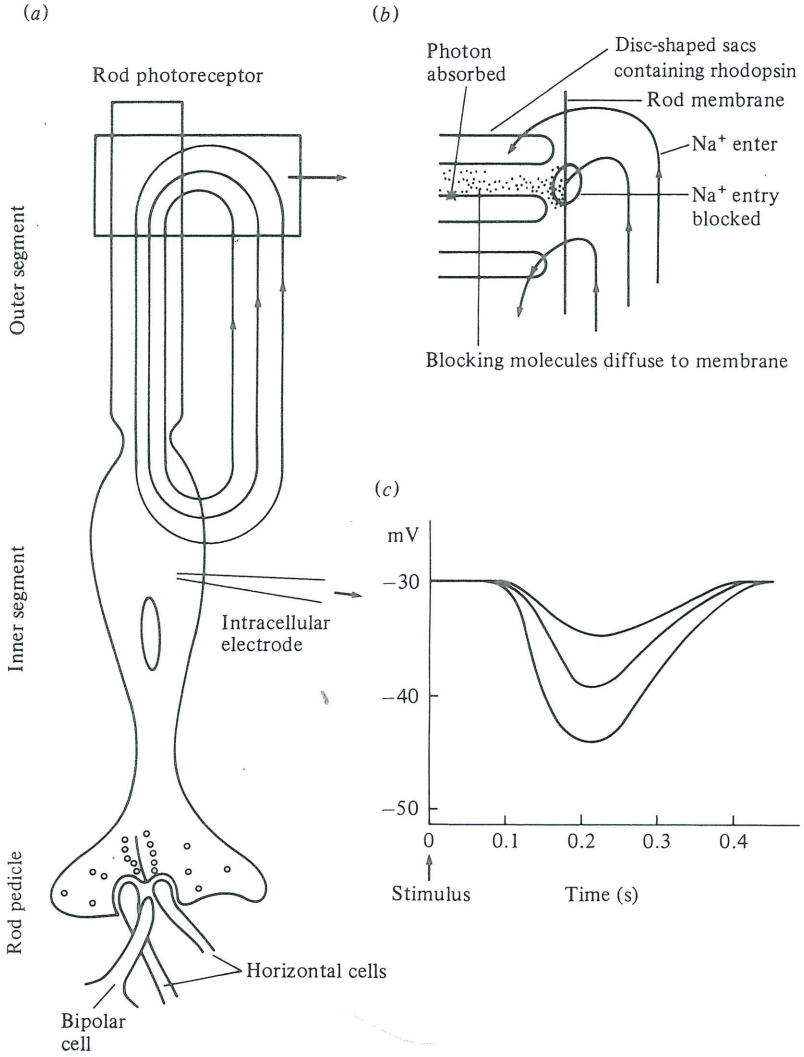

Fig. 6.1. (*a*) Diagram showing how the absorption of light is thought to excite a rod. A metabolic pump in the inner segment extrudes sodium ions; these are free to enter the outer segment, whose membrane has a high conductance for sodium ions in its resting state in darkness. (*b*) When photons are absorbed this high conductance is transiently decreased, perhaps as a result of 'blocking molecules' released at the site of absorption of the photons, though other mechanisms have been proposed (see Chapter 5). The reduction in the entry of sodium ions causes the interior to become more negative leading to the waveforms (*c*) recorded through an intracellular

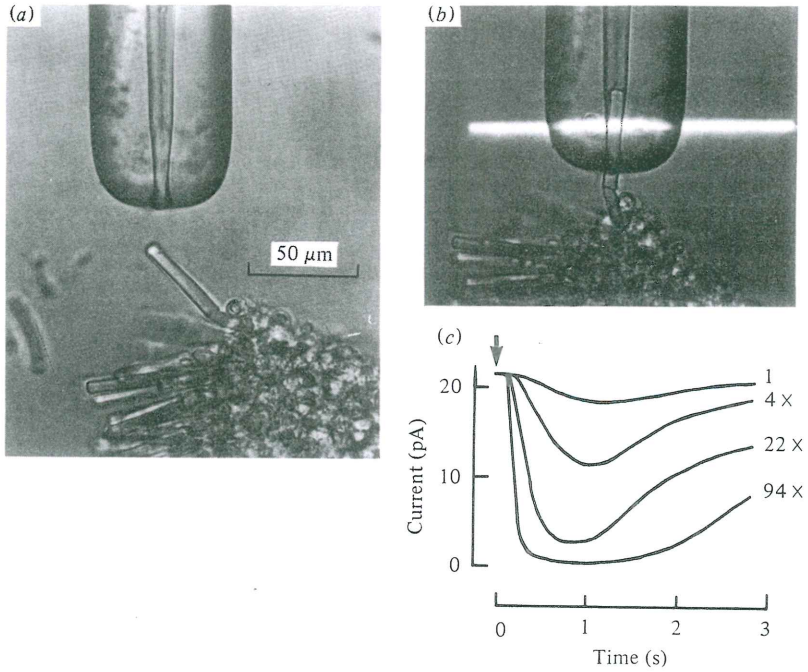

Fig. 6.2. The experiment shown here confirms that the hyperpolarising responses of rods result from blockage of the flow of current into their outer segments. (*a*) The outer segment of a toad rod, which is much larger than a mammalian rod (see 50 μm scale), is sucked into a glass micropipette so that it forms a tight seal at the tip. Almost all the current entering the outer segment has to be supplied through the pipette and can thus be measured. (*b*) When stimulated by a flash of light placed as shown at top right and delivered at the time indicated by the arrow in (*c*), the current is reduced from its resting value of about 20 pA. The reduction is graded with intensity as shown by the four responses illustrated; the strongest intensity is 94 times the weakest, and the entering current is reduced almost to zero at the flattened peak of this response. Much smaller responses than the smallest shown here can be detected, and in fact the sensitivity of the method is such that the responses to the absorption of single photons can be detected (see Fig. 7.8). (After Baylor, Lamb & Yau.)

electrode for three different intensities of flash stimulus. Note that the response to a light stimulus is a graded hyperpolarisation; most sensory receptors respond to stimulation by depolarising. The responses of mammalian receptors at 37 °C are faster than those shown here. (After Penn & Hagins and others.)

measured as it passes into the pipette (except for a small fraction leaking through the seal between the outer segment and the pipette tip). When flashes of light are delivered to the part of the outer segment above the seal there is a reduction of this entering current, and the time courses of these responses for four intensities of flash are shown in Fig. 6.2 (see also Fig. 7.8). Views on the mechanism whereby light blocks the entering current of sodium ions have changed radically over the past decade and are outlined at the end of Chapter 5: in darkness c-GMP holds the sodium channels open, and light decreases c-GMP concentration by activating the hydrolytic enzyme phosphodiesterase through a cascade of other substances. Calcium ions, previously thought to act as an intracellular transmitter closing the sodium channels, are now thought to decrease in concentration during light and thereby mediate light adaptation.

The increased intracellular negativity resulting from the blockage of the current entering outer segments spreads electrotonically throughout the receptor cell and reaches the inner segment and pedicle, which synapses with bipolar cells and horizontal cells. Intracellular recordings from receptors in non-mammals have revealed another unsuspected detail. The rods do not function in isolation, but as already mentioned they are linked to each other by electrical synapses. The result of this arrangement is to pool the excitation reaching a number of receptors, so that the change in intracellular potential of each rod does not depend solely upon the number of quanta absorbed in that particular rod, but rather upon the average number absorbed in the local population of rods, thereby reducing the 'noisiness' of the messages transmitted and making better use of the dynamic range available at the receptor–bipolar synapses.

The pipette technique has been successfully applied to primate and human rods and cones, thereby confirming that they behave in most respects like the non-mammalian receptors upon which most of the pioneering work had been done. There are some important differences, for instance in the fact that the rods of primates do not adapt like those of toads and salamanders, and the method has made possible greatly increased accuracy in the determination of spectral sensitivities.

6.4 HORIZONTAL AND BIPOLAR CELLS

When the photoreceptors absorb more light the hyperpolarisation of their terminals is thought to decrease the release of a chemical transmitter whose identity is so far uncertain. The action on the

postsynaptic cells is variable; the intracellular potential of horizontal cells always moves in the same direction as the receptors (at least in the case of those connected to rods) and therefore the chemical transmitter must have a depolarising action on them. Some of the bipolar cells also hyperpolarise when light is absorbed by the underlying receptors, but other bipolars are depolarised under the same circumstances; for these bipolars the receptor transmitter must cause hyperpolarisation. Fig. 6.3 shows these responses together with a diagram of the synaptic organisation of a vertebrate retina. This figure also indicates the action of the horizontal cells. They are connected to receptors over a much larger area than that within which rods are connected to each other, and they are hyperpolarised when light is absorbed. Their action is to modulate the connection between rods and bipolars, so they carry a signal from rods at a distance from a bipolar cell which opposes that of the receptors immediately underlying it; if one set hyperpolarises the bipolar, the other set depolarises, and vice versa.

There are two particularly interesting points about the organisation and function of the retina described above. The first is that it provides an example of nerve cells interacting with each other by means of graded depolarisations and hyperpolarisations, rather than through all-or-none impulses arriving at synaptic terminals. Previous to this work on the retina it had usually been taken for granted that the input to a synapse was an impulse, and that the output from the postsynaptic neuron was also in the form of impulses propagated down its axon, though it was recognised that the intracellular potential of the postsynaptic neuron represented the graded combination of all its synaptic inputs. Now it is clear that neurons can also interact by graded potentials, and examples are being found elsewhere in nervous systems. Interactions over distances greater than a few millimetres must be mediated by impulses, but over shorter distances graded interaction may prove to be the rule rather than the exception.

The second point of interest is that the role of the horizontal cells appears to be to mediate *lateral inhibition*, which is found very commonly in all sensory pathways. Its action in the spatial domain may be likened to that of the adaptation of sense organs in the temporal domain; both of these mechanisms emphasise change and discontinuity at the expense of uniformity in space or constancy in time. In vision, lateral inhibition plays a part in bringing about simultaneous contrast effects and also the reduction in sensitivity to low spatial frequencies illustrated in Fig. 8.1 and described in that chapter. Though it has only recently been demonstrated that hori-

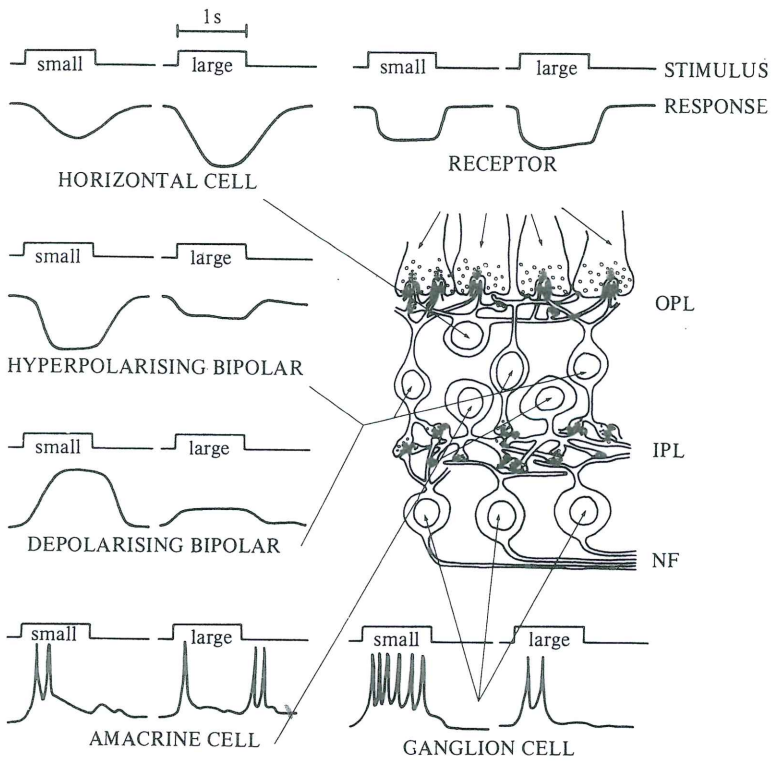

Fig. 6.3. Diagram of the synaptic interconnections in the vertebrate retina based on electron microscopy, and examples of the potentials that can be recorded intracellularly from the different types of cell. For each cell, responses are shown for two types of stimuli, each lasting 1 s as shown by the stimulus traces. The first stimulus is a small spot of light focussed on the centre of the region of retina to which the cell responds. The second is for a large spot which stimulates a wider region of retina. For a receptor the large spot produces a slightly larger hyperpolarisation (downward deflection), because of the lateral interconnections with other receptors, and also because of any stray light that may be present. For horizontal cells this effect is even bigger, because they pick up from an extensive population of rods. But for both types of bipolar cell the large spot produces a smaller response than the small spot; this is because the horizontal cells oppose the action of receptors on bipolars, this taking place in the complex synaptic interconnections occurring in the outer plexiform layer (OPL). The responses so far have all been graded hyper- or depolarisations, but the amacrines and ganglion cells show spikes. The former are characteristically bursts at 'on' and 'off'. The ganglion cell shown here gives a well-sustained burst of spikes

zontal cells are responsible, studies of visual performance showed more than a hundred years ago that such a mechanism must exist.

Some horizontal cells are connected with cones, and they are often connected to two different types of cone in an opponent fashion so that red light causes hyperpolarisation while green light depolarises, or vice versa. The details of such interconnections are not known in man, or any other mammal, but they have been studied in fish.

6.5. AMACRINE AND GANGLION CELLS

So far we have traced the results of light absorption in the receptors only through the outer synaptic, or plexiform, layer to the second order neuron, the bipolar cell. These connect to *amacrine* and *ganglion cells* in the inner plexiform layer (Fig. 2.4), and it is only at this level that impulses are recorded. The ganglion cells generate the streams of action potentials that pass up the optic nerve fibres to the brain. The role of amacrine cells, which also generate spikes, is uncertain but they are probably concerned with the pattern selectivity of ganglion cells. Electron microscopy and intracellular recording have given a preliminary view of these mechanisms, but the account is so far incomplete.

Recordings from optic-nerve fibres have provided some examples of what the mechanisms achieve, and a brief account has been given in Chapter 1. The first point to realise is the great diversity of types of ganglion cell. It was known that this must be the case from the histological studies of the retina by Raman y Cajal in the last century, but it is only in the last few decades that a corresponding diversity of physiological function has been uncovered. Some ganglion cells are amazingly selective in what they will respond to, and only send impulses centrally when a highly specific pattern of stimulation is present in the image falling on the receptors to which they connect (see Fig. 1.6).

It is not certain what ganglion cells the retina of man contains, but the common types found in monkey are as follows. The majority have

which would be transmitted up the optic nerve fibres (NF) to the LGN. Note that there are many other types of ganglion cells (see text and Figs. 1.6 and 1.7); the very complex interactions in the inner plexiform layer (IPL) are probably involved in achieving selectivity for particular trigger features, such as direction of motion. Although the retina is simple compared with many parts of the nervous system, it should not be thought that this diagram covers all types of retinal neuron. (After Dowling, Werblin and others.)

small receptive fields whose centre is predominantly sensitive either to red or to green, with their surrounds sensitive to the complementary colour. Furthermore these surrounds respond at the opposite phase of illumination to the centre and counteract excitation of the centre. Thus if, for instance, the centre is excited by red light when turned on, a response will be elicited from the surround when green light is turned off. Since there are four possible centre types (red, green, and 'on' or 'off' for each) and four surround types, there are sixteen (4×4) possible arrangements, but only four of these are found, namely those for which the surround is opposite to the centre both in spectral type (red or green) and in the phase to which it responds. The mechanism through which this double antagonism is achieved is not certain, but it probably involves the horizontal cells whose contribution to centre-surround antagonism has already been mentioned.

Ganglion cells of this type seem to signal a combination of spatial and colour information. Take a red, on-centre unit with its green, off-surround, for instance. It will not respond to a large, uniform white spot of light, for this excites both centre and surround and these annul each other. But if the large spot is tinted red, the 'on' mechanism will predominate and a response will occur when it is turned on, whereas if it is tinted green a response will occur when it is turned off. However if a white spot is small so that it only fills the centre, then it will elicit responses at 'on' like a large red spot, whereas a white annulus will behave like a uniform green spot and elicit a response at 'off'. The ambiguity in the meaning of impulses from one cell is decreased when the responses of other types are taken into account, and this must be performed centrally by the organised combination of signals from the four different types of unit.

Some colour opponent cells are encountered which lack the spatial opponent feature. The receptive fields of this type are larger than for the other type, and the fields for the two opponent colour mechanisms are the same size. The consequence is that such units cannot signal fine spatial detail, but respond to changes of tint of the light.

In addition to the red–green opponent units, blue–yellow units are found. For these the blue mechanism is derived from the blue-sensitive cones, just as red and green mechanisms are derived from their respective cones in the commoner type of colour-opponent unit. The yellow mechanism, however, appears to be formed by combining signals from red and green cones.

Most of the colour-opponent units have spatial opponency, but as mentioned some do not. There are also units with spatial opponency but no colour opponency. These have rather large

receptive fields with an 'on' centre and 'off' surround, or vice versa. They have another characteristic in that they tend to give brief, poorly sustained, responses to continued stimulation and they are probably analogous to the 'transient' or Y-type cells of cats (Chapters 1 and 8). The exact significance of this system is not understood; possibly they should be regarded as elements that specialise in high temporal resolution and signalling movement while other units with small receptive fields specialise in high spatial resolution.

One of the lessons neurophysiologists have learned is that electrodes do not sample from all neural types in an unbiassed fashion. We know that the types so far described occur in monkey retina, but it is probably not a complete list of the types likely to be present, so it is quite possible that the human retina also has ganglion cells selective for direction of motion and other specific spatiotemporal patterns.

The foregoing brief account of the retina tells us something about its mechanism, but it does not tell us how well it works. The best way to find out what information the retina successfully extracts from the image and transmits to the brain is to measure the overall performance of the visual system, and the next chapters are devoted to this problem.

6.6. SUGGESTIONS FOR FURTHER READING

General references

Dowling, J. E. (1987). *The Retina.* Harvard University Press. (An account of the histology and organisation of the retina by the person who discovered much of it.)

Baylor, D. A. (1987). Photoreceptor signals and vision. Proctor lecture. *Investigative Ophthalmology and Visual Science*, **28**, 34–49. (Nice summary of the photoreceptor work.)

Rodieck, R. W. (1988) In *Comparative Primate Biology*, Vol. 4, pp. 203–78, ed. H. D. Stecklis & J. Erwin. New York: Alan R. Liss (Detailed review of the primate retina.)

Special references

Automatic control systems in retina. Werblin, F. W. (1973) *Scientific American*, **228**, no. 1, 70.

Rod and cone function. Hecht, S. (1937) *Physiological Reviews*, **17**, 239.

Electrical response of photoreceptors. Lamb, T. D. (1984) *Recent advances in Physiology*, ed. P. F. Baker, **10**, 29–65. Edinburgh: Churchill Livingstone.

Types of ganglion cell. De Monasterio, F. M. & Gouras, P. (1975) *Journal of Physiology*, **251**, 167. Shapley, R. & Perry, V. H. (1986) *Trends in Neuroscience*, **9**, 229–35.

CHAPTER SEVEN

Psychophysical measurements of visual performance

H. B. BARLOW AND J. D. MOLLON

When you use your eyes in everyday life what you 'see' is, in one sense, the physical reality of the world around you: the table, book, cat, and so on. But for the sensory physiologist what you 'see' is something very different: it is the pattern of nerve activity, occurring at some level in the brain, that enables you to recognise the table and place your cup on it, to read the print in the book, or to reach out and stroke the cat. What level is involved in this conscious perception is quite unknown, and it is probably over-simple even to talk about it as 'a level in the brain', but what is abundantly clear from the chapters in this book is that a very intricate, very cunningly evolved, sequence of steps intervenes between the physical reality in the world about us and the patterns of nervous activity by which we experience the sight of that reality. The next sections describe the results of measurements that have been made to explore how well this sequence of steps works. How much light do we need to see? How sharp is the picture given by our eyes? How quickly can changes be followed? What is the range of our colour discriminations?

The direct, quantitative study of our sensory performance is called *psychophysics*. Psychophysical measurements of vision are important for two practical purposes: first, one must know how well the normal eye works in order to assess whether an individual is suffering from defective vision; and second, one needs to be able to give the engineer practical guidance about many everyday problems. How much light is needed to read a traffic sign, and how big must the letters be to read it from a certain distance; is the flickering of a light visible when it is very dim; how would a particular type of fluorescent lighting affect the anaesthetist's ability to detect cyanosis in an operating theatre?

But psychophysical measurements are also indispensable theoretically; and indeed they have historically been the primary source of our knowledge of sensory mechanisms. By systematically manipulating the input to the system and by restricting the range of permitted responses, the psychophysicist can learn much about the logic of the

mechanisms within the black box without lifting its lid. Thus psychophysical experiments on the mixture of colours (Chapter 9) allowed the three types of cone photoreceptor to be postulated as 'hypothetical constructs' many years before it was possible to identify them by direct measurements, rather as the gene existed as a hypothetical construct before it could be identified with a particular segment of a DNA molecule.

Despite the glamorous successes of single-unit electrophysiology in the last three decades, psychophysics remains a powerful and complementary source of information. The reason may best be understood by considering the limitations of single-unit electrophysiology. Firstly, the electrophysiologist can never be sure that the electrical response he records is part of the process of seeing: it is easy enough to observe changes in a complex, reactive tissue like the retina when it is excited by light, but it is quite a different matter to establish that the changes you are recording are functional links between physical reality and our perception of it. Secondly, the electrophysiologist can at best record from only a small number of units concurrently and cannot know whether the activity of a given cell has an absolute meaning for later stages of the system or whether its meaning depends on the state of other members of a set of cells. Thirdly, differences between types of cell in morphology and in vulnerability to anaesthetics mean that electrophysiology often yields a badly biassed sample of the full population of cells. The late William Rushton, a distinguished physiologist whose own psychophysical experiments were as elegant as his humour was wry, once likened the electrophysiologist to a person who wishes to discover the foreign policy of a central European country and who therefore crosses the frontier on a dark night, enters a border town and asks random passers-by for their opinion. Psychophysical measurements are important in telling the electrophysiologist what his mechanisms must achieve, how the stimulus should be manipulated and what ought to be the stimulus–response properties of a particular mechanism. The sections on vision that follow are organised according to the *functions* of the visual system: we draw on both psychophysics and electrophysiology (and also anatomy) as suits our local purpose.

The vividness of our visual sensations, and the fact that they almost always prove to be reliable guides to action, tend to make us believe we understand vision and do not need to be told how it works. But although one can gain some knowledge of perception simply by paying attention to one's own subjective experiences as they occur

in a varying world, this source of knowledge is treacherous and cannot be very penetrating. A well-functioning television set usually reproduces faithfully what is before the cameras in the studio, but you are at the mercy of the studio engineers, who can easily deceive you if they wish, and anyway you cannot tell much about the working of television simply by looking at the picture.

The link between the receptors and the brain is at least as complicated as television and one must remember that in this case there is an additional step. The television picture is simply transmitted from studio to receiver, but our visual system not only transmits the picture on the retina, it also interprets it; our conscious perception is only the final product of these processes. The interpretative process involves memory and inference, and is consequently much harder to understand than transmission, but since our perceptions depend on these hazily understood operations we have to very careful how we use them to try to analyse sense organs. Figs. 7.1 and 7.2 reinforce this point.

7.1. MATCHES AND THRESHOLDS

The trick that has served well to show up the properties of the peripheral links in the sensory chain is to ask only the simplest possible questions of these more complex interpretative mechanisms. Thus the experimental subject might be asked to judge whether two stimuli can be distinguished from each other or not; if they appear the same in all respects they are said to *match*, and much valuable information, particularly about colour vision, has been obtained by finding what sets of lights, differing in their physical composition, are nonetheless indistinguishable to the observer's eye. Incidentally, simplifying the task of interpretation is a useful trick for practical purposes, because it leads to more accurate and reliable judgements: if you doubt whether a screw is the right size you will compare it directly with one known to be correct. In clinical medicine there are many such opportunities to improve the reliability of one's observations by substituting an easy direct comparison for a difficult absolute judgement.

Observations of *threshold* are only one step more complicated than matches. In this case the value of a physical parameter of the stimulus, such as its intensity, is adjusted until the subject can distinguish whether the stimulus is present or not with a specified rate of success over a number of trials. More complicated judgements

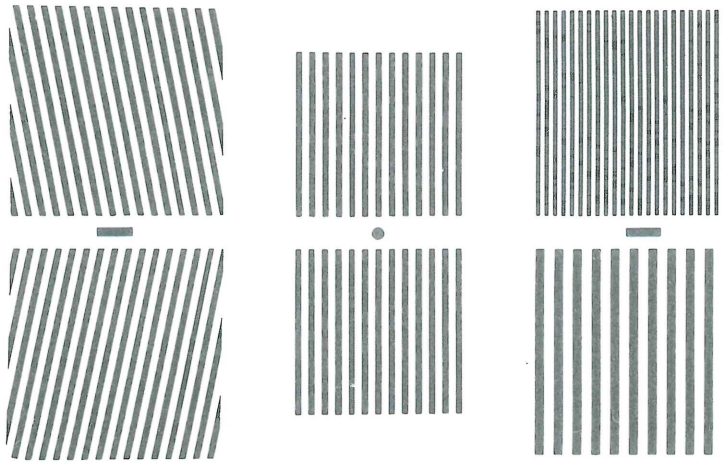

Fig. 7.1. Place the figure at a distance of about 50 cm and fix your eye on the black strip between the tilted gratings (on the left) for at least 30 s. Then transfer your gaze to the round dot between the vertical gratings. Each vertical grating should then briefly appear tilted in a direction opposite to that of the corresponding adapting grating. This effect shows that half a minute's experience of tilted lines can seriously disturb your ability to judge orientation.

Now try looking at the black strip between the right-hand patterns for a minute or so. (Move your eye about a little so that you don't fixate the same point on the strip throughout this adaptation period.) When you now look at the central spot, the lines of the upper grating should appear more coarsely spaced and those of the lower grating, more finely spaced. (A related after-effect is demonstrated in Fig. 8.8.)

The explanation of both these 'negative after-effects' is discussed in Chapter 12. Do the effects spread outside the region of visual field exposed to the adapting stimulus? If one eye only is exposed, do you experience the after-effect when viewing with the other eye? Where in the visual pathway might it occur? (After Blakemore.)

have proved useful, for instance measuring the physical intensities of two lights that appear 'equally bright', even though they differ in colour. Although such judgements can often be made reliably and repeatedly, there is a serious difficulty in interpreting them, for there is a linguistic or verbal element involved in asking people to judge a quality such as brightness in the presence of another quality such as colour that is also variable. This verbal element tends to be even stronger if we ask for more complex judgements, such as expressing

Fig. 7.2. At first you may see no sign of human occupation in this innocent island scene. However its title is 'St Helena', so look again. If you still have no luck, look for Napoleon in the space between the trees on the left. Once you have seen him, for how long can you look at the picture without him obtruding into your gaze? This illustrates first that mental 'set' is important in what you perceive, for without hints one can easily miss Napoleon altogether. Second, notice how Napoleon and the trees are alternative constructs for that part of the figure; you cannot see both simultaneously, and what you see tends to flip from one interpretation to the other. Gestalt psychologists would say that the trees are either 'figure', in which case you see them as such, or 'ground', in which case the space between them forms the figure. Finally you probably would not interpret the space between the trees as Napoleon unless you had previously seen a picture of him in this posture, so you are being influenced by memories from some time in the past. More factors influence perception than we intuitively believe.

brightness by rating it on a 10-point scale. Such procedures necessarily involve interpretative mechanisms, and although they may have their uses, the following sections rely mainly on matches and thresholds, for these give the most reliable information about the early steps.

7.2. FACTORS THAT DETERMINE VISUAL SENSITIVITY

It might seem a simple matter to make a light dimmer and dimmer until it can no longer be seen, and then to record its physical intensity, but many different factors would influence the result and these must be brought under control before a meaningful and consistent figure is obtained. These factors will be described first before discussing what ultimately limits the eye's performance.

Dark adaptation

If one comes into a dimly lit room after being outside in bright sunlight everything appears dark at first, but after a few minutes one's eyes adapt to the darkness and one is often surprised how much can be seen. Recovery is complete in a few minutes after moderate levels of light adaptation, but a recovery curve lasting more than 30 min, as shown in Fig. 7.3, will be obtained if the pre-exposure has been very strong. Note that the recovery occurs in two stages, the first attributable to cones, the second to rods, and note also that threshold drops by a factor of more than 10000 (4 log units) during about half an hour.

There are many causes of these changes. The pupil expands, but this occurs rapidly and can only account for a tenfold change at most. There is also a resynthesis of the photosensitive visual pigments that were bleached during pre-exposure, but the gain in sensitivity is not a simple result of the increased proportion of light absorbed by the increased concentration of pigment. This is very clearly shown in the case of the rods, where it is found that more than a hundredfold drop in threshold is associated with the resynthesis of the final 10% of the rhodopsin, from 90% to 100% of its full concentration. The major factors that increase sensitivity appear to lie in the little-understood intracellular transmitter mechanism that causes changes in conductance of the rod membrane. However there are also interesting changes in the neural connections in the retina.

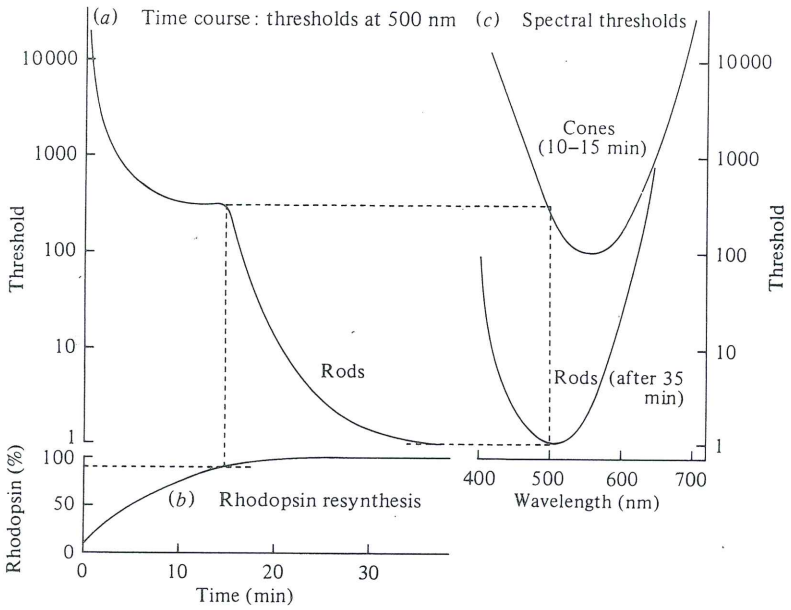

Fig. 7.3. Dark-adaptation curves, the resynthesis of rhodopsin, and spectral sensitivity curves showing the Purkinje shift. (*a*). The drop of log threshold with time following adaptation to a light that bleached a high proportion of rhodopsin in the rods. (*b*). The time course of resynthesis of rhodopsin on the same time scale; notice that less than 10% of the rhodopsin escaped the initial bleach, but 90% had been regenerated after 15 min, when the break occurred in the dark-adaptation curve. (*c*). Two sets of thresholds plotted against wavelength. The upper curve was obtained between 10 and 15 min after starting dark adaptation, and it represents the spectral sensitivity of the cone system. The lower curve was obtained after full dark adaptation and corresponds to the rods. Note that the peak of sensitivity moves (Purkinje shift). These curves represent similar data to V_λ and V'_λ plotted as relative sensitivity in Fig. 5.8, though the latter are obtained by different methods. The fact that the hundred fold drop in rod threshold occurs while the final 10% of the rhodopsin is being resynthesised shows that the change in the threshold is not a simple matter of increased light absorption in the photopigment. (After Rushton and others.)

Spectral sensitivity

If the threshold is measured using monochromatic lights of different wavelengths, results such as those shown in Fig. 7.3 are obtained. Measurements made on the 'cone plateau', within 15 min of intense light adaptation, yield a curve with a minimum threshold near 555 nm wavelength, corresponding to a yellow-green light. If the measurements are repeated after complete dark adaptation, the threshold is much lower and the minimum has shifted to 505 nm, in the blue-green part of the spectrum. This change of the position of maximum sensitivity is called the 'Purkinje shift', after the Bohemian physiologist of the last century who gave his name to many optical effects and anatomical structures: these include the images formed by reflections at the lens surfaces, and the appearance of the shadows of the retinal blood vessels, described in Chapter 3, and also the conducting fibres of the heart, and the neurons named after him in the cerebellum.

The spectral sensitivity curves shown in Fig. 7.3 are of great practical and theoretical importance. They are usually plotted as sensitivity (defined as 1/threshold energy), and they show the relative effectiveness of lights of different wavelengths in stimulating the photopic (cone) and scotopic (rod) systems. They form the basis for calculating the photopic and scotopic *luminance* of a light, for the degree to which a light of physical energy E_λ at wavelength λ nm excites the eye is given by the product $E_\lambda V_\lambda$ in photopic vision and $E_\lambda V'_\lambda$ in scotopic vision, where V_λ and V'_λ are the sensitivities at λ nm relative to the peak of the photopic and scotopic sensitivity curves respectively. This product must then be integrated over the whole spectrum ($\int E_\lambda V_\lambda \, d\lambda$) to assess the luminance of a light containing energy at several wavelengths or continuously distributed over the spectrum.

The curves used for the standardisation of V_λ and V'_λ were mainly obtained by photometric methods different from the threshold determinations suggested in Fig. 7.3, and they differ slightly from these. The shape of V'_λ is theoretically important because it depends primarily upon the absorption spectrum of rhodopsin, and the agreement between the two provides the key evidence implicating this pigment in visual excitation. For cones the situation is more complicated because the photopic sensitivity curve is some kind of average of the sensitivity curves of the red-, green-, and blue-sensitive receptors.

Background luminance

The apparent brightness of a light is much affected by the background against which it is seen, as one knows from the dim appearance of the moon by day, and the invisibility of stars. Fig. 7.4 shows an experiment in which special conditions were chosen to discourage the cones and thus ensure that rods were being utilised over a wide range of luminance levels. The subject saw a large field whose luminance I could be varied over a range of 10^6; this value is plotted horizontally on a logarithmic scale. To this was added a patch of light whose luminance was adjusted to threshold, ΔI, and this value is plotted vertically on a logarithmic scale. Over the middle range the line has a slope very near to 1, which implies that $\Delta I \propto I$. This is an example of Weber's law, which is familiar in many sensory judgements; it should be thought of as an approximate empirical generalisation rather than a basic law of operation of the nervous system, and even where it holds quite accurately its basis is not well understood. In the present case, desensitisation from the background light occurs either in the receptors, or in transmission to bipolars.

Notice that Weber's law breaks down both at low levels and at high. The former may result from spontaneous events mimicking the absorption of light; this is sometimes called 'dark light', since the level of such intrinsic noise can conveniently be expressed as a luminance. The steepening at the upper end is called 'saturation', and may result from the current that enters the outer segments of rods being completely blocked, or from another step in the excitation process being driven nearly to completion. At the very top the curve stops rising so steeply; this is where cones finally enter under these conditions, which were selected to keep them out of the way until a very high background was reached.

Eccentricity

Under photopic conditions the greatest sensitivity is almost always found at the fovea, which is automatically directed to what we wish to see best. But under scotopic conditions this is not so; lowest thresholds are obtained by giving the subject a dim point to fixate his gaze on, and then arranging for the test light to be exposed 10° to 20° in the periphery. The direction selected must not be temporal, for the blind spot is located 15° in the temporal field.

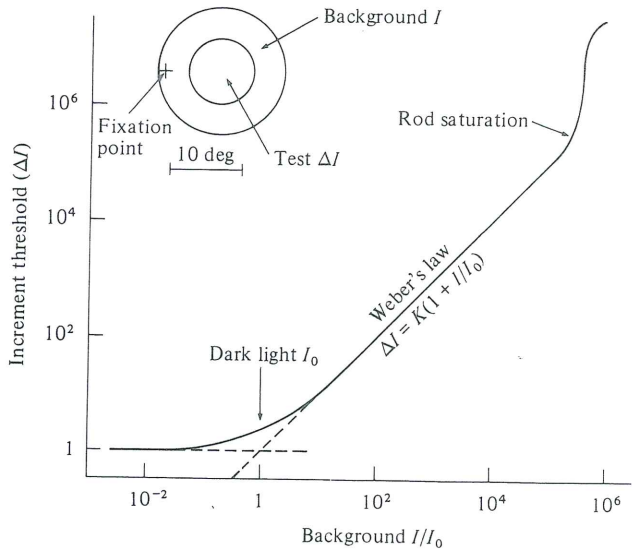

Fig. 7.4. The effect of background luminance on the detection of an added stimulus. The subject fixated on the cross at top left and saw the large uniform background in the right visual field. In the centre of the background a patch of light was added, and adjusted to threshold. Background luminance I is plotted horizontally, and increment threshold ΔI vertically, both on logarithmic scales. To ensure that the threshold was dependent on rods a blue-green light was chosen for the stimulus, together with peripheral location in the visual field, a large stimulus, and long duration exposure. In addition this light was sent into the periphery of the subject's pupil; because of the Stiles–Crawford effect (see p. 130) this light was relatively ineffective for cones. To ensure that the background field had more effect on cones and thus desensitised them more, its colour was orange. Below a certain value of the background, termed the *dark light*, the curve runs almost horizontally, indicating that ΔI is not affected by I. Above this value it rises, and over a range covering a 10000-fold increase in I the line has a slope close to 1, indicating that ΔI is directly proportional to I (Weber's law). Above this the values of ΔI rise more steeply, indicating *rod saturation*, and at higher levels still the values rise less steeply because cones are at last becoming operative. (After Aguilar & Stiles.)

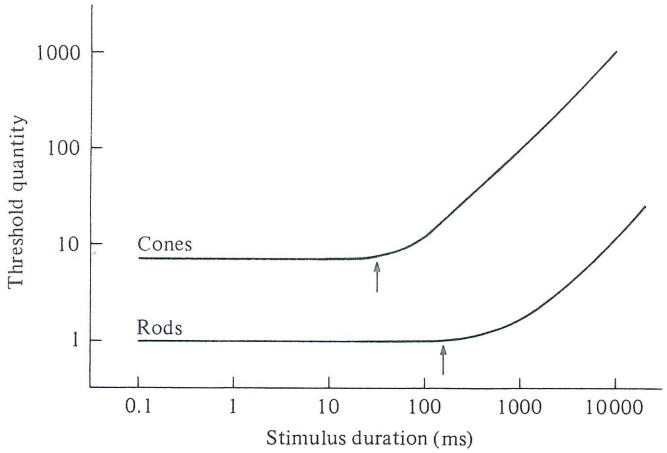

Fig. 7.5. The effect of stimulus duration on visual threshold. Stimuli of variable duration were adjusted in luminance until they could just be seen. This threshold was then multiplied by the duration, and also by the stimulus area, which was held constant, to obtain the threshold quantity of light, and this is plotted vertically against the duration horizontally, both on logarithmic scales. Notice that threshold quantity is independent of duration up to a certain value termed the *critical duration* or *summation time*, and thereafter rises. The summation time for rods is longer than that for cones, so the difference between their thresholds is greater for long-lasting stimuli. The value of the summation time is not a constant but varies with the background upon which test stimuli are superimposed, as well as the system being used.

Pupil diameter

As the pupil expands it admits more light, so under natural conditions the weakest lights can be seen when the pupil is large, provided this does not degrade the image quality to the point where the object's visibility is lost by blurring. In the laboratory it is convenient to use an artificial pupil smaller than the natural pupil, for then the amount of light entering the eye can be calculated without having to measure the natural pupil. The threshold *intensity* of light will be higher than with the natural pupil, but the *quantity* entering the eye will be the same.

Area and duration of test stimulus

Fig. 7.5 shows how the threshold varies with the duration of a stimulus flash. The threshold quantity of light is plotted vertically; this is the product of the threshold intensity, the duration (plotted horizontally) and the area of the test stimulus, which is kept constant in this experiment. Two curves are shown, the lower for rods in the periphery where they are most sensitive, the upper for cones in the fovea. For short durations the threshold quantity does not change, which means that the threshold intensity required is proportional to 1/duration. This is referred to as Bloch's law, and it holds for many photochemical reactions (the Bunsen–Roscoe law). However for durations beyond about 30 ms for the cones and 200 ms for the rods the threshold quantity increases, and at long durations it increases in direct proportion to the duration; at this point the threshold intensity is constant and unaffected by the duration of the stimulus. The point where the curves rise is called the critical duration or summation time. Notice that the threshold for foveal cones is about 7 times that of peripheral rods for short duration stimuli, but rises to almost a hundredfold for long durations because the long summation time for rods gives them a further advantage.

Fig. 7.6 shows the very similar relations that are obtained if threshold is determined as a function of the angle subtended by the

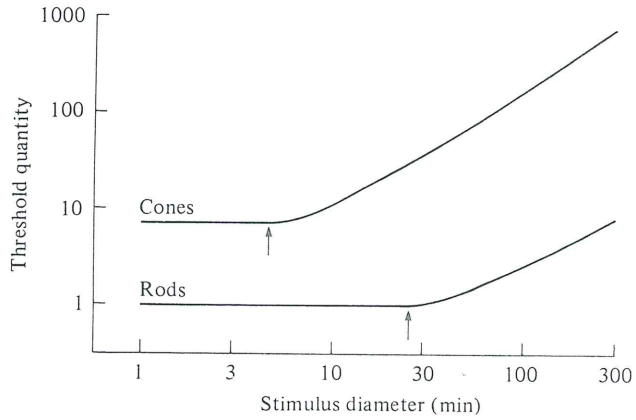

Fig. 7.6. The effect of the size of a test stimulus on threshold. The experiment was done as for Fig. 7.5, but the stimulus diameter was varied and its duration held constant. As before, the threshold quantity is unaffected until the stimuli exceed a certain size called the *critical area* or *summation area*, and thereafter it rises. The summation area is larger for peripheral rods than for foveal cones, so the difference between their thresholds is increased by using large stimuli. As with summation times, summation areas vary with background luminance as well as with eccentricity and the system, rods or cones, which is employed for the threshold tested.

stimulus. Here again the quantity of light required at threshold is constant, provided that the diameter is less than about 5 min for foveal cones and 30 min for rods. This relation implies that threshold intensity is inversely proportional to stimulus area, and is sometimes called Ricco's law after its discoverer. It occurs because the retina and visual pathways have the capacity to pool excitatory effects over a certain area, which is referred to as the 'summation area'. Summation may result from the interconnections between the receptors, from convergence of connections from receptors, through bipolar cells, on to retinal ganglion cells, or possibly from more central interactions. As with summation time, summation areas are reduced in the presence of background lights; in this case it is probably because lateral inhibitory mechanisms are more potent in the light-adapted state.

Summation time and area are reciprocally related to temporal and spatial resolution; a system which integrates over a long time or large area gains sensitivity for persisting and extended targets, but it is unable to specify exactly when or where they occur, so it loses temporal and spatial resolution. In both respects the resolution of cones is better than that of rods, but it would be a mistake to regard summation time and area as fixed and invariable constants for the two systems; they vary with adaptation level, retinal eccentricity, and other characteristics of the stimuli used to measure them.

Reliability of response

It is not altogether easy to decide whether a very weak light can be seen or not, for very weak sensations have a dubious character to them. Fig. 7.7 shows the responses of a subject to lights of six different intensities presented in random order. Some he definitely saw and the percentages of these are marked as circles. Others he was a little uncertain about; if these are included among the 'seen' responses the crosses are obtained. This curve is shifted to the left compared with that for the definitely seen responses, so the effect of including 'uncertains' is to lower the threshold, taking for this the mid-point of the curve corresponding to the intensity detected on 50% of trials. However this gain in sensitivity is achieved by sacrificing reliability; the subject was right to call these sensations uncertain, for he gave a small proportion of 'uncertain' responses to test trials which were actually of zero intensity, whereas he did not claim he definitely saw any of the blank stimuli. The allowable proportion of such false-positive responses is a factor determining the value of the threshold that will be obtained.

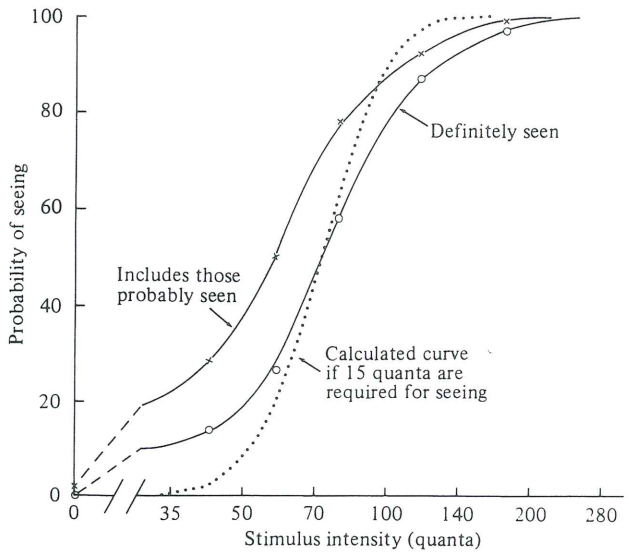

Fig. 7.7. Flashes of light of five different intensities were delivered in irregular order until 100 of each had been delivered. In addition 300 blanks of zero intensity were mixed in. The subject could respond with a definite 'Yes', or could indicate 'Probably yes' if he was not certain. The circles indicate the frequency-of-seeing curve for yes, the crosses the result when probables were added to yes responses. Notice that including probables lowers the threshold, defined as the intensity seen in 50% of trials, from 73 to 59 quanta. But a price was paid for this greater sensitivity because there were three 'Probably yes' replies among the responses to the 300 blanks of zero intensity. Unavoidable fluctuations in the numbers of quanta absorbed from these weak flashes play a part in the uncertainty of seeing near the threshold, but they are not the only cause of variability in responses. The number of photo-isomerisations resulting from 73 quanta entering the pupil is thought to be about 15 on average. The dotted curve shows the predicted frequency-of-seeing curve if the subject had said 'Yes' whenever 15 or more were absorbed, 'No' otherwise. This hypothesis predicts less variability in response than was observed, so there are other intrinsic sources of response variability, or noise. (After Barlow.)

Absolute threshold

The results shown in Fig. 7.7 are the ones we have been aiming towards, for they were obtained under the conditions that yield the lowest possible figure for the quantity of light that yields a visual sensation. To summarise the previous sections, the subject had been

dark-adapted for more than 45 min; light of wavelength 500 nm, at the peak of scotopic sensitivity, was used; there was no background light or other light to elevate the threshold; the test target lay 15° eccentric from the fixation point in the nasal field; an artificial pupil was used of known diameter, smaller than the natural pupil and well within it; the stimulus duration and area were below the upper limits of temporal and spatial summation; and on this occasion the subject used two criteria of acceptability, one of which gave no false responses with 300 blanks, the other three false positives, corresponding to 1%.

The result shows that a stimulus causing an average of 73 quanta to enter the pupil was definitely seen on 50% of trials. The exact result of course varies a bit from person to person but we may take 100 quanta of light of 500 nm as a typical figure for the human absolute threshold. Note first that this represents a very small amount of energy compared with the quantities we customarily handle; for instance the work available from 1 g falling 1 cm is more than 10^{12} times the absolute threshold. The eye is considerably more sensitive than photographic emulsions, and photoelecric devices have only recently surpassed it. However the ear is more sensitive and can detect an even smaller amount of energy.

We can follow further the quanta that enter the eye to cause a sensation of light. Some fail to reach the retina, and some are lost by passing through the retina without being absorbed. Then, of those absorbed, some fail to cause isomerisation of the rhodopsin molecule, which is thought to be the step that initiates excitation. The number of effective absorptions resulting from a just-visible stimulus is thus probably 10 to 15, though this figure cannot be given with great confidence or precision.

When one is dealing with such a small number of events one must expect considerable random fluctuation from trial to trial, and the amount of this variation is readily calculated. If the average number is 15 events, the numbers on individual trials will follow a Poisson distribution* that will have a standard deviation of $\pm\sqrt{15}$; hence

* If the events that *actually* occur are only a small fraction of the events that *might* occur, the numbers of such events in successive trials follow the Poisson distribution $P(n/a) = e^{-a}a^n/n!$ where a is the mean number of events, n the number on a particular trial, and $P(n/a)$ the probability of obtaining that number at that mean rate. The number of events that might occur in the present case is equal to the number of molecules of photopigment in the region of retina considered, and it is clear that only a small fraction of these are isomerised in this type of experiment, so the conditions hold for a Poisson distribution to be followed.

The calculation of the chance of a rod receiving a multiple hit when 15 molecules on average are isomerised in 1000 rods is done by obtaining from the above expression the probabilities of zero and one hit in a given rod; this is raised to power 1000 for the probability that all the rods absorb 0 or 1; then the probability that one or more rods absorb 2 or more quanta is the only remaining possibility and is 1 minus that figure:

$$P = 1-(e^{-0.015}+0.015\,e^{-0.015})^{1000} = 0.1054.$$

The calculation of the probability of obtaining a small bump or missing bump in the experiment illustrated in Fig. 7.8 is simply obtained from the Poisson expression for $n = 1$ or 0, and $a = 0.53$ in this particular case.

it will not be at all unusual for the number on a trial to drop below 10 or rise above 20. The question naturally arises whether this accounts for the fact that a stimulus delivering on average between 50 and 150 quanta to the cornea is sometimes seen, sometimes not seen, as shown in Fig. 7.7. In other words, do statistical fluctuations in quantal absorption cause the variability in response at threshold?

If the condition for seeing is that 15 or more quanta are absorbed one can calculate the expected shape of the frequency-of-seeing curve, and this is plotted in Fig. 7.7 as a dotted line. It is steeper than the observed curve, so one must conclude that quantum fluctuations are not the only factor causing variable responsiveness, though they must of course contribute to it. Other contributory factors are likely to be the excitatory events that occur in the absence of all light ('dark light', see Fig. 7.4), the 'noise' of synaptic transmission in the retina and elsewhere, and the inefficient use of the messages from the eye on the part of the central nervous system.

In following the weak excitatory process a step further one must realise that the 15 isomerisations do not occur in a single rod but are shared between many; how many will depend upon the size of the stimulus, but they could certainly be shared among 1000 rods without the threshold requirement being increased, and one can then calculate the chance of any rod receiving 2 or more isomerisations (see footnote). This turns out to be small (about 11%), so one can reasonably conclude that a rod does not require the absorption of more than a single quantum in order to initiate a signal. Fig. 7.8 shows that this is indeed so; the outer segment of a single rod from a toad retina was sucked into a fine pipette by the technique shown in Fig. 6.2, and the current being drawn into it by the inner segment was measured. A weak flash of light was delivered at regular intervals, and on some trials a change in entering current was recorded. The frequencies of occurrence of small bumps, and missing bumps, fitted well the expectations for a Poisson distribution (see footnote) and they can confidently be identified as the responses to the isomerisation of a single rhodopsin molecule, or none. Thus these neuro-

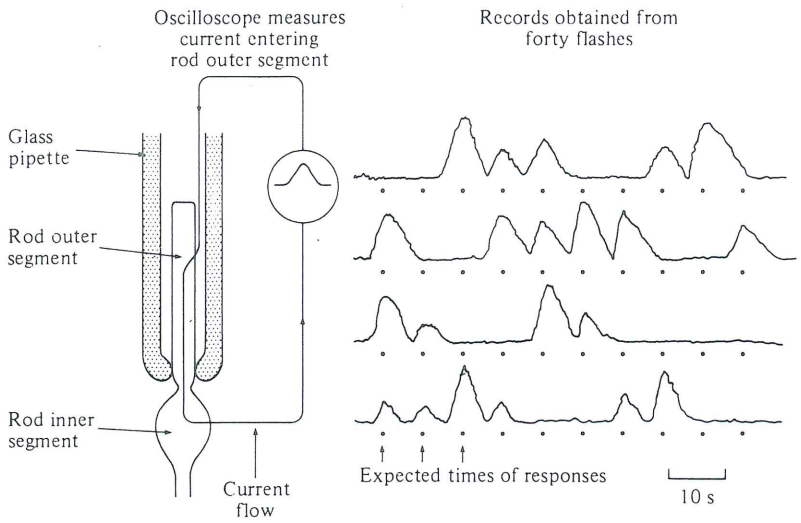

Fig. 7.8. Responses of a rod to the absorption of single photons. The outer segment of a toad rod was sucked into a micropipette by the technique illustrated in Fig. 6.2, and the current entering was measured while a weak flash of light causing an average of 0.53 isomerisations was delivered repeatedly. The records show 40 successive responses. As would be expected for a Poisson distribution with mean 0.53, isomerisations often failed to occur and there was no response. The small-sized bumps correspond to a single isomerisation and occurred at the expected frequency. Large bumps correspond to more isomerisations, but the sizes for more than two cannot be reliably resolved from each other. The very slow, transient, reductions of photocurrent are characteristic of toad rods at 20 °C, but mammalian rods at 37 °C would be much faster. (After Baylor, Lamb & Yau.)

physiological experiments confirm predictions made many years earlier, and they have also confirmed the speculation that the threshold for seeing is greater than the single quantum required by an individual rod because thermal isomerisations of rhodopsin occur at a slow but measurable rate. These would cause frequent false impressions of light if fewer than about 10 isomerisations caused a sensation.

7.3. SENSITIVITY OF CONES

It is worth summarising here the reasons why cones do not function at the low luminance levels that rods do.

(1) The cones are shorter and do not absorb such a high proportion

of the light that enters them. This, however, is partially offset by the fact that each appears to have an optical arrangement that concentrates the light from the pupil on to the pigment in the outer segment. This arrangement is responsible for what is known as the Stiles–Crawford effect: light entering the pupil's centre is, for cones but not for rods, a more effective stimulus than light entering the periphery. It is also responsible for the paradoxical fact that cone photopigments in situ show greater photosensitivity than does rhodopsin in rods; that is, for a given quantal flux, a higher proportion of cone pigment molecules are photochemically changed.

(2) The cone system has a smaller summation area and shorter summation time than rods (see Figs. 7.4 and 7.5).

(3) The electrical response to photon absorption is less.

(4) Whereas single photon absorptions produce very significant and readily detected changes in rods (Fig. 7.7), in cones many photons are required to produce a significant change detectable against the background noise. It is an attractive hypothesis that this high intrinsic noise level is the most important difference between the two types of receptor. The shift to longer wavelengths requires a decrease in the energy barrier that prevents thermal isomerisation occurring in darkness, and although it is only a decrease of about 10% this would be expected to increase the thermal isomerisation rate by a very large factor, about 4000 times. That would be enough by itself to prevent the cones giving useful signals at low light levels, so their unresponsiveness to single photons and the other differences listed above should perhaps be regarded as adaptations to overcome the handicap of a higher intrinsic noise level.

7.4. SUGGESTIONS FOR FURTHER READING

General references

Hochberg, J. E. (1978) *Perception.* New Jersey: Prentice-Hall Inc. (Perception from a psychologist's viewpoint with clear account of Gestalt approach.)

Graham, C. H. (1965) *Vision and Visual Perception.* New York: John Wiley. (A good source for the work on visual psychophysics before 1964.)

Ripps, H. & Weale, R. A. (1976) *On human vision.* In *The eye*, Vol. 2A, *Visual Function in Man*, ed. H. Davson. London: Academic Press.

MacLeod, D. I. A. (1978) Visual Sensitivity. *Annual Review of Psychology*, **29**, 613.

Special references

Tilt and other after-effects. Blakemore, C. (1973) In *Illusion in Nature and Art*, pp. 8–47. London: Duckworth.

Dark and light adaptation. Barlow, H. B. (1971) In *Handbook of Sensory Physiology*, Vol. 7, pt 4, ed. D. Jameson & L. M. Hurvich. Heidelberg: Berlin: New York. Springer. Lamb, T. D. (1988) In *Night Vision*, ed. K. Nordby & R. Hess. Cambridge University Press.

Rhodopsin concentration and threshold. Rushton, W. A. H. (1961) *Journal of Physiology*, **156**, 166.

Spatial and temporal summation. Barlow, H. B. (1958) *Journal of Physiology*, **141**, 337.

Weber's Law and saturation of rods. Aguilar, M. & Stiles, W. S. (1954) *Optica Acta*, **1**, 59.

Reliability, false positives, thermal isomerisation and threshold. Barlow, H. B. (1956) *Journal of the Optical Society of America*, **46**, 634. Baylor, D. A., Matthews, G. & Yau, K-W. (1980) *Journal of Physiology* **309**, 591–621.

Rod responses to single photons. Baylor, D. A., Lamb, T. D. & Yau, K-W. (1979) *Journal of Physiology*, **288**, 613.

Thermal stability of photopigments and Purkinje shift. Barlow, H. B. (1957) *Nature*, **179**, 255.

CHAPTER EIGHT

Spatial and temporal resolution and analysis

J. M. WOODHOUSE AND H. B. BARLOW

Our eyes enable us to recognise and discriminate the shapes of objects around us. We have seen how an image of such objects is formed on the retina and have gone into the factors that determine how much light is required to see. In the first part of this chapter we consider what is known of the mechanisms responsible for spatial resolution and analysis. The first requirement is that the eye should be able to respond separately to different parts of the image; these are the problems of resolution. But the visual system achieves form recognition by combining information obtained from different parts of the image, and we go on to consider the first steps of this process. It must be emphasised that there is a big difference in the level of our knowledge about these two stages; helped by the analogy with physical instruments, we have a good understanding of the eye's resolution, but we hardly begin to know how it proceeds to the analysis and recognition of the objects around us.

Just as the eye responds separately to light entering from different parts of the visual field, so it also responds quickly to light and thus separates events in time. We include problems of temporal resolution in this chapter, and also the problem of detecting movement, which is the simplest example of temporal pattern analysis.

8.1. ACUITY AND CONTRAST SENSITIVITY

The most complete way to represent the eye's resolving power is by determining its *contrast sensitivity function.* The subject looks at sinusoidal gratings (see Chapter 1 and Fig. 1.3), which are usually generated electronically on an oscilloscope screen. For each spatial frequency the contrast (see Fig. 1.3) is adjusted until the subject can just barely see that there is a grating present, as opposed to a uniformly illuminated surface. This is the contrast threshold and for a spatial frequency of 20 cycles deg^{-1} it would have a value of about 0.5% or 0.005. Contrast sensitivity is the reciprocal, 200, and this is what is plotted against frequency as the continuous curve in Fig. 8.1.