Chapter 6

Photoreceptors and Transduction

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In this chapter we leave behind the purely physical aspects of vision – light and optics – and begin a section on retinal physiology. In Chapters 6 and 7 we explore the anatomy, physiology, and function of photoreceptors. In Chapters 8-12 we explore the properties of other retinal neurons. In each case, we first describe the anatomy and physiology of the neurons themselves, and then introduce some of the causal stories of how the characteristics of these neurons leave their marks on the system properties of vision.

Logically speaking, photoreceptors have two major tasks to perform: phototransduction and signal transmission. The first goal of this chapter is to create at least a qualitative (if not quantitative) appreciation of these two processes.

In the phototransduction process, each individual photoreceptor – rod or cone – absorbs quanta of light. A quantum of light – a physical entity – ends its existence, and creates a neural signal. For many vision scientists, including DT, phototransduction has always held a special fascination, because it forms the immediate interface between the physical and physiological worlds. A part of the universe becomes a part of the individual.

The second task of photoreceptors is signal transmission. The absorption of quanta occurs in the outer segment of the photoreceptor. But in order to influence vision, the photoreceptor must transmit a neural signal all the way to its synaptic terminal, at which the photoreceptor communicates with later retinal neurons. The processes involved are complex, and the technical details are really available only to those students with a background in biochemistry and cell biology. However, even if you don’t have the background to understand these processes, we hope to provide at least an intuitive appreciation of them.
Technical advances have allowed vision scientists to carry out physiological recordings from single living, functioning photoreceptors. At low light levels, these recordings show that, amazingly, the absorption of a single quantum in a rod outer segment creates a physiological signal that is sufficient to affect the output of the rod. At higher light levels, they show that the responses of rods increase with increasing light levels, but eventually saturate; that is, they provide evidence for a saturating non-linearity very early in visual processing.

The second goal of this chapter is to continue our analysis of causal stories. How do the properties of photoreceptors leave their marks on the system properties of vision? We will examine three examples. The first deals with the effects of transduction in the rods on the spectral characteristics and wavelength information losses of scotopic vision. The second deals with the effects of the exquisite sensitivity of rods on scotopic absolute thresholds. The third causal story depends upon cones, and concerns the psychophysical consequences of photoreceptor saturation.

Transduction and signal transmission processes in the cones also have profound consequences for color vision and for photopic spectral sensitivity. However, the color story is too long to tell within the present chapter, and is postponed to Chapter 7.

6.1 Family portraits: The anatomy of photoreceptors

As shown in the schematic overview of Figure 1.4A, the photoreceptors lie in the outer portion of the retina, against the back wall of the eyeball. Quanta of light coming in through the lens traverse several other types of neurons before they arrive at the photoreceptors and are finally absorbed.

6.1.1 Rods and cones

There are two basic kinds of photoreceptors in the eye – rods and cones. Figure 6.1 shows some family portraits of rods and cones. Figure 6.1A shows a drawing of a primate cone and two primate rods, as seen through a light microscope. Figure 6.1B shows a scanning electron micrograph of two cones and several rods. Anatomists divide each photoreceptor into three basic parts: the outer segment, the inner segment, and the synaptic terminal.

6.1.2 Retinal distributions of rods and cones

The numbers of rods and cones vary across the retina in different ways, as shown in Figure 6.2. Figure 6.2A shows the concentration of rods and cones as a function of retinal eccentricity. The photomicrographs in Figure 6.2B show the varying sizes and densities of the two types of photoreceptors. In the central fovea (eccentricity 0.0), all of the photoreceptors are cones, and (as we already know) the outer segment diameters of foveal cones subtend only about 30 seconds of arc. At the other eccentricities both rods and cones are present, with the cones being increasingly larger in size, and the rods increasingly more numerous.

Figure 6.3 shows a high power electron micrograph of a rod outer segment. It shows a highly specialized structure of tightly packed membranes, called disks. There are about 1000 disks per rod outer segment. Each disk is composed of two membranes joined at the ends with a space between, like a stack of pita bread. The whole stack of disks is contained within the outer membrane of the rod outer segment. In cones these structures are slightly different (see the inset to Figure 6.3), in
6.1. FAMILY PORTRAITS: THE ANATOMY OF PHOTORECEPTORS

Figure 6.1: Rods and cones. A. Drawings of a rod and a cone as seen under a light microscope. The three basic parts of the photoreceptor – outer segment, inner segment, and synaptic terminal – are shown. The outer segments lie against the pigment epithelium, at the back of the eyeball, and the synaptic terminals lie closest to the center of the eyeball. Light entering the eye passes through the synaptic terminals and inner segments of the photoreceptors before being absorbed in the outer segment. B. A scanning electron micrograph of two cones and several rods. [A from Oyster (1999, Fig. 13.5, p. 550), after Polyak (1941). B from Lewis, Zeevi, and Werblin (1969), via Goldstein (1999, Fig. 2.12, p. 37).]
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Figure 6.2: Distributions of rods and cones across the retina. A. The concentrations of rods and cones as a function of retinal eccentricity. The concentration of cones is highest at the fovea, drops off rapidly out to about 10° eccentricity, and remains roughly constant across the rest of the peripheral retina. The rods are absent from the fovea, increase to a maximum concentration at about 15 to 20° eccentricity, and then taper off toward the far periphery. The blind spot – the region at which the optic nerve exits the eye – contains no photoreceptors of either type. B. Photomicrographs at the level of the inner segment, showing the relative sizes and concentrations of rods and cones at five retinal eccentricities. At zero degrees, in the fovea, all of the photoreceptors are cones. Outside the fovea, the large circles are cones and the small ones are rods. [A adapted from Goldstein (1999, Fig. 2.13, p. 37). B Adapted from Oyster (1999, Fig. 15.12, p. 665). From Curcio et al. (1990).]
Figure 6.3: Membrane specializations in the outer segments of rods and cones. The figure shows a high magnification electron micrograph of part of the outer segment of a monkey rod. The tightly packed horizontal striations are the disks. Inset: Cartoon showing the different arrangements of the specialized membranes in a rod vs. a cone outer segment. In the rod, the disks separate from the cell membrane. In the cone, the cell membrane folds back and forth, making a continuous comb-like structure. [Modified from Dowling (1987, Fig. 7.4, p. 194). Inset modified from Kandel et al. (1991, Fig. 28-2B, p. 403).]
that the “disk” membranes are actually continuous with the outer membrane of the cell (a cone is like a comb).

These highly organized structures hold the machinery for catching quanta and starting neural signals in the photoreceptors. Because of structural differences and other factors, the details of transduction differ slightly between rods and cones. Our descriptions will apply most strictly to rods, but the differences are small.

### 6.2 Phototransduction

#### 6.2.1 The rod photopigment: Rhodopsin

The substance that absorbs quanta of light in the photoreceptor outer segment is called a photopigment. In rods, the photopigment is called rhodopsin. Rhodopsin molecules sit tightly packed in the disks of the outer segments of the photoreceptors, as well as in the surrounding membrane that contains them. In mammalian retina, each rod contains about 1000 disks, and each disk contains about $10^5$ rhodopsin molecules, for a total of about $10^8$ rhodopsin molecules per rod outer segment.

The structure of the rhodopsin molecule is shown in Figure 6.4. It has two parts – the opsins molecule and the chromophore. The opsins is by far the larger part – for those with a background in chemistry, it is a protein composed of 348 amino acids. The molecular weight of the opsins molecule is about 39,000.

As shown in Figure 6.4A, the opsins molecule twists into a helical structure, and loops back and forth through the disk membrane a total of seven times, crossing between the outside and the inside of the disk. As shown in Figure 6.4C, the loops are arranged in a cylindrical conformation, so that each molecule of rhodopsin forms a more or less barrel-shaped structure within the membrane.

The chromophore – also called retinal – is by far the smaller part of the molecule. Retinal is the form of Vitamin A commonly found in carrots and other vegetables. Its molecular weight is 285. As shown in Figure 6.4B, the chromophore commonly exists in either of two forms, called 11-cis and all-trans retinal. These are terms used to describe the atomic connections, and hence the three-dimensional shape, of the chromophore. The two states of the chromophore are called isomers – the chemical composition of the chromophore remains unchanged, but its three-dimensional shape changes. In the 11-cis configuration, the carbon backbone of the molecule is bent at the 11th carbon atom; in the all-trans configuration, this bend is straightened. The chromophore is attached to the opsins within the membrane, in the middle of the seventh loop (as labeled in the rightmost loop in Figure 6.4A). It lies in wait in the 11-cis configuration in the middle of the barrel, primed for action when a quantum of light arrives.

Now, recall that a quantum is an indivisible packet of energy. It cannot be divided up among different photoreceptors, but can only enter a single photoreceptor and be absorbed by a single rhodopsin molecule. Moreover, absorption is an all-or-nothing event: either a quantum is absorbed or it is not. But it is also probabilistic: when the quantum arrives at the outer segment, there is a certain probability that it will be absorbed by a molecule of rhodopsin. That probability varies with the wavelength of the light (the energy in the quantum). For rhodopsin that probability is

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1In an eye that is fully adjusted to the dark, the retina has a rosy appearance – hence the name rhodopsin (= red vision substance) for the rod photopigment. When the eye is exposed to high levels of light, the retina changes color – it loses its color, or “bleaches”. In vision jargon, light is said to bleach photopigments.
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Figure 6.4: The rhodopsin molecule and the disk membrane. A. The structure of rod opsin. The opsin twists into a helical structure, and loops back and forth through the disk membrane seven times, with one end outside the disk and the other inside it. B. The chromophore in its 11-cis and all-trans configurations. C. The three-dimensional shape of a different opsin, this time in a cone membrane, showing the 11-cis chromophore inside the "barrel". [A and B modified from Kandel et al. (1991, Fig. 28-4, p. 405). C from Sharpe et al. (1999, Fig. 1.2, p. 6).]
maximal at about 500 nm, and it falls off sharply at both shorter and longer wavelengths. If the quantum is not absorbed, it is lost to visual processing.

6.2.2 The mechanism of transduction: Cis-trans isomerization

So far, so good. But how does light act on the rhodopsin molecule? When a quantum is absorbed into the structure of a rhodopsin molecule, the energy of the quantum is used to excite an electron, and the decay of the excited electron leads to a change in the conformation of the chromophore. In other words, the only thing light does in the entire visual process is to trigger a change in the shape of the chromophore. Moreover, the change of shape is always the same, regardless of the wavelength of light that has been absorbed.

After the chromophore absorbs the quantum, the rhodopsin molecule goes through a series of very rapid changes in three-dimensional shape, finally including separation of the chromophore from the opsin. With the help of enzymes located in the pigment epithelium, the chromophore eventually gets changed back into 11-cis retinal, and rejoins the opsin in the ultimate recycling process. On average, it takes several minutes for a rhodopsin molecule to reform.

6.3 Signal transmission

As we said earlier, the transduction process is the first of two tasks that each photoreceptor needs to accomplish. The second task is signal transmission: the photoreceptor must create and transmit a signal, passing the information that the quantum has been absorbed, all the way from the rhodopsin molecule to the synaptic terminal.

Photoreceptors are neurons, but it turns out that they are very atypical neurons. In particular, the more typical neurons, of which students have often heard, have axons and fire action potentials (spikes). To work through the properties of photoreceptors, it will be useful to be able to compare them to the properties of typical neurons. In this section, we first review the properties of typical neurons, and then proceed to the unusual properties of photoreceptors.

6.3.1 A typical neuron in a nutshell

Figure 6.5 shows the anatomy and physiology of a typical neuron. A portrait of a typical neuron, with its dendrites, cell body, and axon, is shown in Figure 6.5A. The direction of signal transmission is in through the dendrites, across the cell body and out the axon. The axon ends in a set of structures called the axon terminals, and it contacts the dendrites of the next set of neurons across intercellular spaces called synapses.

How does a typical neuron work? As shown in Figure 6.5B, in its resting state a typical neuron sets up a small electrical voltage across its outer membrane. It does this by maintaining different concentrations of ions with different electrical charges inside vs. outside the cell membrane. Part of the reason for the charge difference is that nerve cell membranes are semipermeable. That is, like the filter in a coffee maker, the openings (channels) in the membrane pass particles of a certain
6.3. SIGNAL TRANSMISSION

Figure 6.5: A typical neuron. A. Anatomy of a neuron: dendrites, cell body, axon, and synaptic terminals. B. A typical neuron maintains different concentrations of different ions (charged particles) on the inside vs. outside of its cell membrane. The inside contains relatively high concentrations of potassium (K+) and proteins (Pr−); the outside contains relatively high concentrations of sodium (Na+) and chloride (Cl−). These charge differences create a resting potential—an electrical voltage—of -70 mV between the inside and the outside of the cell. [A after Levine and Shefner (1991, Fig. 3-11, p. 36); B after Levine and Shefner (1991, Figs. 3-3 and 3-4, p. 38).]
size and electrical charge, and exclude others. So for each kind of channel in the membrane, some chemical ions can enter and leave whereas others cannot. We will be most concerned with the sodium permeable channels.

In addition to the semipermeable membrane, all neurons also have a sodium-potassium pump – an active transport mechanism that pumps sodium ions \((Na^+)\) out of the cell and potassium ions \((K^+)\) in. Because more sodium ions are pumped out than potassium ions are pumped in, the net charge is negative on the inside with respect to the outside. For most neurons, the resting membrane potential – the magnitude of the charge – is about -70 mV, with the minus sign indicating that the inside of the cell is negative with respect to the outside.

How do typical neurons process incoming signals? When a neuron receives a signal across a synapse from a neuron earlier in the causal chain, the incoming signal perturbs the charge across the membrane in the vicinity of the input synapse. These perturbations, called graded potentials, can be either depolarizing (excitatory) or hyperpolarizing (inhibitory). They spread passively along the dendrites and the cell body, with decreasing effect the greater the distance from the input site. Graded potentials from many input sites combine their positive and negative effects across the dendrites and cell body of the neuron.

At the base of the axon there is a specialized location called the axon hillock. When the neuron is depolarized, so that the voltage across the membrane of the cell is sufficiently decreased at the axon hillock, the properties of the axon membrane suddenly change. The mechanisms for this change are well understood, but beyond the scope of this chapter. Suffice it to say that the end product is an action potential or spike – a brief, all-or-none wave of depolarization that travels rapidly along the axon, propagating itself all the way to the synaptic terminal.

A reasonable analogy to a spike traveling down an axon is a flame travelling down a long match. The act of striking the match starts a flame at one end. Each segment of the match that burns provides the energy to ignite the next segment, so that the flame travels all the way down the match to its end. The analogy would be even better if the segments of the match regenerated themselves after the flame had passed, to be ready for the next traveling flame.

At the synaptic terminal, the depolarization brought about by the arrival of the spike produces an increase in the release of a neurotransmitter – a chemical substance specialized to transmit signals across the synapse. The neurotransmitter in turn creates graded potentials in the dendrites and cell bodies of postsynaptic neurons. Any given postsynaptic neuron can receive and combine inputs from thousands of presynaptic cells. The process is repeated countless times throughout the complex neural network of the brain.

In sum, whenever a neural signal must travel long distances, the signal is carried by the patterns of spikes in the axons of typical neurons. We will return to typical neurons in Chapter 8, when we explore the properties of ganglion cells – the neurons whose axons carry information from the eye to the brain.

### 6.3.2 Photoreceptors are not typical neurons

In the meantime, we return to photoreceptors. Vertebrate photoreceptors are extremely atypical neurons – in fact, as we will see, most of their properties differ from those of a typical neuron. Most importantly, photoreceptors do not have axons, and do not produce spikes; they transmit messages only with graded potentials.
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Figure 6.6: The dark current. A. The arrows show the current that flows in darkness, when the sodium permeable (cGMP gated) channels in the outer segment are open. B. In the light the channels close, and sodium ions are excluded from the outer segment. [Kandel, Schwartz, and Jessell (1995, Fig. 22-5, p. 415).]

6.3.3 Photocurrents

The unique physiological properties of photoreceptors are shown in Figure 6.6. The first notable difference between a photoreceptor and a typical neuron is that the resting potential of a photoreceptor is only about -40 mV rather than the -70mV seen in the typical neuron. Why is this so? As with typical neurons, there are sodium permeable channels in the outer membrane of the outer segment of the photoreceptor (shown in Figure 6.6B). In the dark, these channels are open, and they allow sodium to leak in. Meanwhile, the inner segment is permeable to potassium ions. This state of affairs produces an electrical current – a flow of ions – from the outer to the inner segment inside the cell, and back again on the outside of the cell (Figure 6.6A). This continuous depolarizing current, called the dark current, results in the membrane potential of about -40 mV compared to the -70 mV seen in a typical neuron.

In the dark, the constant depolarization produces a constant release of transmitter from the synaptic terminal. This property of photoreceptors is actually consistent with the corresponding property of typical neurons, in which depolarization (at the axon hillock) produces an increase in the release of transmitter (at the synaptic terminal, at the far end of the axon). In summary, in the dark, the resting membrane potential is about -40 mV, the photocurrent flows continuously, and the photoreceptor continuously releases transmitter from its synaptic terminal.

What happens when light is absorbed? It turns out that (for reasons discussed immediately below) sodium channels in the outer segment close, excluding sodium ions, and thus reducing the dark current. In consequence, the cell hyperpolarizes toward -70 mV; and the release of transmitter that occurred continuously in the dark is reduced by the action of light.
Figure 6.7: The chemical cascade. In the dark, cyclic GMP (cGMP) keeps the sodium permeable (cGMP-gated) channels open, so that sodium ions pass into the outer segment, and the dark current flows. When a quantum is absorbed, resulting in isomerization of a molecule of rhodopsin and a set of conformational changes in the opsin molecule, a protein called transducin becomes activated. Transducin in turn activates an enzyme called cGMP phosphodiesterase in the disk membrane, and cGMP phosphodiesterase hydrolyzes cGMP to 5’GMP. 5’GMP cannot hold the sodium permeable channels open, so they close. Sodium ions are excluded from the outer segment, and the dark current slows. The cell hyperpolarizes and the release of transmitter is reduced, signaling to the next cell that a quantum has been absorbed. [Kandel et al. (1995, Fig. 22-3, p. 412).]

We should pause for a minute to consider this mechanism of action. Intuitively, most of us would probably have guessed that increased light on the photoreceptor would yield an increase in transmitter release from the photoreceptor. But in fact the opposite is the case – increased light absorption in the photoreceptor yields a decreased signal from the photoreceptor. Is this a logical problem? Not really. The fact that the signal for an increase in light level is a decrease of transmitter (and vice versa) is logically perfectly OK. It is the change of transmitter release with the change of light level that matters, not the absolute direction of change.

6.3.4 The chemical cascade

Returning now to the outer segment: what happens after a photon is absorbed? In particular, how does the message that light is absorbed get from the rhodopsin molecule to the outer membrane of the cell, and bring about a closing of the sodium channels? To make a long and highly technical story short, the absorption of a quantum triggers a complex series of biochemical changes, called the chemical cascade, that results in the closing of sodium permeable channels in the outer membrane of the outer segment of the photoreceptor.

For those with some biochemical background, the details of the chemical cascade are shown
6.4. PHYSIOLOGICAL RESPONSES RECORDED FROM RODS

in Figure 6.7. From our perspective, the bottom line is that the chemical cascade produces an enormous amplification of the signal. Absorption of a single quantum in the outer segment of a rod results in the closing of several hundred sodium permeable channels, and each closed channel blocks the entry of as many as 10,000 sodium ions per second into the rod’s outer segment. As we will see, the change in sodium flux is so large that it causes a detectable change in the charge across the photoreceptor membrane, as well as in the output of the photoreceptor.

6.4 Physiological responses recorded from rods

In the 1970s, a remarkable new technique was developed: the suction electrode. A suction electrode preparation is shown in Figure 6.8. Using an excised retina, it is possible to draw the outer segment of a rod or a cone into a closely fitting hollow glass electrode. The membrane current that would ordinarily flow along the outside of the cell then flows inside the electrode, and changes in the current can be measured. By shining lights of various intensities and wavelengths on the outer segment of the photoreceptor within the electrode, one can record the changes in current flow in response to light, all the way down to the responses to absorption of an individual quantum. This work was extended to primate photoreceptors, including human photoreceptors, in the early 1980’s.
6.4.1 Low light levels: Responses to single quanta

Suppose that a rod outer segment has been drawn into a suction electrode, and the current flowing through the photoreceptor is being recorded. Now suppose that the experimenter produces a series of flashes of light so dim that on average only a single quantum of light will be absorbed by the photoreceptor. Because of the quantal nature of light, the actual number of quanta absorbed will vary from one flash to the next – sometimes zero, sometimes one, sometimes two, and occasionally more than two. If the response of the photoreceptor to a quantal absorption is consistent and repeatable, then the change in current on each flash should take one of only a few stereotyped forms, corresponding to the absorption of zero, or one, or two, or (occasionally) higher numbers of quanta.

The results of such an experiment are shown in Figure 6.9A. The upper tracing shows the current recorded as a function of time. The tick marks under the tracing show the times at which the flashes were nominally delivered – a little more than one flash every 10 seconds. Notice that the response of the cell is variable from one flash to the next, as predicted. Changes in the membrane current occur on some but not all trials; and when they occur, they are usually of a stereotyped form, either small or large in size. In sum, and remarkably, rod photoreceptors can indeed initiate a measurable signal from the absorption of a single quantum of light.

Similar experiments show that the photocurrent produced in a rod by a single quantal absorption is the same regardless of the wavelength of the quantum. Figure 6.9B shows responses to flashes of 550 and 659 nm lights that each produced one quantal absorption.

6.4.2 Higher light levels: A saturating non-linearity

What about the photoreceptors’ responses to multiple photons at higher light levels? Figure 6.10 shows photocurrents measured from dark adapted primate rods and cones, measured with suction electrodes. The traces in Figure 6.10A show current flow in response to lights of varying radiances. For both rods and cones, as light levels increase, the amplitude of the current decreases. The time course of the response also changes with the light level. For rods, as the quantal catch increases, latency decreases. The cone response is biphasic but shows the same trend. Eventually, at high enough light levels all of the sodium channels are closed, the current is reduced to zero, and no further changes in current amplitude can occur.

Figure 6.10B shows the peak change in the membrane current of rods and cones as a function of the number of quantal absorptions. In each case, the size of the response increases with the number of quanta absorbed, but the response eventually saturates. That is, photoreceptors show a saturating non-linearity.

The dynamic range of the photoreceptor is defined as the range of inputs over which the photoreceptor’s output changes. Dynamic ranges for both rods and cones are shown in Figure 6.11. Defined in terms of the peak change in current flow, the dynamic ranges of both the rod and the cone cover about a factor of 100, or two log units: from about 1 to about 100 quanta absorbed for rods, and from about 200 to 20,000 for cones. We will see in Chapter 10 that these descriptions

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3In cones as in rods, single quanta are caught by single photopigment molecules, and single quantal absorptions must initiate functional physiological signals. But a rod produces a much larger signal than a cone does in response to the absorption of a single quantum. Some estimates suggest that the difference in the magnitude of current produced is as much as 100/1. Thus, the magnitudes of the cone responses to individual quanta are too small to measure, even with suction electrodes.
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Figure 6.9: The responses of rods to very dim flashes of light. A. Responses to a series of very dim flashes spread over a 200 second period. The ordinate shows the change in the photoreceptor current in picoamps (pA; 1 picoamp = 10⁻¹² amperes). The responses of the photoreceptor come in three sizes, corresponding to the absorption of zero, one, or two quanta from each particular flash. The response to one isomerization is about one pA. B. The response to capture of single quanta, on an expanded time scale. The responses to quanta of different wavelengths, such as the 559 and 659 nm cases shown here, are identical. [A from Ricke and Baylor (1998, Fig. 4, p. 1030); B from Baylor, Nunn, and Schnapf (1987) via Wandell (1995, Fig. 4.17, p. 92).]
Figure 6.10: Saturation in rods and cones. A. Superimposed responses to flashes of light of increasing intensity, recorded from a monkey rod with a suction electrode. The average number of quanta absorbed per photoreceptor per flash increases by a factor of two from each trace to the next. In the top panel, for traces 1-7, the higher the intensity the higher the peak membrane current. For traces 7-9, the peak response shows little if any additional increase; these traces reveal physiological saturation in the rod. B. A similar trend can be seen in the responses of cones. [After Baylor (1987, Fig. 11, p. 42).]
Figure 6.11: Dynamic ranges of rods and cones. Peak responses of a rod (left) and a cone (right) to flashes of light of increasing intensity. The abscissa shows the number of photoisomerizations per rod or per cone. $Q_{1/2}$ is the light level required to produce a half-maximal response; this is about 55 quanta for rods and 495 quanta for cones. Both rods and cones show saturating nonlinearities. The range over which the cell’s response changes with changes in the light level is called the dynamic range of the cell. [Schnapf, personal communication.]

strictly apply only to the dark-adapted rod and the dark-adapted cone, and things become more complex when light adaptation processes are included.

### 6.5 Three causal stories

In this section we discuss three causal stories concerning how photoreceptors leave their marks on perception. The three stories illustrate the effects of our three major properties of photoreceptors. The first rests on the properties of transduction; the second on signal transmission; and the third on the saturating nonlinearity. The first two rest on the properties of rods; the third, on the properties of cones.

#### 6.5.1 Transduction and wavelength information

In Chapter 2, we introduced two major system properties of scotopic vision. First, scotopic spectral sensitivity varies with the wavelength of light, with a maximum at about 500 nm and a sharp falloff of sensitivity to either side. And second, the ability to preserve wavelength information is lost in scotopic vision – lights of all wavelengths look whitish, and they can be matched psychophysically to one another – made indiscriminable – simply by adjusting relative light levels. Some people
Figure 6.12: The dark adapted human spectral sensitivity curve and the absorption spectrum of rhodopsin. The psychophysical data have been corrected to compensate for differential absorption by the lens of light of short wavelengths. There is a close correspondence between the biochemical data and the behavioral data.[From Wandell (1995, ig. 4.9, p. 79).] See these two properties as intuitively contradictory – how can sensitivity vary with wavelength if wavelength information is lost? In fact, the transduction process precisely accounts for both.

Figure 6.12 shows a comparison of the scotopic matching curve of human subjects to the absorption spectrum of rhodopsin. In this figure, the psychophysical data have been corrected for the differential absorption of light of different wavelengths by the optics of the eye (Figure 4.8). Both curves have their maxima at just about 500 nm, and fall off virtually identically, both at shorter and at longer wavelengths. The fit between the two curves is remarkable, particularly given that one data set is psychophysical and the other biochemical. In short, the absorption spectrum of rhodopsin – the probability of a cis-trans isomerization as a function of wavelength – perfectly predicts the shape of the psychophysical spectral sensitivity curve.

At the same time, the transduction process discards wavelength information. When a rod absorbs a quantum, an isomerization occurs, but the effect is exactly the same regardless of the wavelength of the quantum. It follows that the rod has equivalence classes – sets of stimuli which, even though they are physically different from each other, are rendered identical by the transduction process. Any set of stimuli that lead to equal numbers of quanta caught are in an equivalence class for the rod. It is these quantal equivalences that lead to the suprathreshold discrimination failures seen in scotopic vision. So these two properties of transduction – the variation of the probability of quantal absorption with wavelength, and the loss of wavelength information at the instant of quantal absorption – are exactly sufficient to model the two system properties of scotopic vision –
the shape of the spectral sensitivity curve, and the existence of equivalence classes.

By what criteria do we evaluate the quality of a causal story? The more fully established the facts at both levels, the better the match of details between the two sets of facts, the fewer the free parameters, and the fewer the reasonable alternative explanations, the more compelling the causal story. In this case, both the rhodopsin spectrum and the psychophysical spectral sensitivity curve are known from direct measurements, and equivalence classes exactly like the ones originally discovered psychophysically can be demonstrated physiologically by recording rod signals to light of different wavelengths (Figure 6.9B). The story fits together perfectly, with no questionable assumptions and no free parameters. In short, this is one of the most compelling causal stories in vision science.

6.5.2 Signal transmission and absolute thresholds

In 1942, Hecht, Schlaer, and Pirenne carried out a psychophysical experiment on absolute detection thresholds. The stimulus was a test spot that subtended 10 minutes of visual angle. It was placed 20 degrees eccentric to the fovea, near the region of maximum density of rod photoreceptors (Figure 6.2). After the subject adjusted fully to the dark, detection thresholds were measured using the Yes/No method of constant stimuli.

Hecht and his colleagues then made careful calibrations of the light source, and combined these with estimates of the fractions of quanta that are lost within the eye vs. absorbed by the rod photoreceptors. Based on these calculations, Hecht et al. concluded that the subjects could detect the test spot when only a total of 5-10 quanta were absorbed by the whole set of photoreceptors covered by the test spot. Going back to the information retention proposition we discussed in Chapter 1, this system property implies that the absorption of 5-10 quanta by a set of neighboring photoreceptors is sufficient to initiate a signal that traverses every stage of processing in the visual system.

Moreover, comparisons to retinal anatomy showed that the 10 minute-of-arc test spot covered several hundred rod photoreceptors. Hecht et al. calculated that with only 5-10 quanta required for detection, the probability was very low that any one rod would have absorbed two or more quanta. Thus, they also concluded that the absorption of a single quantum must be sufficient to make a detectable signal in an individual rod. Half a century later, this prediction was confirmed by direct physiological measurements, as we know from Figure 6.9 above.

The causal story, then, is that the detection of lights that yield a quantum catch of only 5-10 quanta over a 10' field is mediated by the exquisite sensitivity of individual rod photoreceptors, plus of course the preservation of this signal throughout the visual projection system. To psychophysics chauvinist DT, the fun of the story is that the psychophysics came first, and yielded a strong

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4 More complicated arguments supporting the same conclusions were also made by comparing the slopes of the actual psychometric functions to slopes predicted on the basis of quantal fluctuations. These arguments are presented in elegant detail by Cornsweet (1970).

5 The claim of such exquisite sensitivity was not immediately accepted by all vision scientists. DT and a friend both went to graduate school in the early 1960's. DT in psychology and the friend in biochemistry. It turned out that we were both assigned to read the Hecht, Schlaer, and Pirenne paper (for the friend it was part of an examination question on cell biology). The friend argued that the energy in a quantum was not sufficient to make a signal that could traverse the whole rod photoreceptor, and therefore that Hecht et al's conclusion must be wrong. DT maintained, on the basis of a bumblebees-can-fly argument, that a single quantum must be sufficient; and that new mechanisms of photoreceptor function, consistent with the psychophysical data, must remain to be discovered. The photocurrent and the amplification provided by the chemical cascade eventually resolved the argument.
prediction about the sensitivity of the individual rods. Direct verification of the exquisite sensitivity of rods was a much sought after goal in retinal physiology for many years. Now that the prediction has been confirmed, this property of photoreceptors changes its status from deduced to observed.

6.5.3 Photoreceptor non-linearities and the detection of gratings

Finally, are there psychophysically detectable effects produced by the saturating nonlinearities seen in photoreceptors? In Chapter 5, we introduced the experiment on the neural CSF executed by He and MacLeod (1996). Remember that He and MacLeod analyzed the interferometric CSF into three regions: a veridically perceived region below about 60 cy/deg, attributed to the ordinary mechanisms of pattern vision; a high spatial frequency region above 60 cy/deg, attributed to alias patterns; and an intermediate region in the neighborhood of 60 cy/deg, attributed to a putative compressive non-linearity, with the explanation for the latter postponed to the present chapter. We now return to this topic.

The model proposed by He and MacLeod is shown in Figure 6.13. Figure 6.13A, at the bottom, shows a diagram of luminance across space for two stimuli: a uniform field and a sinusoidal grating with the same space-average luminance. Figure 6.13B shows a compressive nonlinearity, with the output growing more and more slowly as the input increases. The thin dashed lines projected upward from Figure 6.13A represent the minimum and maximum luminances of the grating, and the luminance of the uniform field. Note that on the Input axis of Figure 6.13A, the minimum and maximum differ equally from the average.

The thin dashed lines projected rightward from Figure 6.13B show the levels of output for the minimum, maximum and average luminances after passing through the compressive nonlinearity. Because of the nonlinearity, the signal strength for the maximum is closer to the average signal strength than is the signal strength for the minimum. Figure 6.13C shows the result: the space average signal from the grating (shown by the heavy dashed line) is now smaller than the signal from the uniform field (shown by the heavy solid line). This would not occur if the system was linear. In sum, He and MacLeod argue that a compressive nonlinearity in the photoreceptors can produce a spatially uniform change in the magnitude of the neural signal arising from the stimulus field. This change could underlie the detection of non-resolvable gratings in the range of spatial frequencies around 60 cy/deg. This argument provides us with a theoretical account of the heavy solid line that bridges the Nyquist frequency in Figure 5.14.

This causal story has a couple of minor glitches. First, the nonlinearity that has been seen physiologically in cones is saturating rather than compressive (Figure 5.1B). But either one will work in the He-MacLeod model, provided that the luminance values are well chosen. Second, it turns out that there are later stages of retinal processing at which the signals from individual cones remain separated from each other (as we will see in Chapter 7, and these stages could in principle provide alternative loci for the nonlinearity. But in the meantime, the He-MacLeod model, modified to use a saturating nonlinearity, provides a convincing account of interferometric detection thresholds in the vicinity of the Nyquist limit.

6.6 Linking propositions

As far as DT can see, there are no new linking propositions involved in these three causal stories. All three psychophysical experiments depend only on either threshold or matching judgments, and
Figure 6.13: The effect of a compressive nonlinearity. A (bottom). A sinusoidal grating, with symmetrical variations of intensity above and below the mean value. The input grating has the same average intensity as a uniform field. B. The grating and the uniform field both pass through a compressive non-linearity. C. The average output for the grating ($R'$) is less than that of the uniform field ($R$). When the uniform test field is replaced by the grating, a compressive nonlinearity can yield the perception of a still-uniform test field, with a change in intensity at the moment of transition. [From He and MacLeod (1996, Fig. 2, p. 1140).]
all three causal stories therefore rely only on Identity propositions. The first story, on spectral sensitivity and equivalence classes, also includes an Analogy between the psychophysical spectral sensitivity curve and the rhodopsin spectrum (Figure 6.12).

6.6.1 The Nothing Mucks it Up proviso

However, we now want to discuss another important linking proposition, having to do with boundary conditions. Philosophers call these the ceteris paribus conditions – other (unspecified) things being equal, the argument holds. DT (Teller, 1980) calls it the Nothing Mucks It Up proviso. It is the implicit assumption that nothing else in the visual system interferes with the control of the identified physiological processes over the psychophysical phenomenon under study.

For example, in the case of scotopic detection thresholds and equivalence classes, the Nothing Mucks It Up proviso would include the assumption that the rods are the only photoreceptors that mediate vision across the whole range of conditions tested. That is, no neural elements exist that are more sensitive than the rods at any wavelength. Moreover, no code transformations occur that interfere with the Analogy between the psychophysical and physiological spectral sensitivity curves. In fact, we know that the human retina contains cones as well as rods. And in fact, they do “muck up” the causal story at higher light levels, as we will see in Chapter 7.

6.7 Summary: Photoreceptors and system properties

In this chapter, we introduced the anatomical structure of rods and cones. We learned that rods contain the photopigment rhodopsin, which has a narrow absorption spectrum with a maximum at about 500 nm. We described the molecular structure of rhodopsin, and the cis-trans isomerization of the rhodopsin molecule. It is this small change in the shape of the molecule that accomplishes the transduction from light to physiological signals.

We then reviewed the properties of typical neurons, in order to stand them in contrast to the properties of photoreceptors. Technical stories were developed at the intuitive level, concerning the photocurrents that flow around photoreceptors in the dark, and the way they are changed by the action of light. A brief description was also provided for the chemical cascade, the set of molecular processes that carries the neural signal from the rod disk to the outer membrane, and provides the amplification required to produce a measurable signal in the photoreceptor.

We then had a look at actual physiological recordings from individual photoreceptors. In particular, we saw that the responses to individual quantal absorptions can indeed be recorded from photoreceptors. The changes in photoreceptor response with light levels and the saturating nonlinearities of photoreceptors were also shown in direct physiological recordings.

Finally, we presented three Causal Stories about how rod photoreceptors leave their marks on our visual perception. The first proposes that the transduction process in the rods accounts for the two system properties of scotopic vision developed in Chapter 2 – spectral sensitivity and equivalence classes. The second concerns signal transmission – how the capacity of a rod to signal the absorption of a single quantum determines the value of the absolute threshold of human vision. And the third concerns how a compressive or saturating non-linearity in the cones can provide a model of the detection of interference fringes in the vicinity of 60 cy/deg, covering the notch between veridical detection and the detection of alias patterns. All three causal stories seem highly
credible. We are on a roll, and the question becomes, how much longer can we go on before our causal stories begin to leave more room for doubt?

In Chapter 7, we turn to another of the major ways in which the cone photoreceptors leave their marks. In particular, we examine the consequences that the presence of three cone types has for the processing of wavelength information and for color vision.