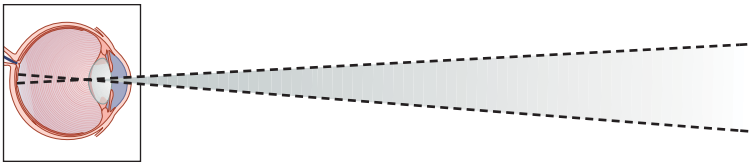

3

The Duplex Retina

The human visual system operates over a remarkably broad range of light levels (Table 3–1). At one extreme, we are able to detect a star on a dark, moonless night, while at the other, we can see a jet flying in the bright midday sky. This constitutes an adaptational range on the order of **10 log units** (Boynton, 1979).

How much of this adaptation is due to changes in the pupil's diameter? Suppose the pupil diameter increases from 3 to 9 mm. By using the formula for the area of a circle, we can calculate the increase in light reaching the retina. For a 3-mm-diameter pupil, we have

$$A = \pi r^2$$
$$A = \pi(1.5)^2$$
$$A = 2.25\pi$$

When the pupil is 9 mm in diameter, the area is

$$A = 20.25\pi$$

The ratio of the pupil area under dim illumination to that under bright illumination is

$$20.25\pi/2.25\pi = 9.0$$

This calculation shows that changes in pupillary area account for only a small portion of adaptation, approximately 1 log unit out of the 10-log-unit range. The remaining adaptation is due largely to the existence and properties of two classes of retinal photoreceptors, rods, and cones.

TABLE 3–1. **VISIBLE LIGHT INTENSITIES (APPROXIMATE VALUES)**

Stimulus	Luminance (candelas/m^2)		
Sun	10^{10}	↑	
	10^9	Tissue damage possible	
	10^8		
	10^7	↓	
100-W bulb filament	10^6	↑	
Sunlit paper	10^5		
	10^4	Photopic vision	
	10^3	↓	(Optimal acuity)
This page (normal lighting)	10^2		(Rod saturation)
	10	↑	
	1	Mesopic vision	
Moonlit paper	10^{-1}	↓	
	10^{-2}		
Starlit paper	10^{-3}	↑	
	10^{-4}		
	10^{-5}	Scotopic vision	
Threshold light	10^{-6}	↓	

BASIC DISTINCTIONS BETWEEN SCOTOPIC AND PHOTOPIC VISION

Scotopic vision occurs under dim (nighttime) lighting conditions. Exquisite sensitivity to very dim lights, poor visual acuity (20/200 vision), and the absence of color discrimination characterize scotopic vision, which is mediated by rods.

Photopic vision, which occurs under bright (daytime) lighting conditions, shows poor sensitivity to dim lights; however, it is characterized by both excellent visual acuity (20/20) and color discrimination. Cones mediate photopic vision.

The existence of two classes of photoreceptors, each operating under different lighting conditions, leads to what has been referred to as a **duplex retina.** Under twilight **(mesopic)** conditions, both rods and cones contribute to vision.[1]

MORPHOLOGICAL DISTINCTIONS BETWEEN RODS AND CONES

Figure 3–1 displays schematic drawings of rods and cones. Figure 3–2 is a scanning electron micrograph of these two classes of photoreceptors. Note that rods and cones share several features. Both have an outer segment consisting of disc-like

1. It is an oversimplification to think that rods and cones always operate independent of each other. Under certain conditions, interactions between rods and cones occur.

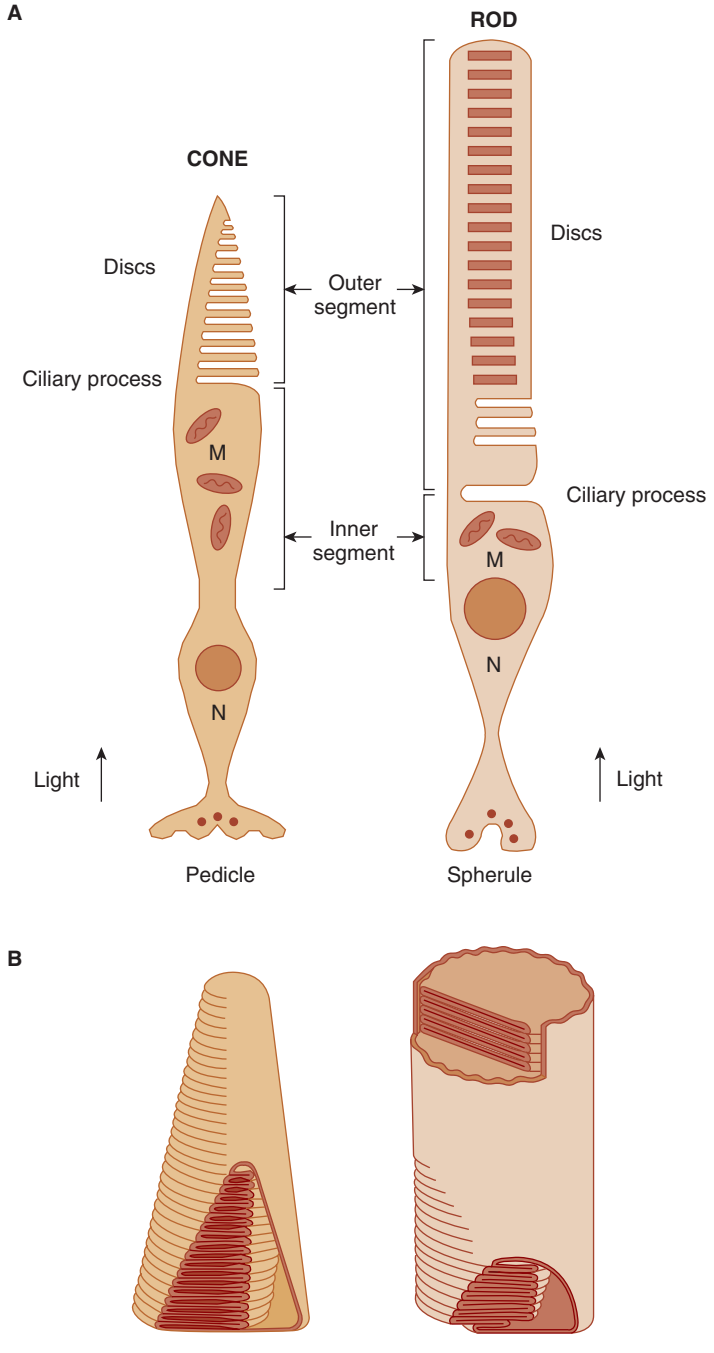

Figure 3–1. **A.** Schematic drawings of a cone (left) and a rod (right). The nucleus is designated by "N" and the mitochondria by "M." **B.** Schematic drawings of the outer segments of a cone and rod (Young, 1970).

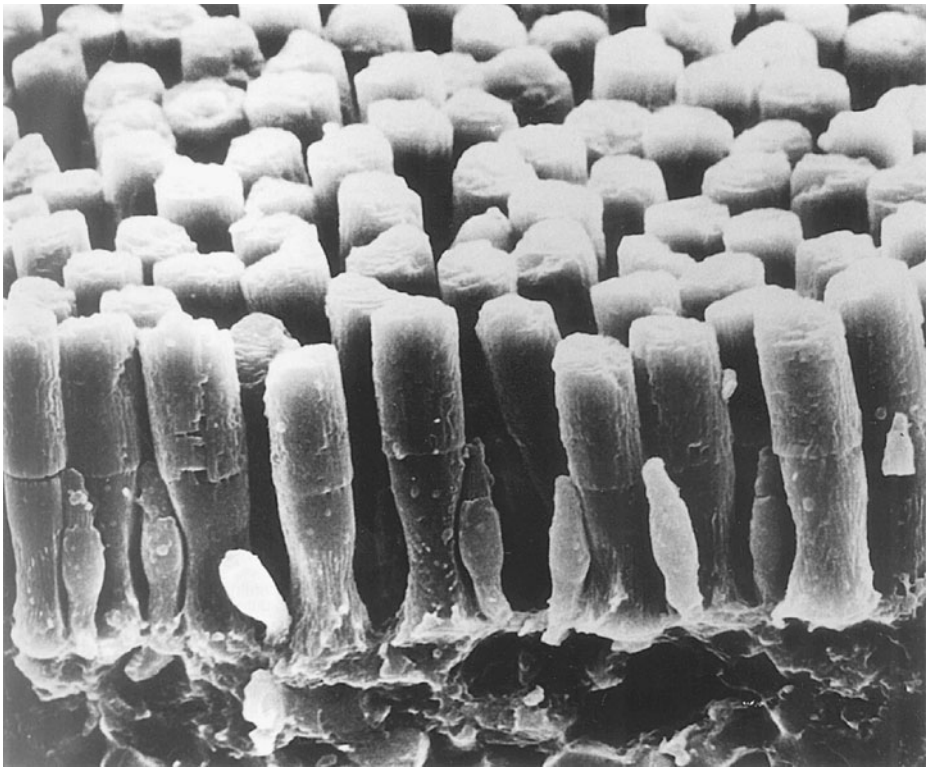

Figure 3–2. Scanning electron micrograph of photoreceptor outer segments in the tiger salamander. The larger outer segments are rods and the smaller are cones. In humans, the rod and cone outer segments are more similar in size. (*This scanning electron micrograph was made by Scott Mittman and Maria T. Maglio and is reprinted with their permission.*)

structures. Within these discs is photopigment that absorbs light quanta, initiating those processes that ultimately lead to vision.

The outer segment is connected to the inner segment by a thin ciliary connection. Within the inner segment are cellular organelles, excluding the cell nucleus. The innermost aspects of rods and cones synapse in the outer plexiform layer, with the rod and cone synaptic endings taking the forms of a **spherule and pedicle,** respectively.

Although there are similarities in the morphology of rods and cones, there are also important differences. Consider the outer segments. True to their respective names, rod outer segments are rod shaped, whereas cone outer segments are cone shaped. The outer segment discs represent infoldings of the cellular membrane. They are generated in the region of the ciliary connection and migrate outward (Young, 1970, 1971). In the rods, these discs break away and become free-floating as they migrate outward (appearing somewhat like a stack of poker chips). The cone discs, as indicated in Fig. 3–1, remain attached to the cone outer segment as they migrate outward—they do not become free-floating.

The discs are continuously produced and shed, and subsequently phagocytized by the retinal pigment epithelium, which lies outer to the rod and cone outer segments (Young, 1971). Rod discs are shed at the rate of approximately 10% per day. Rod discs tend to be shed during the day, and cone discs tend to be shed at night (Young, 1978).

Clinical Highlight

Phagocytosis of photoreceptor discs is essential to maintaining retinal health. In the absence of effective phagocytosis, metabolic waste products collect, thus damaging the rods and cones. This may be the case in **retinitis pigmentosa,** a rod–cone degenerative disease that can result in the progressive loss of vision, with scotopic vision typically affected first (Apple and Rabb, 1991). Although there is currently no effective treatment for retinitis pigmentosa, there is considerable ongoing research. Retinal tissue transplantation (Radtke et al., 2008), gene therapy, and retinal prostheses may hold promise.

Figure 3–3 shows how a retinal prosthesis (epiretinal design) could be used to provide vision in a patient whose photoreceptors have been destroyed in retinitis

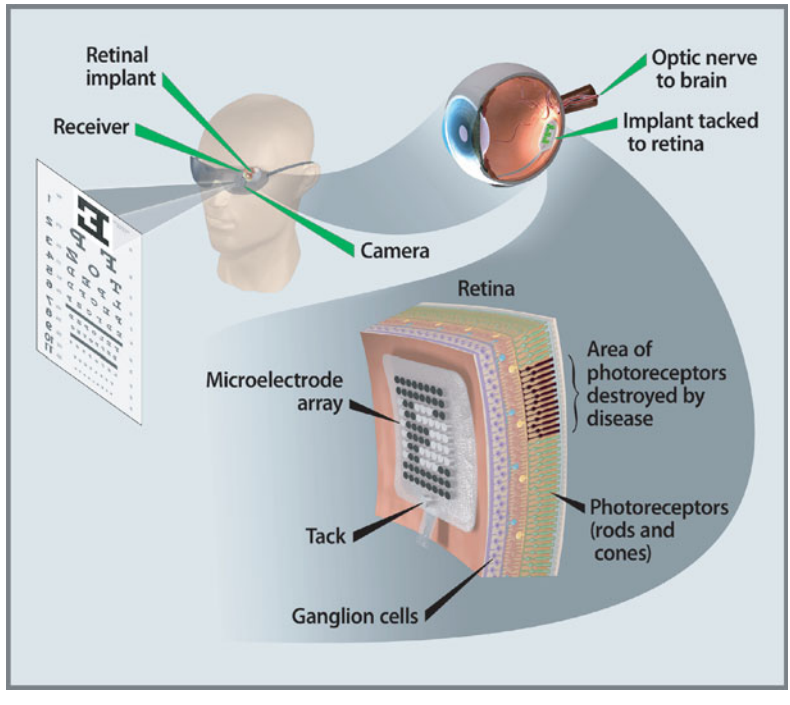

Figure 3–3. Epiretinal implant design. The microelectrode array sits on the innermost aspect of the retina and directly stimulates ganglion cells. In the alternative subretinal design (not shown), the implant is situated at the level of the damaged photoreceptors, thereby stimulating the outer aspects of ganglion and bipolar cells. (*Source: U.S. Department of Energy's Artificial Retina Project, Washington, DC*)

pigmentosa or some other outer retinal disease. Through a camera mounted in a spectacle frame, an image is transmitted to a microelectrode array tacked onto the retinal nerve fiber layer. The electrodes stimulate ganglion cells axons, mimicking signals produced when photoreceptors are activated (Lowenstein et al., 2004). Other devices utilize a subretinal design in which the microelectrode array is implanted within the retina, at the depth of the damaged photoreceptors. In this case, activation of the microelectrodes stimulates the outer aspects of retinal ganglion and bipolar cells. Early data suggests that retinal implants can restore rudimentary vision in blind patients (Humayun et al., 2003).

PHOTOPIGMENTS IN RODS AND CONES

The absorption of light quanta by the photosensitive pigment in the outer segment causes the photoreceptor to become hyperpolarized. This is the first step in a sequence of events that ultimately leads to vision.

Rod Photopigment

The photopigment **rhodopsin** is contained within the discs of the rod's outer segment.[2] A disc contains approximately 10,000 molecules of rhodopsin. Because each rod has approximately 1000 discs and an eye contains 120 million rods, there are approximately 10^{15} molecules of rhodopsin per eye (Boynton, 1979). Each molecule of rhodopsin is capable of absorbing one photon of light, and the absorption of one photon is sufficient to activate a rod. The large number of rhodopsin molecules provides the eye with a tremendous ability to capture light and contributes to our exquisite sensitivity under nighttime lighting conditions.

Figure 3–4 shows the absorption spectrum for rhodopsin and the manner in which this curve could theoretically be generated. A fixed quantity (e.g., 100 quanta) of monochromatic light is incident upon a container of rhodopsin. The ratio of transmitted light to incident light is calculated. This procedure is repeated for many wavelengths (e.g., 400 nm, 401 nm, 402 nm, and so forth) across the spectrum. The results are plotted as a curve that shows the proportion of light transmitted as a function of wavelength (Fig. 3–4B).

Light quanta that are incident on the rhodopsin, but not transmitted, have been absorbed. Consequently, the absorption curve is the reciprocal of the transmission curve (Fig. 3–4C). Note that wavelengths in the region of 507 nm are most likely to be absorbed by this photopigment.

A molecule of rhodopsin becomes bleached (i.e., transparent) when it absorbs light. The absorption of only one quantum of light is required to bleach a molecule of rhodopsin (Hecht et al., 1942). When a rhodopsin molecule is in the bleached

2. An older term for rhodopsin is visual purple.

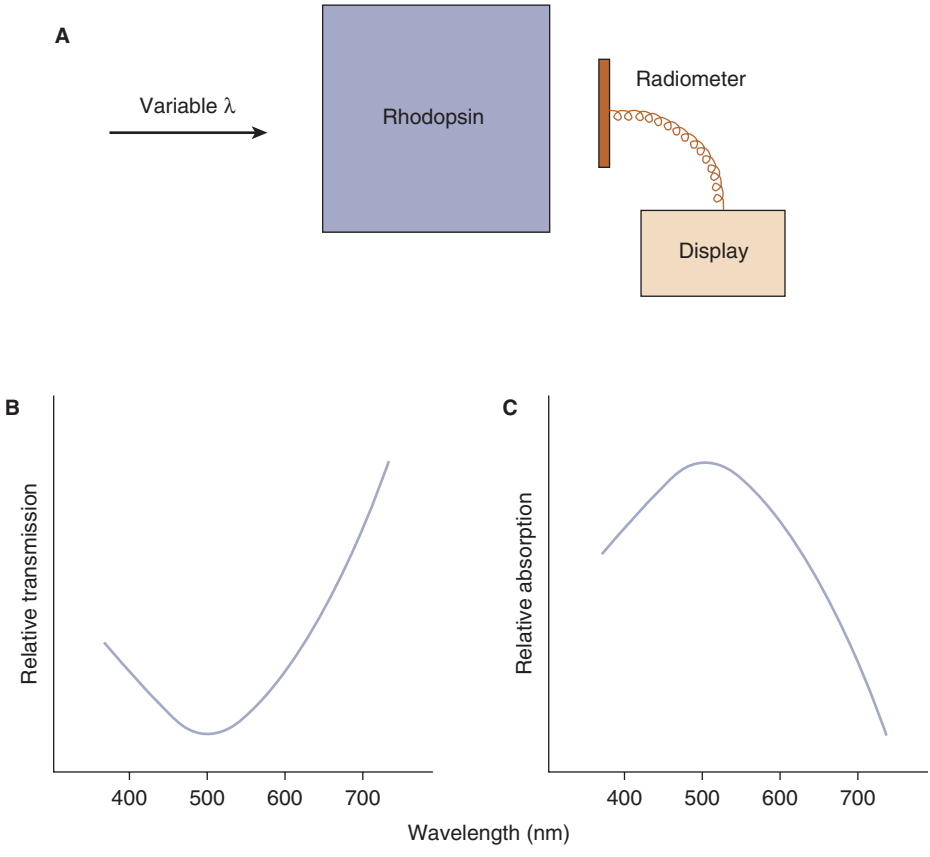

Figure 3–4. **A.** Monochromatic light incident upon a container of rhodopsin. The amount of transmitted light is determined as a function of wavelength. **B.** Transmission curve for rhodopsin. **C.** This absorption spectrum for rhodopsin is the reciprocal of the transmission curve.

state, it is not capable of capturing another quantum—it will transmit a quantum of light incident on it. A bleached molecule will spontaneously revert back to the unbleached state. The probability that a molecule of bleached rhodopsin will revert to the unbleached state within a 5-minute period is 0.50 (Rushton, 1965a). Therefore, if a quantity of rhodopsin is bleached, 50% of the rhodopsin will recover in 5 minutes. In commonly used terminology, the half-life for rhodopsin regeneration is 5 minutes.

Let us consider the rhodopsin absorption spectrum, which shows the probability of absorption (indicated as relative absorption on the ordinate) as a function of wavelength, in more detail (Fig. 3–4C). Quanta of 507 nm have the highest probability of absorption. This is due to quantum mechanics: the rhodopsin molecule and a quantum of 507 nm "fit together" well, thus increasing the probability of absorption.

Does this not mean that quanta of other wavelengths cannot be absorbed by rhodopsin? Not at all! Other wavelengths are absorbed, but with less probability. To illustrate this point, compare the effects of 1000 quanta of 507 nm and 1000 quanta of 680 nm that are incident on a container of rhodopsin. Assume that the rhodopsin absorption curve gives a probability of 0.20 that a quantum of 507 nm will be absorbed and a probability of 0.10 that a quantum of 680 nm will be absorbed. The 507 nm will bleach 200 rhodopsin molecules, whereas the 680 nm will bleach 100 molecules. (Multiply 1000 quanta by the proportion absorbed at each wavelength.)

If the intensity of the 680-nm light were doubled to 2000 quanta, it would produce the same number of absorptions as does the 1000 quanta of 507 nm. Consequently, 1000 quanta of 507 nm produce the same effect as does 2000 quanta of 680 nm.

Once a quantum of light is absorbed, all information regarding its wavelength is lost, a principle referred to as **univariance.** Whether a molecule of rhodopsin is bleached by a photon of 680 or 507 nm, the effect is the same. Analogous is a bathroom scale that is designed to make a loud noise when it registers 10 pounds. Although the sound tells us that the scale registers 10 pounds, it does not tell us what is on the scale—it could be 10 pounds of lead or 10 pounds of feathers.

Scotopic Spectral Sensitivity

The ability to detect stimuli under scotopic conditions is determined by the rhodopsin absorption curve. This can be demonstrated by measuring a person's scotopic spectral sensitivity (i.e., sensitivity as a function of wavelength). First, we dark-adapt an individual by asking him or her to sit in a dark room for 45 minutes, thereby maximizing the regeneration of the rhodopsin. Subsequently, the minimum amount of energy required for the person to detect stimuli of various wavelengths is determined. The minimum amount of energy required for detection of a stimulus is referred to as the **threshold** for that stimulus.

A curve showing threshold as a function of wavelength and another showing sensitivity as a function of wavelength, both obtained under scotopic conditions, are given in Fig. 3–5. The sensitivity curve is simply the reciprocal of the threshold function. A low threshold indicates high sensitivity. Note that this scotopic spectral sensitivity curve has essentially the same form as the rhodopsin absorption spectrum (Wald, 1945).[3] This similarity in form suggests that the human scotopic spectral sensitivity function is determined by the absorption characteristics of rhodopsin.

Absolute Sensitivity of Vision

One quantal absorption is sufficient to activate one rod. Ten such activated rods are sufficient to activate a ganglion cell, with the result that the stimulus is detected. However, a stimulus that emits only 10 quanta is not visible because many quanta

3. The scotopic spectral sensitivity curve may differ slightly from the rhodopsin absorption curve due to absorption by the ocular media.

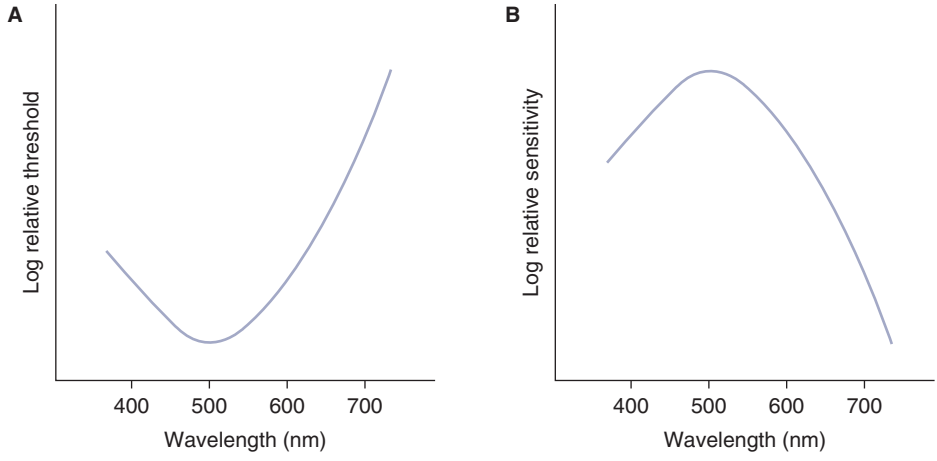

Figure 3–5. **A.** Scotopic threshold as a function of wavelength. **B.** Scotopic sensitivity as a function of wavelength.

are either reflected or absorbed by tissue inner to the photoreceptors (preretinal and retinal) or not absorbed by the rhodopsin. Less than 20% of the quanta incident on the retina are absorbed by rhodopsin (Hecht et al., 1942). For 10 quantal absorptions to result in detection, they must occur within certain space and time constraints. These constraints reflect the limits of spatial and temporal summation of the visual system, which are discussed in more detail later in this chapter.

Cone Photopigments

In a typical human eye, there are three fundamental cone photopigments, cyanolabe, chlorolabe, and erythrolabe, which show maximal absorption at approximately 426, 530, and 557 nm, respectively (Fig. 3–6A).[4] Each cone contains only one photopigment.

It is common to speak of three different classes of cones, each containing a different photopigment. The cyanolabe-containing cones are referred to as short wavelength-sensitive cones (SWS- or S-cones), the chlorolabe-containing cones as middle wavelength-sensitive cones (MWS- or M-cones), and the cones containing erythrolabe as long wavelength-sensitive cones (LWS- or L-cones).[5] The cone photopigments recover from bleaching at a faster rate than does rhodopsin. It takes

4. There are two variants of erythrolabe, with some individuals inheriting a variant that shows maximal absorption at 552 nm, and others manifesting a form that has maximal absorption at 557 nm (Merbs and Nathans, 1992).
5. The three classes of cones are also improperly (and all too frequently) referred to as blue, green, and red cones. Because the cones are not these colors and do not necessarily signal these colors, this terminology is discouraged.

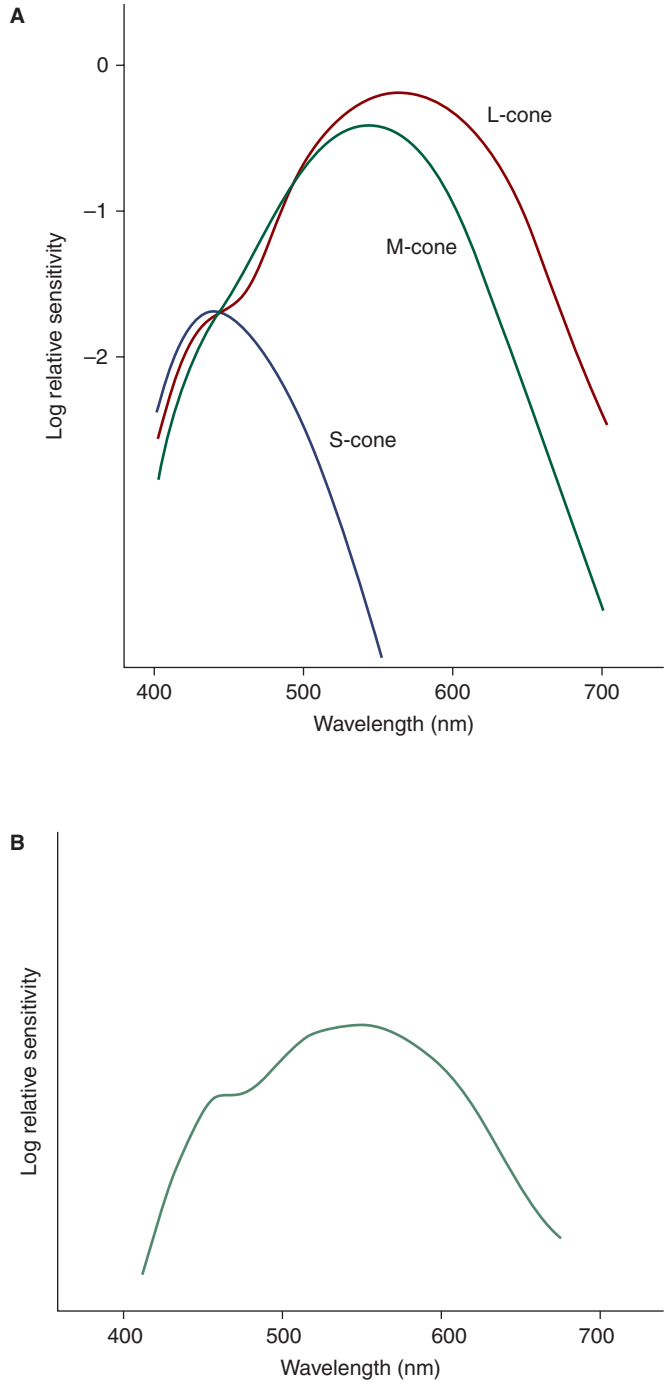

Figure 3–6. **A.** Approximations of the absorption spectra of cyanolabe (S-cone), chlorolabe (M-cone), and erythrolabe (L-cone) based on the data of Smith and Pokorny, (1975). (*From Boynton RM.* Human Color Vision. *New York: Holt, Rinehart, and Winston; 1979. Reprinted with permission of Dr. Boynton.*) **B.** An approximation of photopic sensitivity as a function of wavelength.

approximately 1.5 minutes for 50% of a cone photopigment to recover following bleaching (Rushton, 1963b).

Photopic Spectral Sensitivity

The photopic spectral sensitivity curve (or function) can be determined much the same way as the scotopic function, with a primary difference being that it is measured under brighter lighting conditions. Photopic sensitivity as a function of wavelength is given in Fig. 3–6B. Note that the photopic spectral sensitivity curve shows a single broad peak in the region of **555 nm** (Wald, 1945).

The photopic spectral sensitivity curve apparently represents the addition of M- and L-cone absorption spectra. Absorption of light quanta by either of these cones contributes to this function. It is thought that S-cones make little, if any, contribution to spectral sensitivity (Cavanagh et al., 1987).

Photochromatic Interval

Figure 3–7 shows scotopic and photopic spectral sensitivity functions plotted on the same graph. Thresholds were determined after the subject underwent dark adaptation, thereby allowing both rhodopsin and the cone photopigments to fully regenerate. The curves represent absolute sensitivity in that each is obtained under conditions that lead to the highest possible sensitivity. Two thresholds are present at each wavelength: a threshold for colorless scotopic vision and a threshold for chromatic photopic vision.

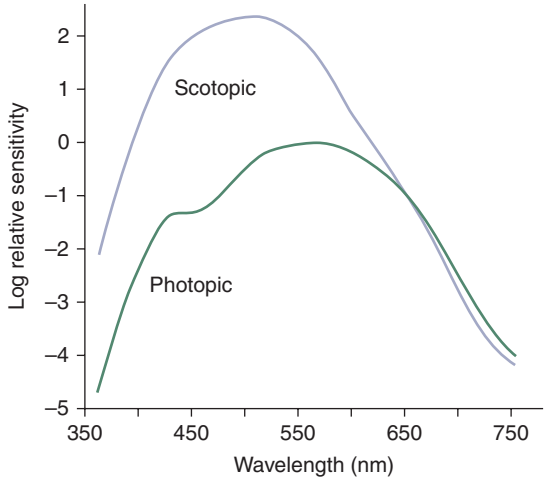

Figure 3–7. Scotopic and photopic spectral sensitivity functions. These functions represent the absolute sensitivities of the two systems. Note that for long wavelengths, the photochromatic interval is close to zero (Wald, 1945).

Consider a stimulus of 500 nm as its intensity is slowly increased. It is first detected by the scotopic system and seen as colorless (achromatic). As its intensity is further increased, it is eventually seen as colored (chromatic), thus indicating detection by the photopic system. The difference in sensitivity between scotopic and photopic systems, for a given wavelength, is referred to as the **photochromatic interval.**

Note that the scotopic system is more sensitive than the photopic system at all wavelengths, except in the long-wavelength (red) region of the spectrum. In this area, the photochromatic interval is approximately zero and rods and cones are almost equally sensitive. (Curiously, beyond 650 nm, the photopic system is slightly more sensitive than the scotopic system.)

Purkinje Shift

As lighting conditions change from scotopic to photopic, the wavelength to which we are most sensitive increases from 507 to 555 nm. This is the basis for the **Purkinje shift,** the relative increase in the brightness of longer wavelength stimuli as lighting conditions change from scotopic to photopic.

Consider an example. A dark-adapted individual views an array of monochromatic stimuli (400–650 nm) that each emits the same number of quanta. These stimuli are very dim, ensuring that they are detected only by the scotopic system. Because of the absorption spectrum of rhodopsin, the 507-nm stimulus is brightest. Next, the intensity of each stimulus is increased by the same amount so that they are all detected by the photopic system.[6] Which stimulus is now the brightest? Since the photopic spectral sensitivity peaks at 555 nm, the stimulus of this wavelength is brightest.

RETINAL DISTRIBUTION OF PHOTORECEPTORS

The human retina contains approximately 120 million rods and 6 million cones. As illustrated in Fig. 3–8, rods are most densely packed at approximately 20 degrees from the fovea, where they reach a peak density of approximately 150,000 rods/mm^2. There are no rods in the fovea, which results in the inability to see a small, dim object, such as a star, when it is foveally fixated under scotopic conditions. Looking slightly to the side of a faint star, causing its image to fall outside of the fovea onto the surrounding rods, increases its visibility. Whereas the number of retinal cones may remain stable as the eye ages, the number of rods decreases (Curcio et al., 2000).

Unlike rods, M- and L-cones are most concentrated in the foveal center, where their density ranges from approximately 115,000 to 225,000 cones/mm^2 (Putnam et al., 2005). Although the density of cones is substantially reduced outside the fovea,

6. By increasing equally the intensity of all the stimuli, they will each continue to emit an equal number of quanta.

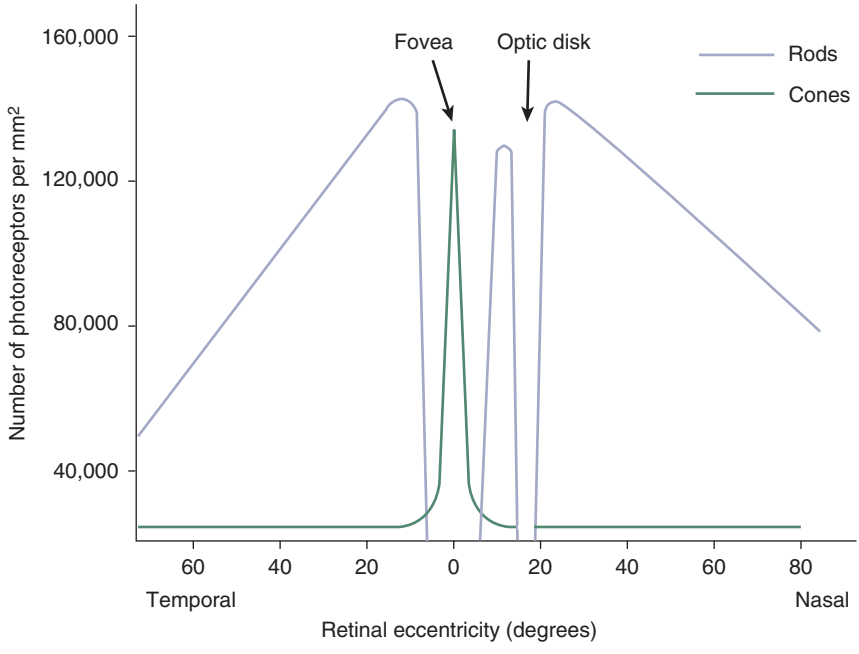

Figure 3–8. Retinal distribution of rods and M- and L-cones (Østerberg, 1935).

they are present throughout the retina. About only 5% of the total number of retinal cones are located in the fovea. A similar percentage of retinal ganglion cells are located in the fovea (Azzopardi and Cowey, 1996).

The ratio of L- to M-cones varies from person to person and has been found to range from 1:1 to 16:1 in individuals with normal trichromatic vision (Roorda and Williams, 1999; Hofer et al., 2005). This normal variation is dramatically illustrated in Fig. 3–9, which shows cone mosaics for two color normal males.

S-cones show a different retinal distribution than other cones (Calkins, 2001). Not only are they considerably less numerous than either M- or L-cones, constituting approximately 5% to 10% of the cone population, they are not found in the central 0.3 to 0.4 degrees of the human fovea (Curcio et al., 1991; Roorda et al. 2001). Peak density, approximately 2000 cells/mm^2 is at approximately 0.5 degrees from the foveal center.

DARK ADAPTATION

The Basic Curve

Most of us have had the experience of entering a dark movie theater on a sunny afternoon. Immediately on entering the theater, we are virtually blind. Yet, after

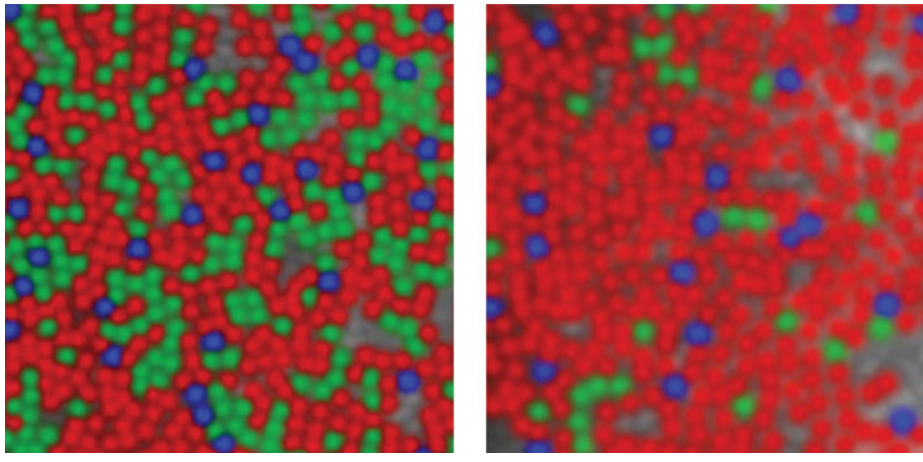

Figure 3–9. False-color images of cone mosaics at an eccentricity of 1 degree for two male subjects. The subject on the left shows a L:M cone ratio of 1.9:1 and that on the right a ratio of 16.5:1. Both have normal trichromatic vision. Note the relative scarcity of S-cones. (*Images courtesy of Dr. Heidi Hofer. Data from Hofer H, Carroll J, Neitz J, Neitz M, Williams DR. Organization of the human trichromatic cone mosaic.* J Neurosci. *2005;25:9669–9679.*)

several minutes, vision recovers to the point where we can walk down the aisle and find an empty seat. This gradual improvement in vision, after exposure to a bright-adapting light (in this case the sun), is referred to as **dark adaptation.**

Following exposure to an adapting light, rods and cones recover sensitivity at different rates. The dynamics of this recovery are made clear in dark adaptation experiments. Dark adaptation has proven useful in the clinical diagnosis of various retinal disorders.

Figure 3–10 is a typical dark adaptation curve. To generate this curve, an individual is exposed to a bright-adapting light that is designed to bleach most of his or her photopigment. The adapting light is then turned off, and detection threshold is determined as a function of time for a stimulus flashed against a totally dark background. In this case, the stimulus is large (e.g., 10 degrees) and centrally fixated, with a wavelength of 420 nm. During these experiments, it is important that the room remains perfectly dark and that the individual is not exposed to ambient light.

There are several important features of the dark adaptation curve in Fig. 3–10. Perhaps most obvious is that over a period of approximately 35 minutes, threshold improves by approximately 5 log units (i.e., after approximately 35 minutes in the dark, the person is 100,000 times more light sensitive). Another key feature is its division into two sections, the first showing a rapid reduction in threshold up to approximately 10 minutes, where the curve plateaus **(cone plateau).** This first section represents photopic thresholds. At approximately 12 minutes, there is an abrupt change in the slope of the curve, referred to as the **rod–cone break,** that is followed by a slow reduction in threshold out to approximately 35 minutes, where the curve

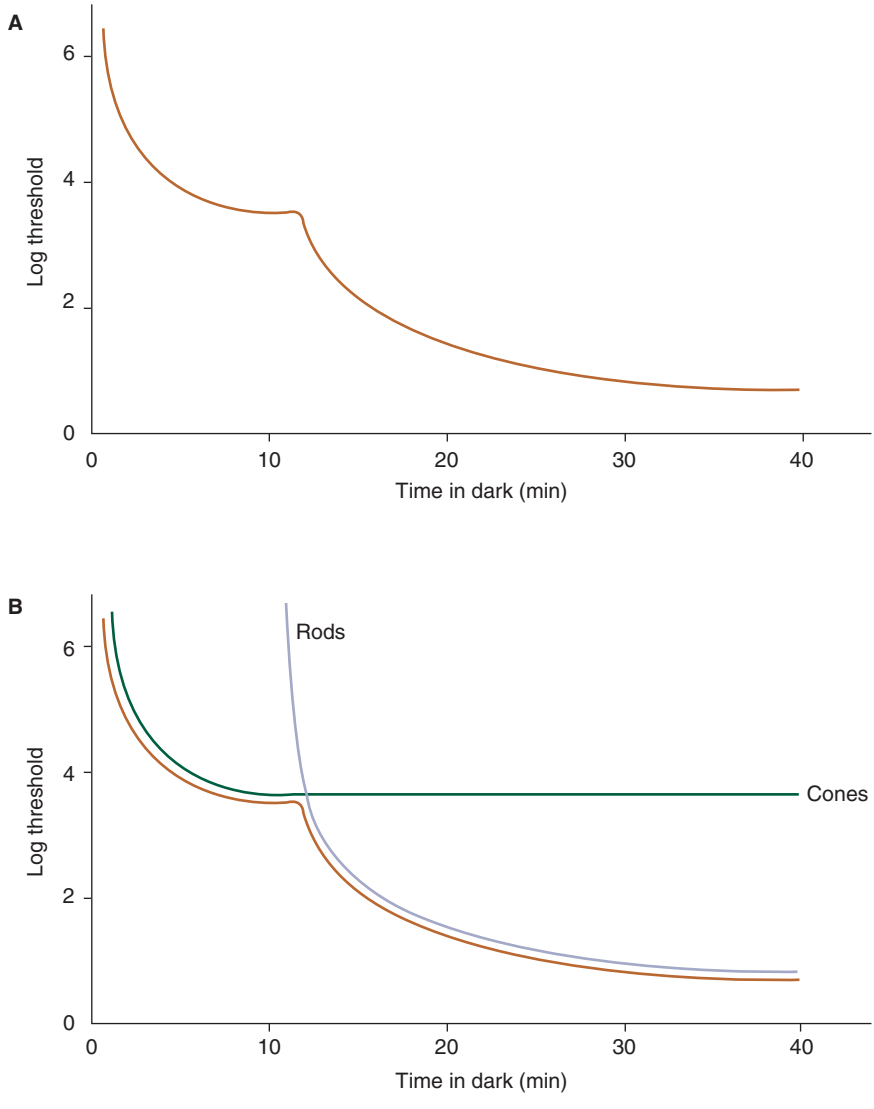

Figure 3–10. **A.** Typical dark adaptation curve. The stimulus is 420 nm and large. **B.** This diagram shows the thresholds for both cones and rods over the duration of dark adaptation. The dark adaptation curve represents the lowest threshold at any given point in time, whether determined by cones or rods. Note that early in dark adaptation, the threshold for rods is infinitely high. The photochromatic interval for 420 nm is the distance between the cone and rod plateaus.

again plateaus **(rod plateau)** (Hecht et al., 1937, 1942). This second portion of the curve represents scotopic thresholds. The rod–cone break occurs at that point in time when the rods become more sensitive than the cones. Prior to this point, the cones detect the stimulus. After this point, the rods detect it.

The photochromatic interval can be read directly off the dark adaptation curve; it is the difference between the cone plateau, which represents the minimum photopic threshold for a stimulus, and the rod plateau, which represents the minimum scotopic threshold for this same stimulus. For the 10-degree, centrally fixated, 420-nm stimulus used to generate the dark adaptation curve in Fig. 3–10, the photochromatic interval is approximately 3 log units.

The recovery in sensitivity that occurs during dark adaptation is related to the regeneration of photoreceptor photopigments. As discussed later, however, photopigment regeneration does not fully explain dark adaptation.

Effects of Stimulus Wavelength

The dark adaptation curve given in Fig. 3–10 was obtained with a stimulus of 420 nm. What form does the dark adaptation curve take if the stimulus is 650 nm (Fig. 3–11)? This curve is substantially different: it shows only a cone portion—the rod aspect is missing. This result should not be surprising after reconsidering Fig. 3–7, which shows that the photochromatic interval for a 650 nm is zero. Because the scotopic system is not more sensitive than the photopic system, there is not an obvious rod–cone break (Hecht et al., 1937). In contrast, the photochromatic

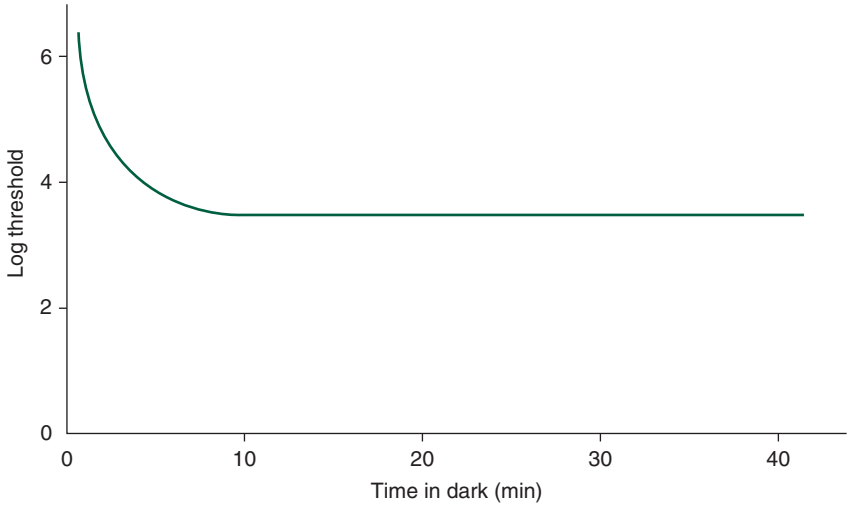

Figure 3–11. Dark adaptation curve obtained with a stimulus of 650 nm. Since rods are not more sensitive than cones to this stimulus, there is no rod–cone break.

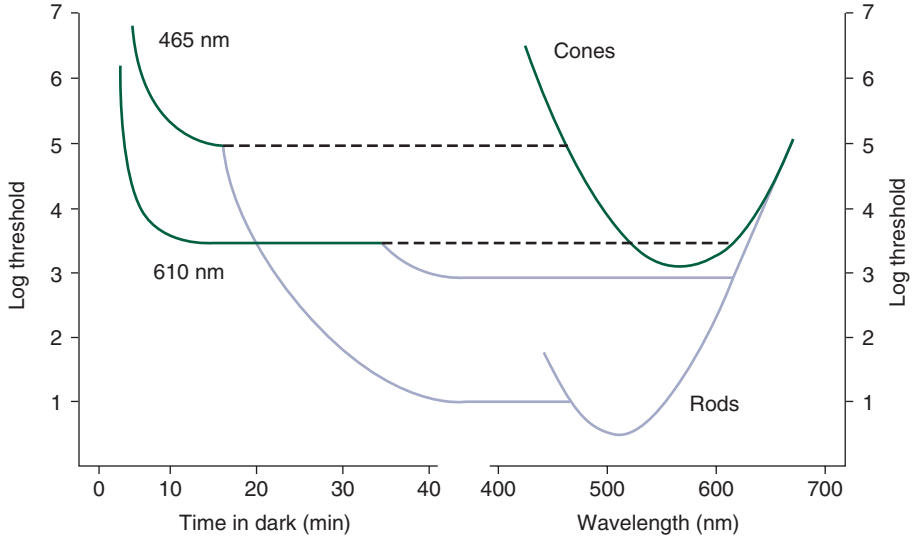

Figure 3–12. Dark adaptation curves for stimuli of 465 and 610 nm as they relate to photopic and scotopic threshold functions.

interval for the 420-nm stimulus is large; consequently, this stimulus produces a dark adaptation curve with a prominent rod–cone break (see Fig. 3–10).

The role of stimulus wavelength in determining the form of a dark adaptation curve is further examined in Fig. 3–12. On the left of this figure are dark adaptation curves for stimuli of 465 and 610 nm; on the right are threshold scotopic and photopic functions. These threshold functions are the reciprocal of the sensitivity curves given in Fig. 3–7.

Consider the 465-nm stimulus. After approximately 15 minutes of dark adaptation, the cone plateau is reached, representing the minimum threshold (or maximum sensitivity) for the photopic system. The dotted line, which extends from this cone plateau and intersects the photopic threshold function at 465 nm, shows that the cone plateau corresponds to a specific point on the photopic threshold function. The rod portion of the dark adaptation curve for 465 nm levels off at approximately 40 minutes, and has been extended to intersect the scotopic threshold function. This type of analysis is useful because it illustrates the photochromatic interval in terms of both dark adaptation curves and spectral threshold functions. For a dark adaptation curve, the photochromatic interval is the separation of the cone and rod plateaus. When viewing the spectral threshold functions, this same photochromatic interval is the difference between scotopic and photopic thresholds.

Why is the rod–cone break for the 465-nm stimulus more prominent and earlier than for the 610-nm stimulus? Part of the answer relates to the absorption properties of rhodopsin. As illustrated by Fig. 3–4C, the probability that a molecule of

rhodopsin will absorb a quantum of 465 nm is relatively high. Therefore, early during dark adaptation, after relatively little rhodopsin has regenerated, the sensitivity of the scotopic system surpasses that of the photopic system. The situation is different for 610 nm. It is considerably less probable that a molecule of rhodopsin will absorb a quantum of 610 nm. Only after a relatively large amount of rhodopsin has regenerated—late during dark adaptation—has the scotopic system recovered to the point where it is more sensitive than the photopic system.

Stimulus Size and Location

It was assumed in the preceding examples that the stimulus was centrally fixed and that its size was such that it covered both the fovea and a portion of the surrounding retina. For example, a 10-degree diameter stimulus would produce the results discussed so far.

Making the stimulus very small, say 0.5 degrees, and confining it to the fovea has a predictable effect: only a cone function is obtained (Fig. 3–13). The absence of a rod function reflects the absence of rods in the fovea.

Physiological Basis of Dark Adaptation

How can we account for the slow recovery in sensitivity that follows exposure to a bright adapting light? During dark adaptation, the regeneration of photopigment increases the probability of quantal absorptions, thereby increasing sensitivity. The **photochemical explanation** of dark adaptation holds that this photopigment

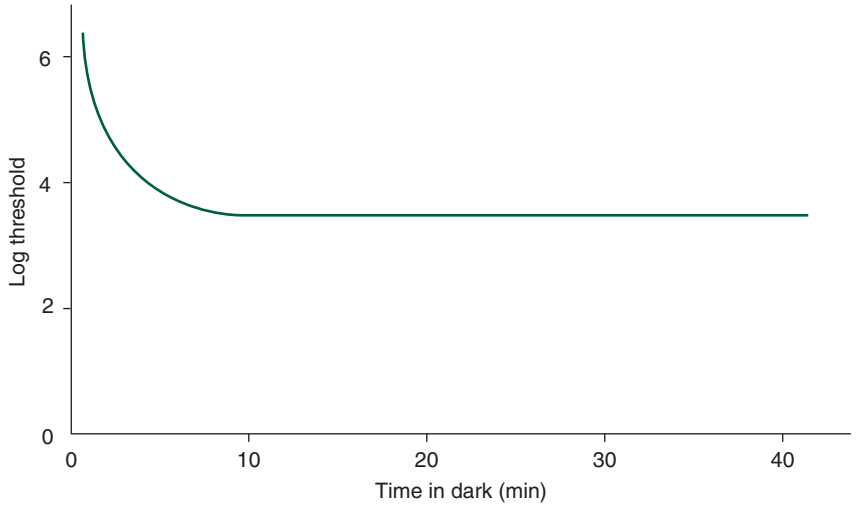

Figure 3–13. Dark adaptation curve for a small stimulus, confined to the fovea. Note the absence of a rod–cone break.

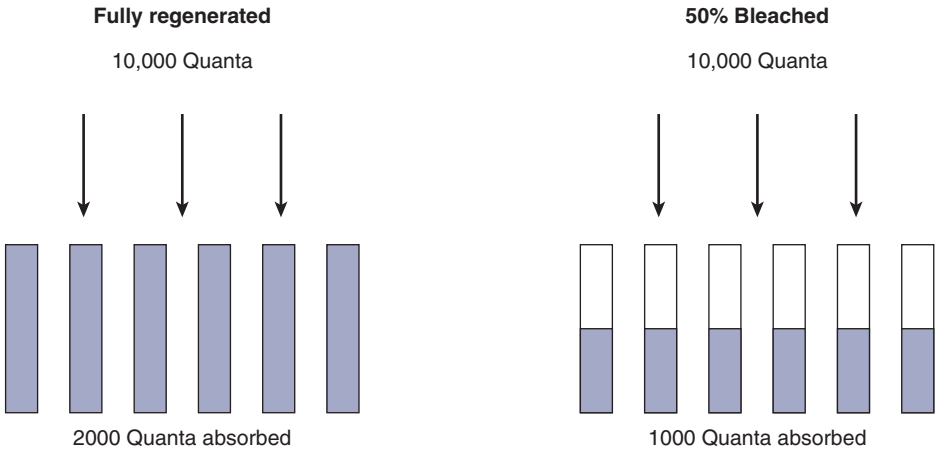

Figure 3–14. Fifty percent bleaching of rhodopsin decreases the probability of quantal absorption by a factor of one-half. Yet, the threshold is increased by a factor of 10^{10}.

regeneration fully explains the recovery of sensitivity that occurs during dark adaptation (Hecht, 1937).

The photochemical explanation is schematically illustrated in Fig. 3–14, which shows rods that have had one-half of their rhodopsin bleached. Compared with the unbleached state, there is a 0.50 probability that a quantum of light will be captured by the rhodopsin. Therefore, based purely on photopigment considerations, a 50% bleaching is predicted to double the threshold. If we were to conduct the experiment, however, we would find that this is not close to being correct—the threshold actually increases by a factor of approximately 10^{10}!

We can gain further understanding of dark adaptation by studying the visual system of a person with **rod monochromacy,** who is born with only rods.[7] The filled circles in Fig. 3–15 show the recovery of rhodopsin in such an individual, while the dashed line shows his dark adaptation curve.[8] A normally sighted subject's dark adaptation curve is given for comparison. It can be seen that bleaching 50% of the rhodopsin (right-hand ordinate scale) is expected to increase the threshold by 10 log units, rather than only doubling it, as predicted by the photochemical explanation.[9] Factors other than photopigment regeneration (both receptoral and postreceptoral) apparently contribute to the complex dynamics of dark adaptation (Schnapf and Baylor, 1987).

7. Rod monochromacy is discussed in more detail in Chapter 6.
8. These data were obtained with retinal densitometry. A weak measuring light is shined onto the retina, and the amount of the reflected light is measured (Rushton, 1965a). By comparing the amount of incident light to the amount of reflected light, the proportion of bleached pigment can be determined.
9. Also note that at the rod–cone break, approximately 90% of the rhodopsin has regenerated.

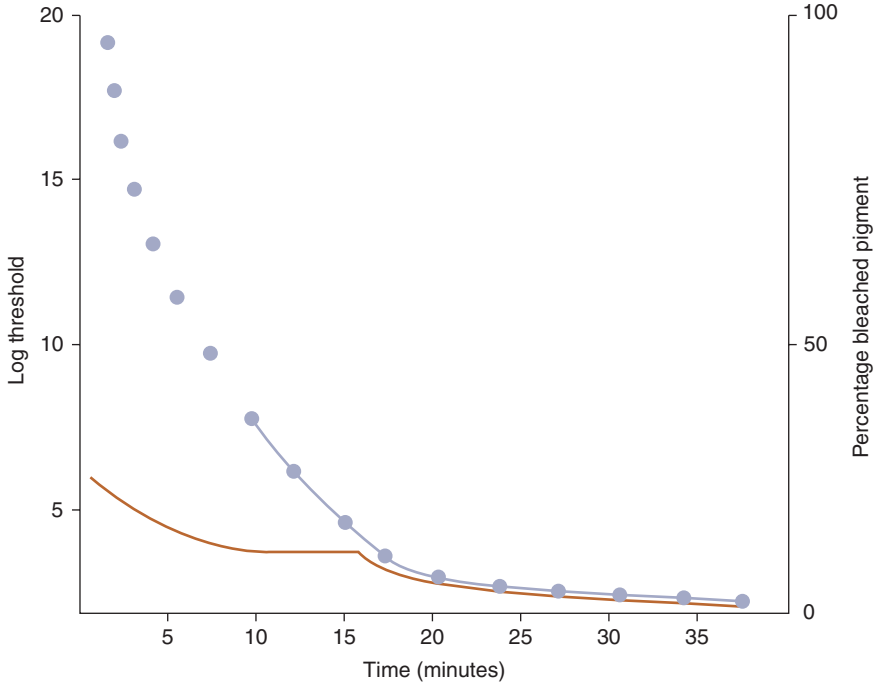

Figure 3–15. Solid circles show retinal densitometry results for a person with rod monochromacy, while the blue lines show thresholds for this subject. A dark adaptation curve for a normally sighted subject is given for comparison (Rushton, 1965a).

Clinical Highlight

Patients with rod monochromacy may have symptoms similar to those of patients with retinitis pigmentosa. A clue to the differential diagnosis lies in when the condition first presents. While retinitis pigmentosa may manifest as early as the first decade of life, rod monochromacy is fully developed at birth. The patient with rod monochromacy will have a history of visual acuity never developing beyond 20/200. Additionally, nystagmus, photosensitivity, poor or absent color vision, and night blindness are present early in life.

LIGHT ADAPTATION

When you step outside on a sunny day, the amount of light reflected into your eye and focused onto your retina increases by a factor of several thousand. In spite of this tremendous change in light levels, the appearance of objects remains the same (e.g., your classmate's hair appears black whether viewed indoors or outdoors on a sunny day). Within a very brief period—so fleeting that you are unaware of it—your visual system adapts to the changes in illumination levels, a process referred to as **light adaptation.**

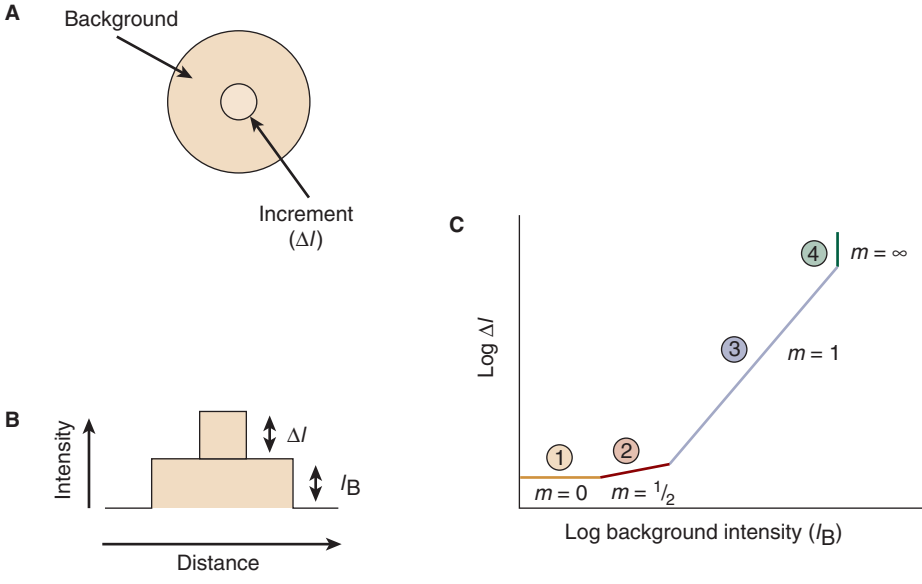

Figure 3–16. To determine a light adaptation curve, an increment, ΔI, is presented on a background that has an intensity of I_B. **A.** Face-on view of the stimulus used in such an experiment. **B.** Intensity profile of this stimulus. **C.** Simplified light adaptation curve. Only the scotopic portion is illustrated.

Light adaptation may be studied with an **increment threshold** procedure (Fig. 3–16). Threshold is determined for a flash of light—an increment—that is presented on a background of a given intensity.[10] After a threshold has been determined, the background intensity is increased and the threshold measurement is repeated. This procedure is performed for background light levels ranging from darkness to extreme brightness, resulting in a light adaptation curve that shows increment threshold (ΔI) as a function of the background adapting (I_B) intensity.

Scotopic Light Adaptation

Figure 3–16C shows the four sections of the scotopic light adaptation function. The explanations for the first two sections are rather technical, and we will only briefly touch on them. The first section, for which the slope (m) is zero, is that range of light levels where detection is limited by the neural noise inherent within the visual system. The background is practically black, and internal neural noise produces as much so-called dark light as does the background itself[11] (Barlow, 1956; Fechner, 1860).

10. An increment threshold (ΔI) is sometimes referred to as a **just noticeable difference** or a **difference limen.**
11. To experience this "dark light," close your eyes and note that you do not experience pure darkness, but see various visual phenomena.

The second section, having a slope of 1/2, reflects quantal fluctuations in the background (DeVries, 1943; Rose, 1948). The background is so dim that fluctuations inherent in the light source that produces it play a primary role in determining threshold. This is frequently expressed as the **DeVries–Rose law,** which predicts that ΔI is equal to $(I_B)^{1/2}$.

The third section, which covers a 4-log-unit range, has a slope of approximately 1, revealing that **Weber's law**[12] is followed (Aguilar and Stiles, 1954; Barlow, 1965; Walraven and Valeton, 1984). As the background brightness is increased, the increment intensity must be increased such that the ratio of the increment intensity (ΔI) to the background intensity (I_B) remains constant. This constant ratio, $\Delta I/I_B$, is referred to as Weber's fraction or Weber's constant.

The Weber fraction for scotopic vision is approximately 0.14 (Cornsweet, 1970). If the background intensity is 100 units, the increment must have an intensity of 14 units ($\Delta I = 14$) to be detected. If the background is increased to 1000 units, the increment intensity must increase to 140 units ($\Delta I = 140$) to maintain a Weber fraction of 0.14 and thus remain visible. Although the *relative* sensitivity of the visual system (0.14) does not change as the illumination increases, there is a reduction in the *absolute* sensitivity (the threshold goes from 14 to 140 units). This tradeoff between relative and absolute sensitivity is referred to as **sensitivity regulation.**[13]

As discussed in Chapter 7, the ratio of the increment intensity to the background intensity (i.e., relative sensitivity) is referred to as **contrast.** Saying that the visual system follows Weber's law is the same as saying that the threshold contrast remains constant as the illumination changes.

The final section of the scotopic portion of the light adaptation curve, section 4, has a slope of infinity. This indicates that the rods are saturated (Aguilar and Stiles, 1954). At this background illumination, it is not possible for the rods to signal the increment stimulus, no matter how bright it is, because they are overwhelmed by the brightness of the background. On first analysis, you might suppose that **rod saturation** occurs when all the rod photopigment has been bleached. In actuality, only about 10% of the rhodopsin is bleached at the point of rod saturation (Rushton, 1965a).

The bleaching of rhodopsin molecules results in the closure of sodium channels located in the rod outer segment. This reduces the flow of sodium into the outer segment, leading to rod hyperpolarization.[14] The magnitude of this hyperpolarization is dependent, up to a point, on the intensity of the stimulus. Because the number of sodium channels is finite, the amount of the rod hyperpolarization is limited

12. Weber's law is discussed in more detail in Chapter 11.
13. The physiological basis of sensitivity regulation, at the level of the photoreceptor, is beginning to be elucidated. It appears that calcium plays an important role in this process (Fain and Matthews, 1990).
14. Photoreceptor physiology is discussed in more detail in Chapter 12.

(Baylor et al., 1984). When approximately 10% of the rhodopsin molecules are bleached, all the sodium channels are effectively closed and further bleaching of rhodopsin produces no further hyperpolarization (i.e., the rod is saturated).

Photopic Light Adaptation

Weber's law is also followed under photopic conditions. The Weber fraction is approximately 0.015, indicating that the photopic system is more sensitive to contrast than the scotopic system (which has a Weber's fraction of approximately 0.14) (Stiles, 1953). Although the photopic system is more sensitive to contrast than the scotopic system, its absolute sensitivity is less.[15]

SPATIAL RESOLUTION AND SPATIAL SUMMATION

Basic Concepts

Do humans see better under photopic or scotopic conditions? Your initial response may be that vision is better under photopic conditions. Certainly, the ability to resolve details is substantially superior—photopic visual acuity is on the order of 20/20, whereas scotopic acuity is approximately 20/200, a 1-log-unit difference. Moreover, contrast sensitivity is higher under photopic conditions, with a Weber fraction for photopic vision of 0.015 (compared to 0.14 for scotopic vision).

But visual resolution and contrast sensitivity are not the whole story. The ability to *detect* a stimulus is much superior under scotopic conditions. For a 500-nm stimulus to be detected under photopic conditions, it must be approximately 3 log units (1000 times) more intense than is required for detection under scotopic conditions (see Fig. 3–7). While visual resolution and contrast sensitivity are superior under photopic conditions, absolute sensitivity is greater under scotopic conditions. The trade-off between visual resolution and visual sensitivity is, to a large extent, due to the manner in which the rods and cones are connected to the postreceptoral elements of the retina. Rods are connected in such a manner as to sum up information over space. This produces great sensitivity, but poor resolution. Cones, on the other hand, manifest connections that maximize visual resolution at the expense of sensitivity.

Figure 3–17 schematically illustrates rod and cone connections to a ganglion cell. (Rods and cones do not actually synapse on a ganglion cell, but this simple model

15. A dim stimulus that can be seen under scotopic conditions may not be visible under photopic conditions.

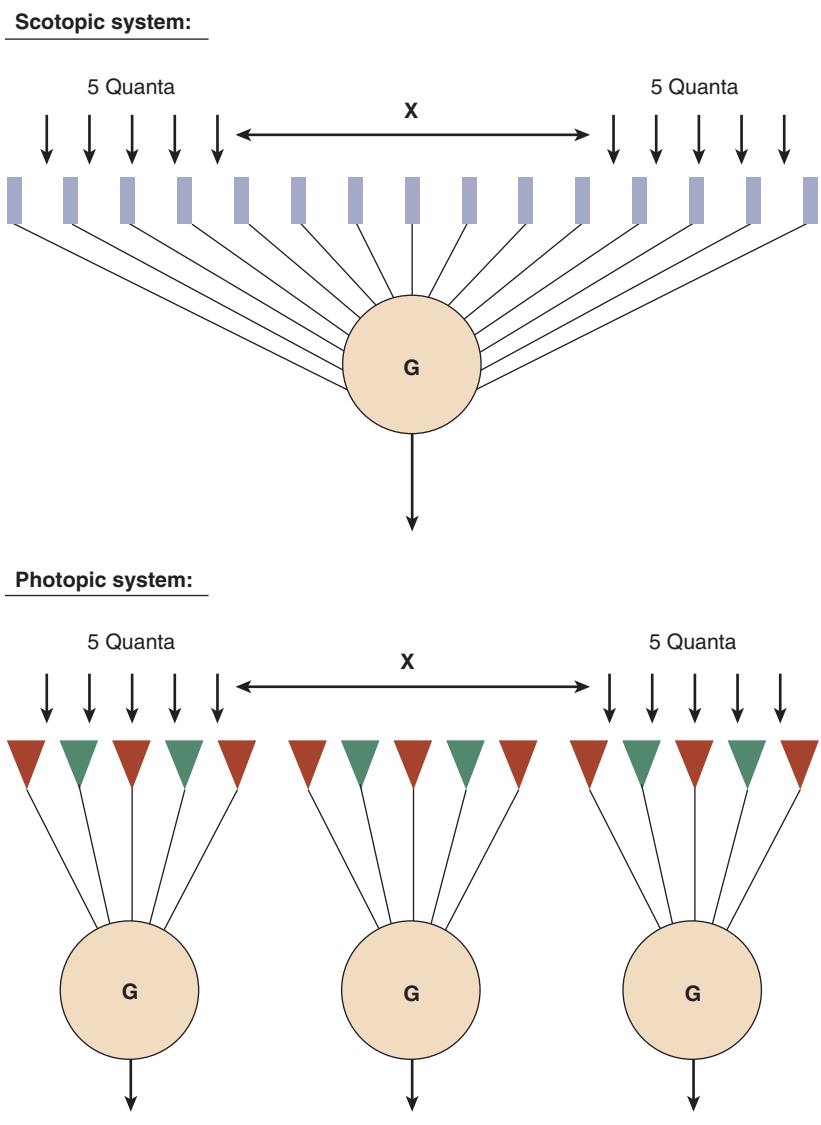

Figure 3–17. Schematic illustrations of scotopic and photopic retinal organization. The scotopic system manifests greater spatial summation than the photopic system. (A ganglion cell may sum information from hundreds of rods.) The explanation in the text, which is associated with these diagrams, is best applied to the peripheral retina.

is useful for instructional purposes.) A major distinction between the scotopic and photopic systems, as depicted by this diagram, is the number of photoreceptors that communicate with a single ganglion cell; many more rods communicate with a ganglion cell than is the case for cones. This illustrates that the scotopic system, to a greater extent than the photopic system, sums up information over space—it manifests greater **spatial summation.**

The following example shows how spatial summation contributes to high scotopic sensitivity. Suppose that for a ganglion cell to signal an event, a total of 10 quanta must be absorbed by the photoreceptors that feed into it, with each photoreceptor absorbing only 1 quantum. Furthermore, assume that these quanta are delivered in two flashes of light, separated by the distance *x*, and each flash contains 5 quanta. Finally, assume that all the incident quanta are absorbed.[16]

By observation of top schematic in Fig. 3–17, it is seen that this stimulus arrangement causes the scotopic system to reach threshold. The two spots of light produce a total of 10 quantal absorptions, and the ganglion cell sums this information to produce a signal that indicates the presence of a single light. It does not signal the presence of two lights; this information is lost because of spatial summation. The scotopic system has excellent sensitivity (a stimulus is seen), yet poor spatial resolution (only one stimulus is seen).

Now consider the situation for the photopic system with the same stimuli (bottom schematic in Fig. 3–17). In these circumstances, no stimulus is seen because the limited spatial summation of the photopic system prevents it from adding up the information contained in both spots of light. A ganglion cell requires 10 quantal absorptions to signal an event, but each of the ganglion cells in this example has input reflecting only 5 absorptions. Therefore, the ganglion cell threshold is not met.

What happens if we double the number of quanta contained in each spot of light. The two ganglion cells, in the photopic case, each reach threshold and signal the presence of a stimulus; consequently, two stimuli are seen. For the scotopic condition, the ganglion cell also reaches threshold; however, because all the rods converge on only one ganglion cell, the two spots of light are not resolved, and one stimulus is seen.

In summary, the scotopic system shows excellent spatial summation. This contributes to its high sensitivity, but results in poor spatial resolution. Consequently, we can see a dim star at night, yet have a scotopic acuity of only 20/200. In contrast, the photopic system shows less spatial summation, resulting in poor sensitivity, but excellent spatial resolution (20/20).

Ricco's Law

Spatial summation classically is demonstrated by the following experiment. An observer is presented with a very small spot of light, and the threshold number

16. As we have learned, less than 20% of the quanta incident on the retina are absorbed by rhodopsin (Hecht et al., 1942).

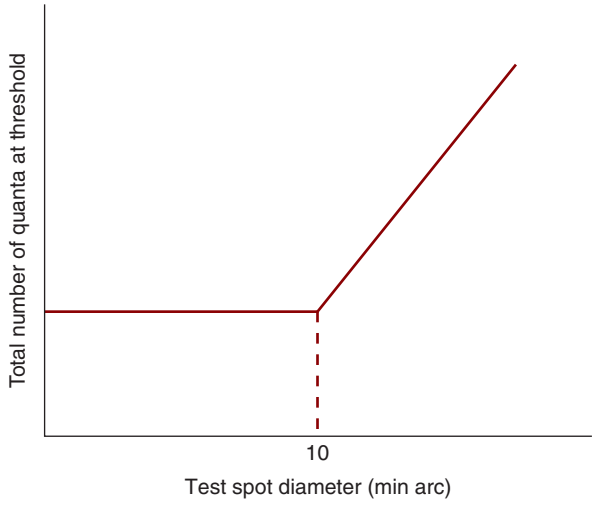

Figure 3–18. Classic expression of Ricco's law regarding spatial summation (scotopic conditions).

of quanta necessary to detect this light is determined. The experiment is then repeated with spots of increasing size, resulting in a function like that in Fig. 3–18, which shows the threshold number of quanta required for detection as a function of test spot diameter. These data are for the scotopic system. Note that for stimuli up to 10 minutes of arc in diameter, the total number of quanta necessary for detection is constant (Barlow, 1958). This means that the threshold number of quanta could be delivered in a 1-minute arc test spot or spread out over a larger area, up to 10-minutes arc, the so-called **critical diameter.** The scotopic system manifests total spatial summation for stimuli that fall within the critical diameter.

Total spatial summation is represented mathematically by Ricco's law:

$$IA = K$$

where

I = stimulus intensity (quanta/area)
A = stimulus area
K = constant

The difference in spatial summation between the scotopic and photopic systems manifests as a difference in the critical diameters for these two systems. It should not be surprising that the critical diameter of the photopic system is smaller than that for the scotopic system, reflecting the reduced spatial summation capability of the photopic system.

TEMPORAL RESOLUTION AND TEMPORAL SUMMATION

Scotopic and photopic vision also demonstrate significant differences in their temporal (time-related) properties. The scotopic system sums up information, over time, to a greater extent than the photopic system. It shows greater temporal summation. The photopic system, however, is better able to distinguish two flashes of light separated by a brief interval in time. It has superior temporal resolution.

Let us examine this in more detail. Figure 3–19A shows two subthreshold pulses of light presented under scotopic conditions. Each pulse of light, by itself, would not be seen. Assume that these pulses are separated by an interpulse interval of 120 milliseconds and that the temporal summation (integration) period of the scotopic system is 100 milliseconds. On the basis of this information, it is expected that no stimulus will be seen because the pulses do not both fall within the temporal summation period. If the two subthreshold pulses, however, are separated by 90 milliseconds, they will be summed up to reach threshold; the subject will report seeing a stimulus (see Fig. 3–19B). Since both pulses occur during the temporal summation period, the subject reports only one flash of light, not two.

If the flashes both fall within the temporal integration period, increasing the intensity of the pulses such that they are above threshold (suprathreshold) still does not allow the subject to perceive two flashes of light (see Fig. 3–19C). The scotopic system's high degree of temporal summation limits its ability to resolve distinct temporal events. Only when these two suprathreshold pulses are separated by greater than 100 milliseconds, as indicated in Fig. 3–19D, are two flashes seen.

The photopic system, as indicated in Fig. 3–20A, shows a shorter period of temporal summation. As a consequence, the two subthreshold stimuli are not summed up to reach threshold. They need to be presented closer in time, as indicated in Fig. 3–20B, to produce a percept of a single flash of light.

Although the photopic system demonstrates poor temporal summation, it does manifest superior temporal resolution. As indicated in Fig. 3–20C, two suprathreshold pulses, separated by only 50 milliseconds, are distinguishable as two flashes. The scotopic system, with its high degree of temporal summation, would not be able to resolve these stimuli.

The high degree of temporal summation of the scotopic system is consistent with its greater absolute sensitivity. It sums information over both space (spatial summation) and time (temporal summation) to obtain excellent sensitivity. In contrast, the photopic system shows limited spatial and temporal summation. This, however, provides it with excellent spatial and temporal resolution. It is evident that there is a trade-off between summation and resolution.

Bloch's Law

Bloch's law, the temporal equivalent of Ricco's law, is illustrated in Fig. 3–21. This graph shows that within the so-called **critical duration,** or **critical period,** there is

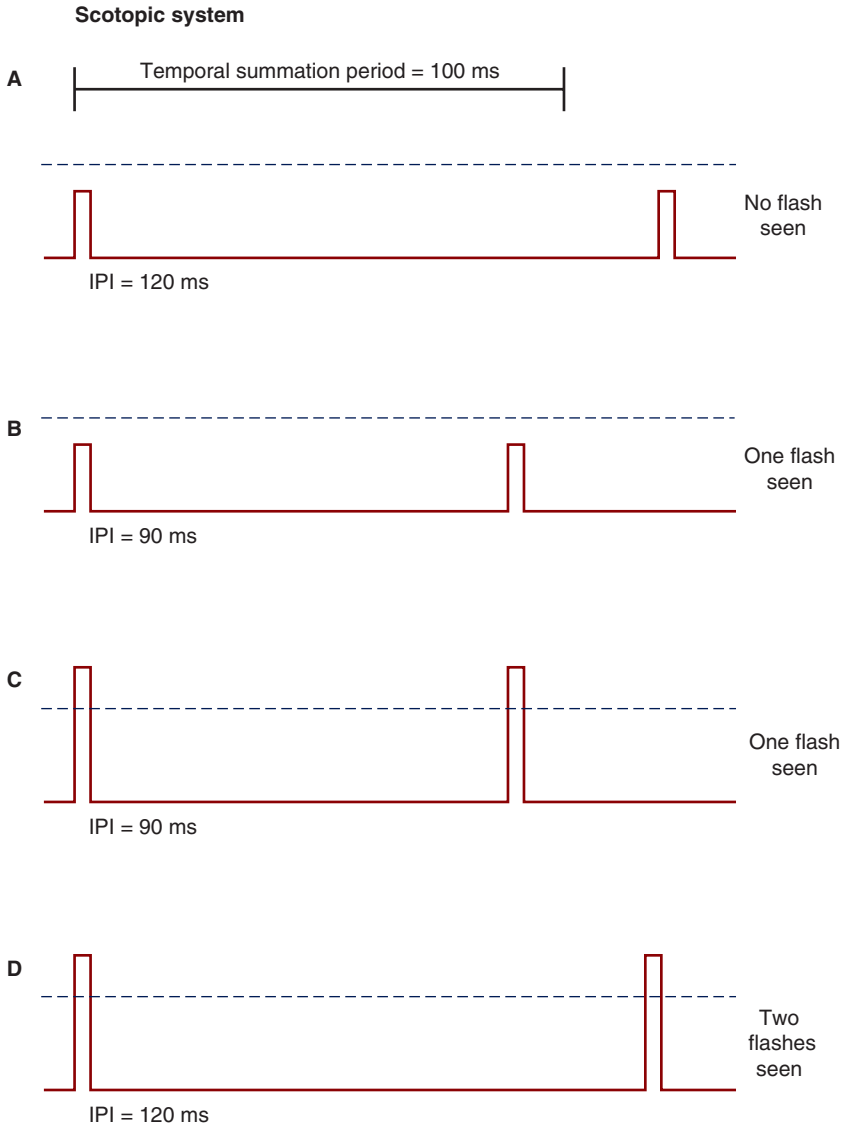

Figure 3–19. Temporal properties of the scotopic system assuming a temporal summation period of 100 milliseconds. The dashed line represents threshold for a single pulse. **A.** Two subthreshold pulses, separated by an interpulse interval (IPI) of 120 milliseconds, do not sum to reach threshold. A stimulus is not perceived. **B.** Two subthreshold pulses, presented within the temporal summation period, result in the perception of a single flash. **C.** Two suprathreshold pulses, presented within the temporal summation period, result in the perception of only a single flash. **D.** Two suprathreshold pulses, presented with an IPI of 120 milliseconds, are perceived as two flashes.

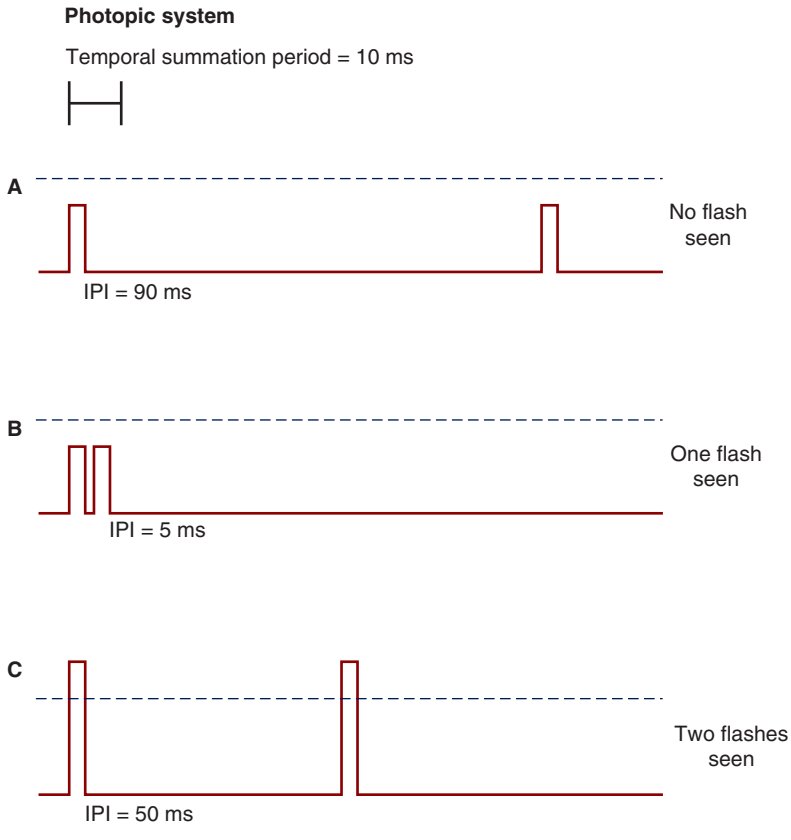

Figure 3–20. Temporal properties of the photopic system assuming a temporal summation period of 10 milliseconds. **A.** Two subthreshold pulses, presented with an interpulse interval of 90 milliseconds, do not sum to reach threshold. **B.** Two subthreshold pulses, presented within the summation period, are summed to reach threshold. **C.** Two suprathreshold pulses, separated by 50 milliseconds, are perceived as two flashes.

total temporal summation. As long as the threshold number of quanta are delivered within this critical duration, it does not matter how they are delivered. They could be presented in one or more flashes. Multiple flashes presented within this critical duration are not resolved, and only one flash is seen.

Bloch's law can be expressed mathematically as follows:

$$It = K$$

where

I = stimulus intensity (quanta/time)
t = stimulus duration
K = constant

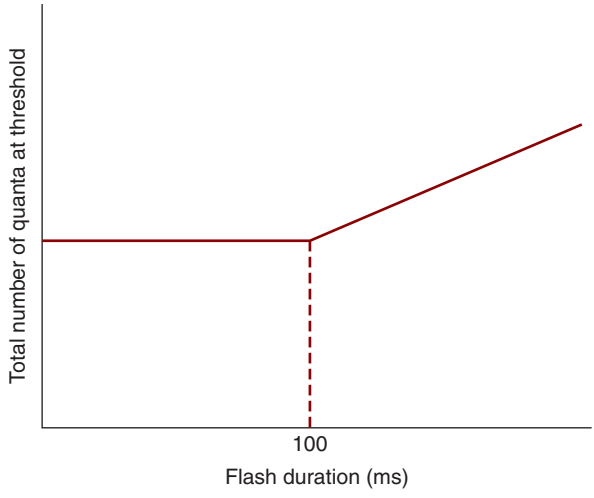

Figure 3–21. Classic expression of Bloch's law regarding temporal summation (scotopic conditions).

Predictably, the scotopic and photopic systems manifest different critical durations. Scotopic vision, with its greater degree of temporal summation, shows a critical duration of approximately 100 milliseconds, whereas photopic vision manifests a critical duration on the order of 10 to 50 milliseconds (Sperling and Jolliffe, 1965; Krauskopf and Mollon, 1971; Swanson et al., 1987).

STILES–CRAWFORD EFFECT OF THE FIRST KIND

To be maximally effective at bleaching photopigment, a light ray must strike a cone perpendicular to its surface. In comparison, the angle at which a light ray strikes a rod is much less critical.

If an observer is asked to view a point source of light through a pinhole that is centered in front of the pupil, the light rays strike the photoreceptors perpendicular to their surface (Fig. 3–22A). If, however, the pinhole is decentered, as in the bottom diagram of 3-22A, the light rays strike the same photoreceptors at an oblique angle. Under scotopic conditions, the subject notes relatively little difference in brightness, demonstrating that the angle at which light rays are incident on rods is relatively insignificant (Van Loo and Enoch, 1975).

The same experiment repeated under photopic conditions produces a different result. Light rays that strike cones perpendicular to their surface (pinhole centered) are perceived as brighter than those that do not strike perpendicular to the surface (pinhole decentered) (Fig. 3–22B). This effect, which is strongly manifested by

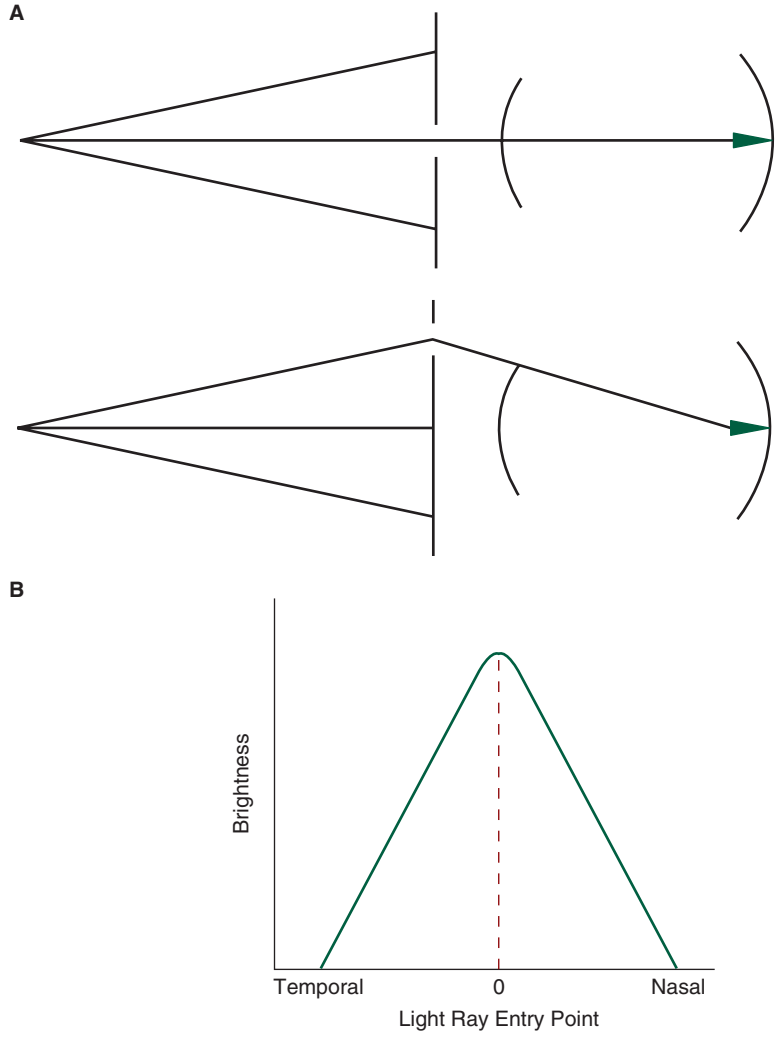

Figure 3–22. Stiles–Crawford effect of the first kind. **A.** A centered pinhole (top) causes the light ray to strike the foveal cone perpendicular to its surface, whereas a decentered pinhole (bottom) causes the ray to strike the cone at an oblique angle. **B.** Under photopic conditions, the centered pinhole produces a brighter image than the decentered pinhole.

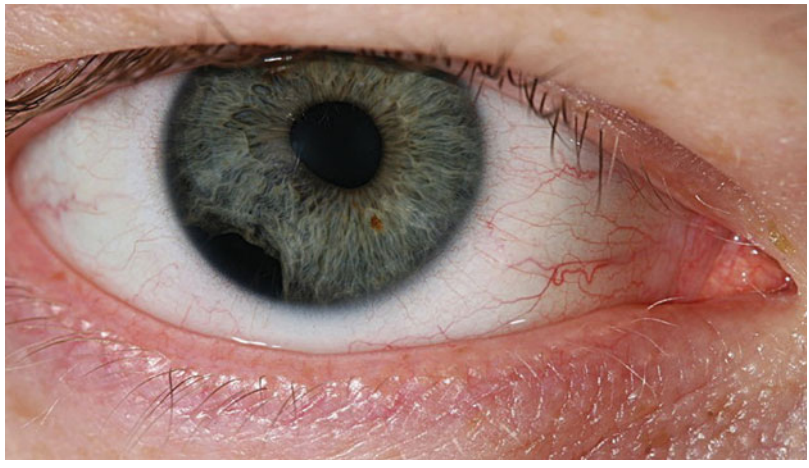

Figure 3–23. Decentered pupil secondary to an eye injury. The Stiles–Crawford effect of the first kind is expected to be abnormal in such an injury. (*Petr Novák, Wikipedia; Wikimedia Commons, Creative Commons Attribution ShareAlike 2.5. http://creativecommons.org/licenses/by/2.5/.*)

cones, is referred to as the Stiles–Crawford effect of the first kind (Stiles, 1939; Applegate and Lakshminarayanan, 1993).[17]

The effect is probably due to waveguide properties of the cones (Enoch and Fry, 1958). The physical dimension of a quantum of light is such that it approaches the size of a cone, making critical the angle of entry of a ray of light into the funnel-shaped cone. Any deviation from an orthogonal entry reduces the effectiveness of light rays at bleaching photopigment and, consequently, reduces the perceived brightness of these rays.

Under normal circumstances, cones point toward the center of the pupil, maximizing their effectiveness. What are the consequences of a chronically decentered pupil, as illustrated in Fig. 3–23?[18] Do the cones point toward the normal pupil position, or do they point toward the location of the decentered pupil? The Stiles–Crawford effect manifested by these eyes is displaced,[19] suggesting that the cones point toward the location of the decentered pupil (Applegate and Bonds, 1981; Enoch and Birch, 1981; Smallman et al., 2001). Taking this a step further, if an adult with a normal Stiles–Crawford effect is fit with a contact lens that has a decentered pupil, as illustrated in Fig. 3–24, the cones eventually point toward it, resulting in a displaced effect. When the contact lens is removed, the cones return to their original state. These results tell us that the cones are mobile and that they orient

17. The Stiles–Crawford effect of the second kind refers to changes in hue and saturation of monochromatic light as the point of entry into the pupil is changed.
18. A decentered pupil can be congenital or secondary to trauma.
19. When the Stiles–Crawford effect is displaced, the maximal sensitivity is no longer at a light entry point of zero (Fig. 3–22B).

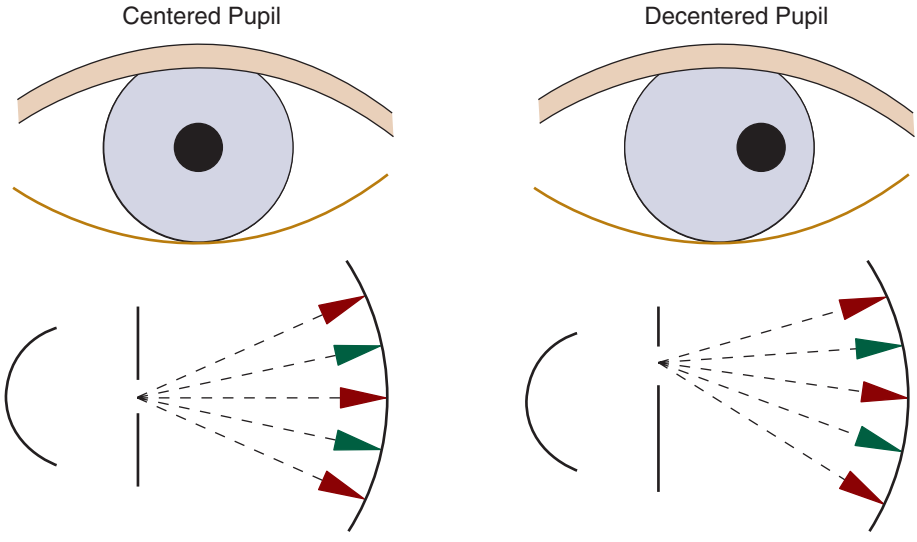

Figure 3–24. When a (pharmacologically dilated) eye is fit with a contact lens that has a decentered pupil, the cones point toward the center of this pupil. Following removal of the contact lens, the cones point toward the normal location of the pupil.

themselves to light; if the pupil becomes decentered, the cones reorient themselves such that they now point toward the center of the pupil, thereby maximizing their effectiveness in capturing photons of light.

Retinal disease may cause disruption of cone orientation, leading to an abnormal Stiles–Crawford function. The function may be abnormal in areas affected by disease (e.g., regions of retinal traction), but normal in unaffected areas.

ADDITIONAL CLINICAL CONSIDERATIONS

Visual Field Testing

Clinical Highlight

Visual field testing is a common and important clinical procedure that is critical for the diagnosis and management of many neurological diseases that affect the visual system, including glaucoma. It allows the clinician to assess the integrity of the visual pathways through noninvasive means. Damage to the visual pathways may produce generalized or localized loss of vision (visual field defects), the latter referred to as a **scotoma.** Careful analysis of the visual field defect can assist the clinician in localizing the damage within the visual pathway and determining its cause. Figure 3–25 shows the visual field defects expected for lesions in various regions of the visual pathway.

The clinical procedure used to plot visual fields is referred to as **perimetry.** During this procedure, which is conducted under photopic conditions, the patient

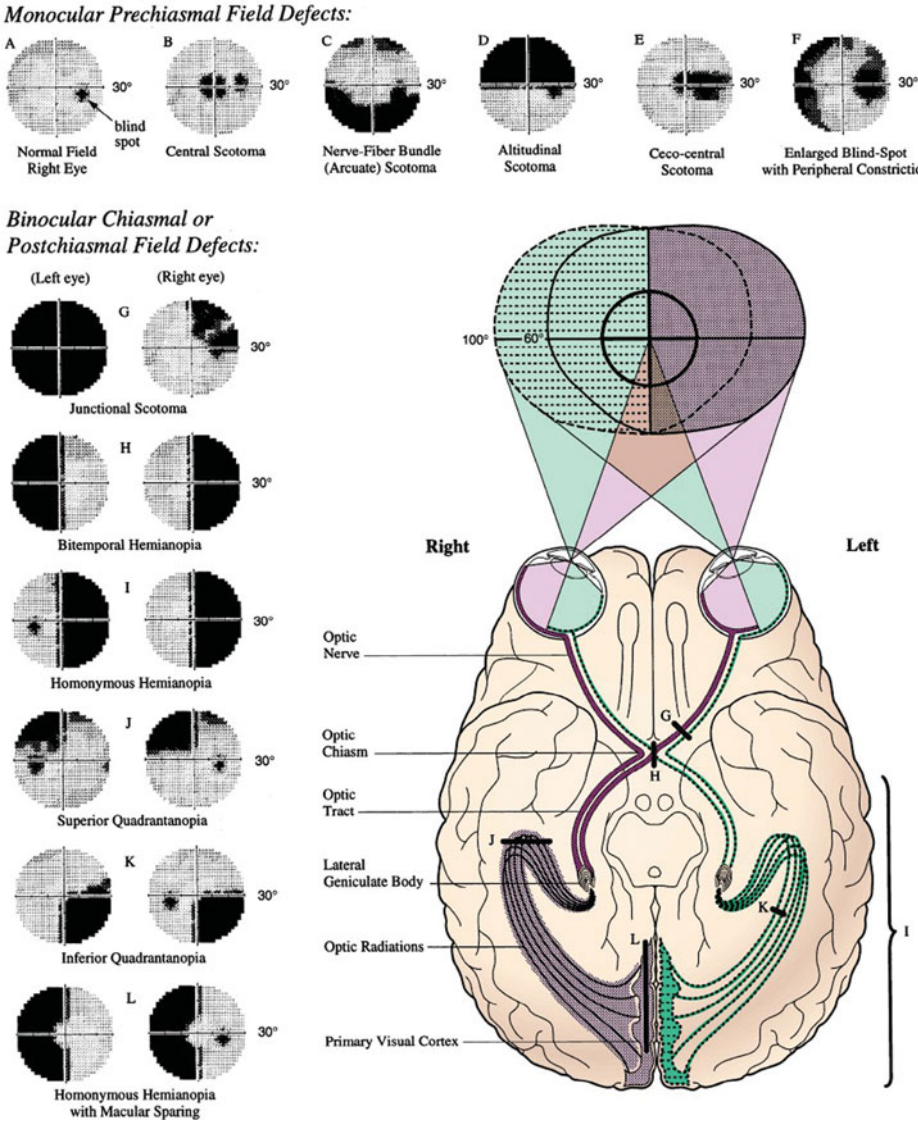

Figure 3–25. The location of a lesion within the visual pathway determines the nature of the field defect. Threshold is indicated by shading, with darker shading indicating higher thresholds (lower sensitivity). (*Reproduced with permission from Fauci et al.*. Harrison's Principles of Internal Medicine. *17th ed. New York: McGraw-Hill, Inc; 2008.)*

views a fixation target while a stimulus is presented in another region of her visual field. In **static perimetry,** the patient is asked to push a button to signal when she sees the stimulus, which appears as a flash of light. Using an algorithm specified by the perimeter's manufacturer, stimuli of various intensities can be presented at each of the tested points, thereby allowing the threshold for each of these points to be determined.[20] The stimulus is an increment (ΔI) flashed on a steady background (I_B), similar to that in a light adaptation experiment (see Fig. 3–16A). In essence, increment sensitivity is determined at a large number of retinal locations. These thresholds values are compared to norms established by the manufacturer of the device. An example of a static visual field in glaucoma is given in Fig. 3–26.

To enhance the diagnostic utility of the device, software programs allow visual sensitivity for various regions of the visual field to be compared with other regions. For instance, sensitivity in the superior nasal field may be compared with that in the lower nasal field. This is particularly helpful in diagnosing glaucoma, a disease in which visual field loss frequently shows vertical asymmetry, with either the superior or inferior visual nasal field first affected.

Compared to static perimetry, where the stimulus remains stationary, for **kinetic perimetry** the stimulus is slowly moved from a non-seeing to a seeing region of the visual field. In Goldmann perimetry, for example, the examiner slowly moves a stimulus of a specific size and intensity from the patient's periphery toward central fixation until the patient can see it. This procedure is repeated (using the same stimulus) for various visual meridians, and the points are connected to plot what is called an **isopter.** For all points that fall on an isopter, the visual system has equal sensitivity.

A less visible target (i.e., one that is smaller and/or dimmer) results in an isopter with a smaller diameter because the stimulus is not detectable by the less sensitive peripheral retina, but is detectable by the more sensitive central retina. Likewise, a more visible stimulus results in a larger isopter because the peripheral retina is able to detect this target. By using stimuli of various sizes, the clinician can plot various isopters.

When sensitivities for all points in the visual field are measured, we obtain the sensitivity profile in Fig. 3–27, which shows sensitivity as a function of visual field location in three dimensions. Sensitivity is greatest centrally and falls off in the periphery, resulting in a profile that looks like a hill, often referred to as the **hill of vision.** The dashed lines, which run circumferentially around the island, represent the various isopters.

Do the age-related reductions in retinal illumination that are secondary to senile miosis[21] and nuclear sclerosis affect visual field thresholds (ΔI)? The answer is no if the measurements are made at background light levels (I_B) where Weber's law

20. Thresholds are commonly determined using the staircase psychophysical method, which is discussed in Chapter 11.
21. The pupil diameter decreases and it becomes less responsive to light in the elderly, a condition referred to as senile miosis.

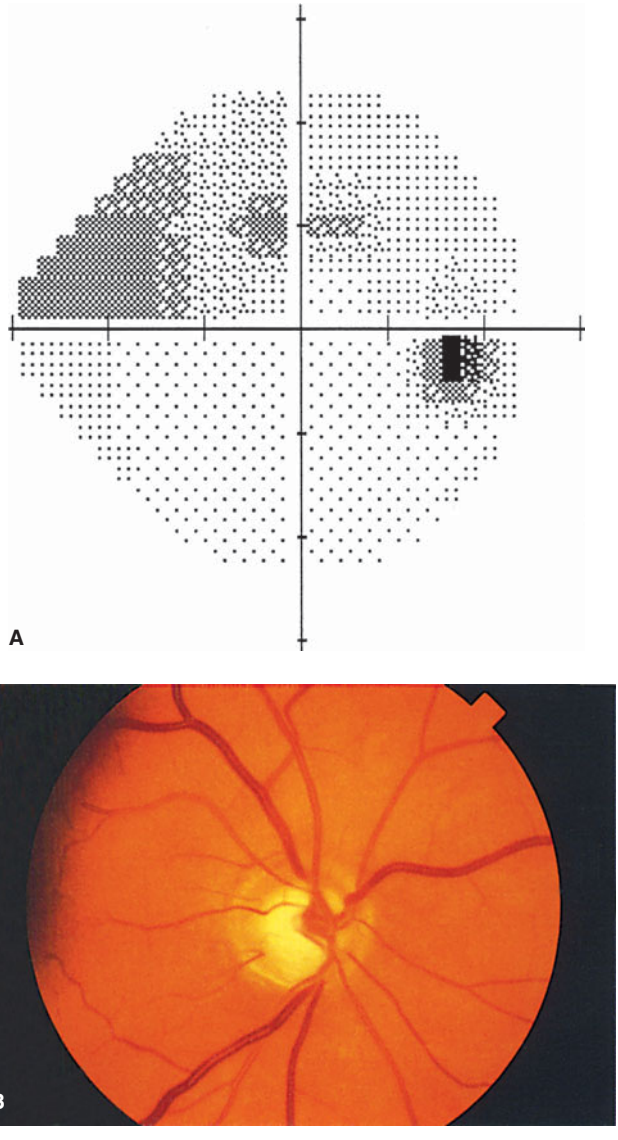

Figure 3–26. **A.** Right eye static visual field in a patient with early glaucoma as determined with a Humphrey visual field device. Threshold is indicated by shading, with darker shading indicating higher thresholds (lower sensitivity). The physiological blind spot is the dark area located temporal and inferior to the fixation point (center of the diagram). The shading located nasally and superiorly reveals a nasal step, which is strongly indicative of glaucoma. (*Image courtesy of Dr. Leon Nehmad.*) **B.** Right eye fundus photograph showing inferior notching of the optic nerve. This notching, which is due to neural atrophy, would be consistent with a nasal-step field defect as illustrated in **A.** (*Reproduced with permission from Fingeret M, Lewis TL.* Primary Care of the Glaucomas. *2nd ed. New York: McGraw-Hill, Inc; 2001.*)

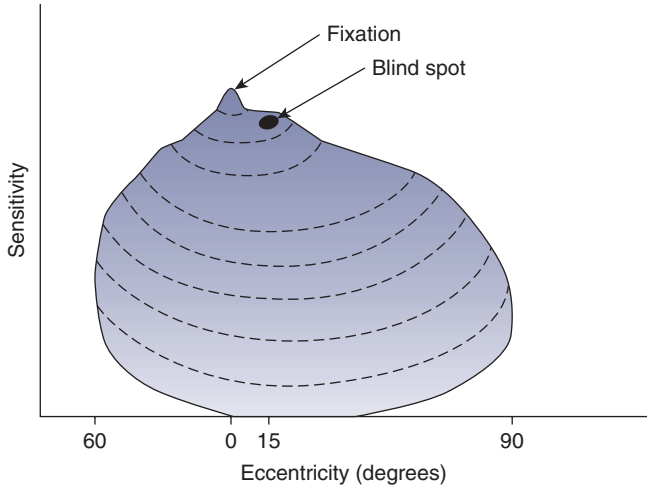

Figure 3–27. Hill of vision obtained under photopic conditions for a right eye. Note the peak at fixation, representing the fovea, and the blind spot produced by the optic disc.

is followed. Because senile miosis and nuclear sclerosis reduce the *retinal illumination* produced by the increment and background by the same amount, the Weber fraction of the *retinal image* remains unchanged.

Dark Adaptation

Used in conjunction with the electroretinogram[22] and other electrodiagnostic tests, dark adaptation may be useful in the diagnosis of retinitis pigmentosa (RP), congenital stationary night blindness,[23] and certain other rod–cone degenerations and diseases (Fig. 3–28). Measurements suitable for clinical applications may be obtained using a commercially produced dark adaptometer such as the Goldmann–Weekers or scotopic sensitivity tester (SST-1) dark adaptometer.

In RP, rods are typically affected prior to the cones. This may lead, early in the disease, to a dark adaptation curve with a rod portion that takes an abnormally long time to level off and/or plateaus at a higher than normal threshold. An abnormal dark adaptation curve is consistent with certain symptoms typical of RP, including night blindness and slow visual recovery following exposure to a bright light. The latter is particularly evident following ophthalmoscopy; patients with RP are often visually incapacitated for several minutes.

22. The ERG is discussed in Chapter 16.
23. CSNB is an inherited disorder characterized by rod dysfunction. Visual acuity may be normal or reduced.

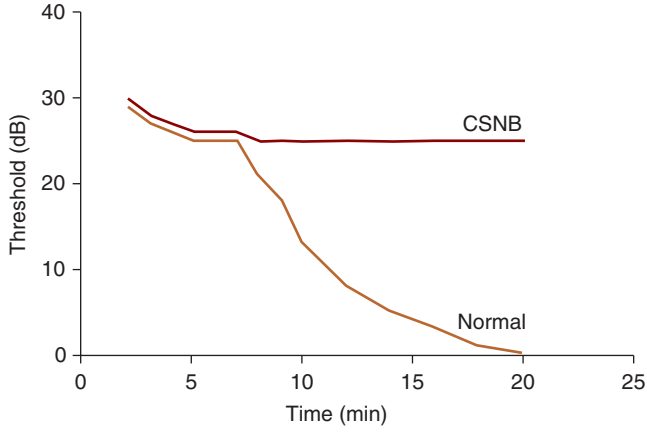

Figure 3–28. Dark adaptation as obtained with a SST-1 for a healthy patient and one with congenital stationary night blindness. Note the elevated rod threshold. (*Original black and white figure is courtesy of LKC Technologies, Inc., Gaithersburg, MD*)

TABLE 3–2. SUMMARY OF FEATURES OF THE SCOTOPIC AND PHOTOPIC SYSTEMS

Property	Scotopic System	Photopic System
Receptor	Rods	Cones
Outer segment morphology	Free-floating discs	Discs attached to cell membrane
Weber's fraction	0.140	0.015
Photopigment(s) and peak absorption	Rhodopsin (507 nm)	Erythrolabe (552 or 557 nm) Chlorolabe (530 nm) Cyanolabe (426 nm)
Maximal sensitivity of the system	507 nm	555 nm
Chromatic discrimination	Colorblind	Color discrimination
Sensitivity	Very sensitive to dim lights, not to bright lights	Not sensitive to dim lights, but to brighter lights
Spatial resolution (resolution acuity)	Poor (20/200)	Excellent (20/20)
Spatial summation	Excellent	Poor
Temporal resolution (CFF[a])	Poor (20 Hz)	Excellent (70 Hz)
Temporal summation	Excellent	Poor
Contrast sensitivity	Low (0.140)	High (0.015)
Stiles–Crawford effect	Minimal	Yes

[a]Critical flicker fusion.

SUMMARY

Not only do the rods and cones manifest different morphologies, photopigments, and retinal distributions, the postreceptoral organization of the rod system is fundamentally different than that of the cone system (Table 3–2). The result is a duplex retina: a rod-dominated system operates under dim (scotopic) lighting conditions and a cone-dominated system functions under daylight (photopic) conditions. This duplex retina allows us to have usable vision on both a dark evening and a sunny day, even though there may be up to a 10-log-unit difference in the light levels under these two conditions.

Scotopic vision shows extraordinary absolute sensitivity, largely because of its high degree of spatial and temporal summation; however, this high degree of spatial and temporal summation limits scotopic spatial and temporal resolution. Photopic vision, on the other hand, displays substantially greater spatial and temporal resolution, but poorer spatial and temporal summation.