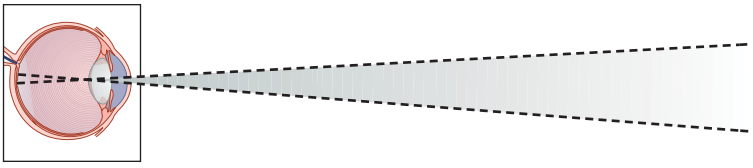

2

Introductory Concepts

This chapter is for readers who do not have training in ocular physiology and the physics of light or who require a review of this material. Not intended to be comprehensive, it presents an introductory background critical to the study of visual perception.

VERY BASIC OCULAR ANATOMY

Three Ocular Layers: Sclera, Uvea, and Retina

Figure 2–1 shows a horizontal cross section of the human eye. At birth, the average eye has an **axial length** (cornea to retina) of 17 mm and grows to an average length of 25.4 mm (1 in) in the adult.

The eye consists of three concentric layers. The outermost is the sclera, the middle is the uvea, and the innermost is the retina.

The sclera is the white portion of the eye that is apparent on gross observation. It consists largely of collagen and provides support and protection for the internal elements of the eye. The sclera is continuous with the cornea, which is the transparent tissue at the most anterior aspect of the eye.

The highly vascularized uvea consists of the iris, ciliary body, and choroid. Within the **iris** are the sphincter iridis and the dilator pupillae muscles that control the diameter of the pupil, thereby helping to regulate the amount of light that enters the eye. The **ciliary body** contains the ciliary muscle, which focuses the crystalline lens for near vision—a process referred to as **accommodation.** It is also the source of the **aqueous humor,** a liquid substance that provides nourishment to certain eye structures, including the cornea and crystalline lens. The blood supply for the outer retina comes from the **choroid,** which is continuous with the ciliary body.

The innermost tissue layer of the eye is the **retina,** an exceedingly complex, multilayered neural element only 0.2 mm thick. The eye's optical elements focus an image on the retina, which then begins the thorny task of analyzing this image.

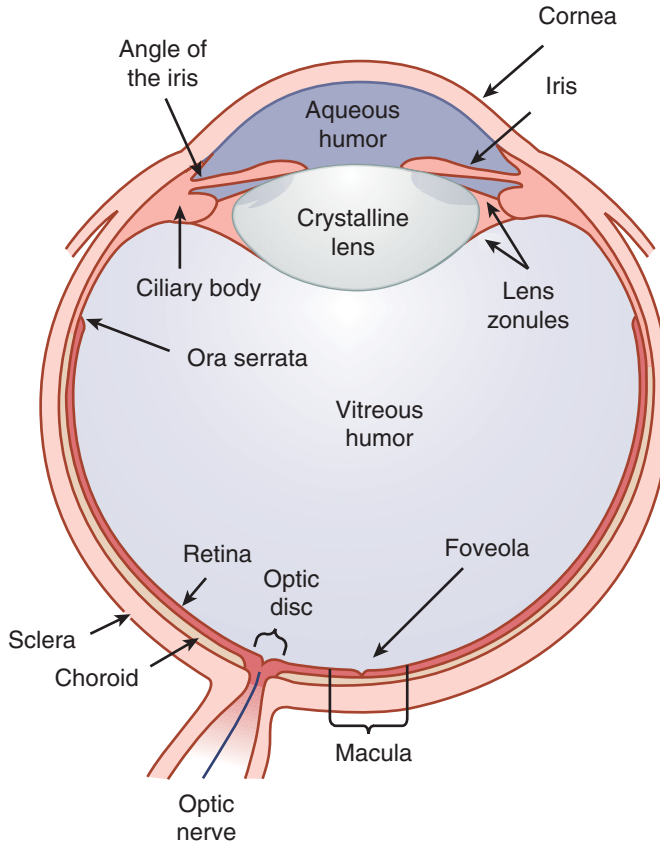

Figure 2–1. Cross section of the human eye.

Ocular Anatomy: Anterior to Posterior

The most anterior aspect of the eye is the **cornea,** a transparent structure that provides approximately two-thirds (40 diopters) of the refractive power (focusing power) of the eye (which has a total power of 60 diopters) (Millodot, 1982). For the cornea to remain transparent, its hydration must be maintained at a fairly constant level. Conditions disrupting this process can lead to corneal swelling and consequent light scatter, which can profoundly reduce image quality.

The aqueous humor is contained within the **anterior** and **posterior chambers** of the eye. (The anterior chamber is bound by the posterior surface of the cornea and the anterior surfaces of the crystalline lens and iris, while the posterior chamber is bound by the posterior surface of the iris and the anterior surface of the vitreous humor.) The aqueous is continuously produced by the ciliary body and

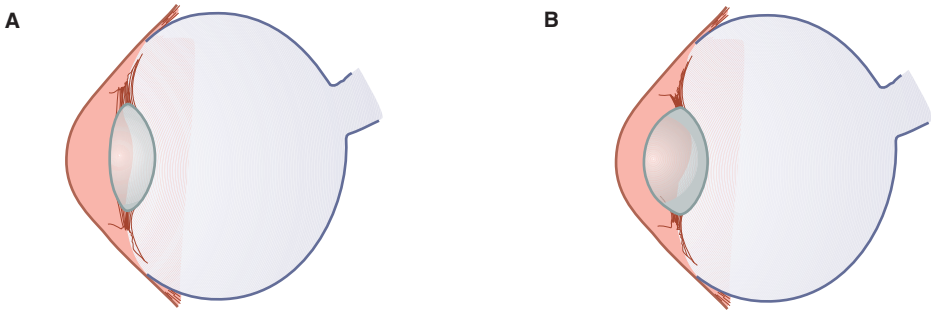

Figure 2–2. **A.** When the distant objects are viewed, the anterior surface of the crystalline lens is at its flattest, thereby minimizing the lens' refractive power. **B.** When near objects are viewed, the sphincter-like ciliary body constricts; this reduces the tension on the zonules, thereby allowing the anterior surface of the lens to bulge forward. As a result, the dioptric power of the lens is increased. (*Reproduced with permission from Schwartz SH.* Geometrical and Visual Optics: A Clinical Introduction. *New York: McGraw-Hill, Inc; 2002.*)

drained by the **canal of Schlemm,** which is located in the angle that is formed by the iris and cornea—the **angle of the iris.** The canal of Schlemm runs circumferentially.

The aqueous humor exerts a pressure, referred to as the **intraocular pressure (IOP),** of approximately 16 mm Hg that helps maintain the structural integrity of the eye. In certain forms of **glaucoma** the IOP is elevated, presumably leading to retinal damage. Elevated IOPs can result from the overproduction of aqueous, poor drainage of aqueous from the eye, or a combination of these factors.

Posterior to the iris is the **crystalline lens,** which contributes approximately one-third (20 diopters) of the dioptric power of the eye. Through accommodation, the dioptric power of the lens increases, thereby focusing near objects on the retina. Accommodation occurs when the ciliary muscle constricts, releasing tension on the **lens zonules** and allowing the lens to assume a more "natural" position in which its anterior surface bulges forward (Fig. 2–2). The radius of curvature of the anterior lens surface is thereby decreased, increasing the dioptric power of the lens and, consequently, the eye itself.

Clinical Highlight

As we age, the ability to accommodate diminishes due to reduced elasticity of the crystalline lens secondary to its continuous growth throughout life. By the time most people are in their mid forties, the ability to accommodate has diminished to the point where they cannot read without plus lenses, a condition referred to as **presbyopia.**

The crystalline lens becomes less transparent with age, presumably due to the destructive oxidative effects of free radicals. When decreased lens transparency becomes significant and results in a loss of visual acuity, the patient is said to have

a **cataract.**[1] During cataract surgery, one of the most common surgical procedures, the crystalline lens is removed and replaced with a synthetic lens.

The **vitreous humor** makes up the bulk of the eye volume. It consists largely of collagen and hyaluronic acid and has a gel-like structure. The vitreous provides structural and nutritive support for the retina in addition to filling a dioptrically critical space.

Posterior to the vitreous humor is the retina. It is on this tissue that the visual world is focused. For the study of visual perception, this is the most important ocular tissue.

BASIC RETINAL ANATOMY AND POSTRETINAL PATHWAYS

In a rudimentary sense, the eye can be considered analogous to a camera. Both focus the world on a light-sensitive element. This analogy falls apart when we scrutinize the respective roles of a camera's photosensitive element and the retina. The former acts as a passive receiver of light: it records a point-by-point representation of the light falling upon it. In comparison, the retina is an elaborate neural structure that actively analyzes the image that is focused on it. The signal that is sent to the brain is not merely a point-by-point representation of the retinal image—certain information is highlighted, while other information is disregarded.[2] The information processing that occurs within the retina is discussed extensively in this book.

Retinal Layers

Figure 2–3A is a schematic flowchart of retinal processing. Photoreceptors (rods and cones) respond to light, transforming radiant energy into electrical activity. They synapse on retinal bipolar cells, which feed into retinal ganglion cells. The comparatively long axons of the retinal ganglion cells leave the eye, form the second cranial nerve (the optic nerve), and synapse in the lateral geniculate nucleus.

This photoreceptor → bipolar cell → ganglion cell arrangement reflects the feedforward, or **centripetal,** nature of retinal organization. There are also lateral interconnections that provide for the horizontal transmission of retinal information. As indicated in Fig. 2–3, **horizontal** and **amacrine** cells are involved in this lateral integration.

In addition to the feedforward and lateral interconnections, there is feedback transmission of information. In this pathway, referred to as the **centrifugal pathway,**

1. Cataracts can be congenital or secondary to aging (senile cataracts), injury, infection, systemic disease (e.g., diabetes), or environmental exposure to ultraviolet radiation.
2. In lower animals with smaller brains, proportionately more visual processing takes place in the retina than is the case for higher animals. The frog retina is, for example, capable of detecting a bug and triggering the decision to strike it with the frog's tongue (Lettvin et al., 1959).

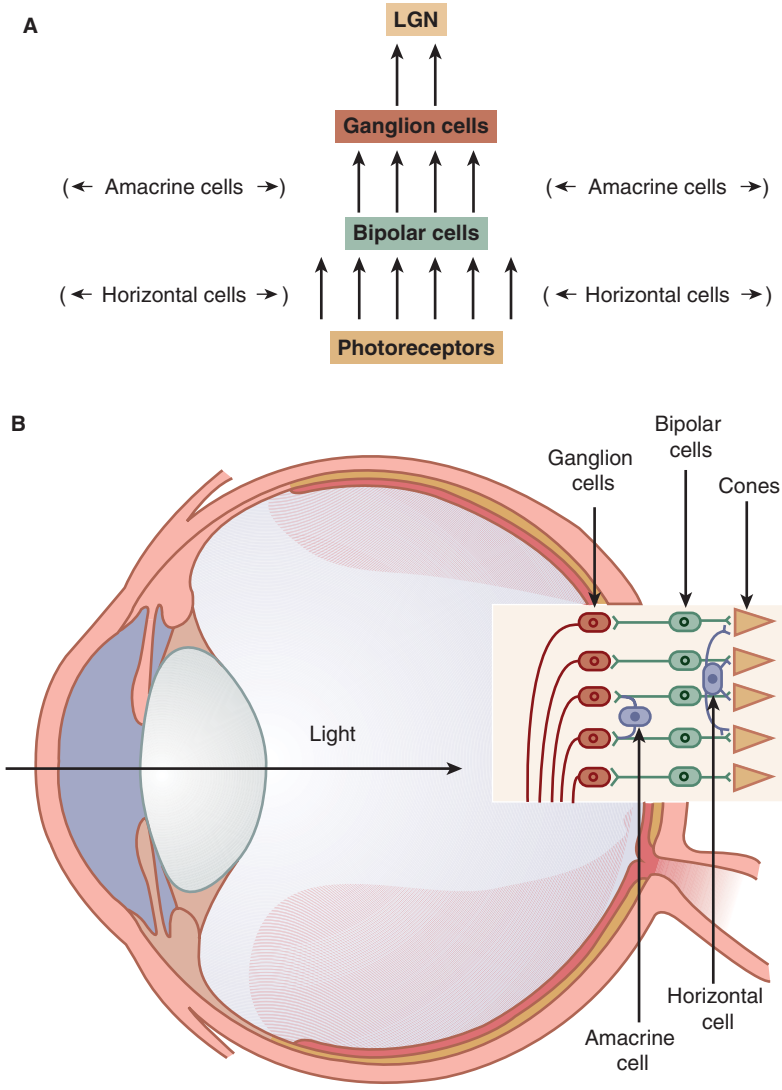

Figure 2–3. **A.** Schematic flowchart of retinal processing. The feedforward (centripetal) pathway consists of *photoreceptors → bipolar cells → ganglion cells → lateral geniculate nucleus (LGN)*. Horizontal and amacrine cells participate in lateral integration within the retina. **B.** Magnified schematic of the retina in the region of the fovea. The photoreceptors absorb light quanta and convert this radiant energy into electrical activity. They synapse on bipolar cells, which in turn, can stimulate ganglion cells, thereby sending action potentials along the optic nerve to the LGN. Note that the incident light travels from inner to outer retina, while the electrical signal travels in the opposite direction.

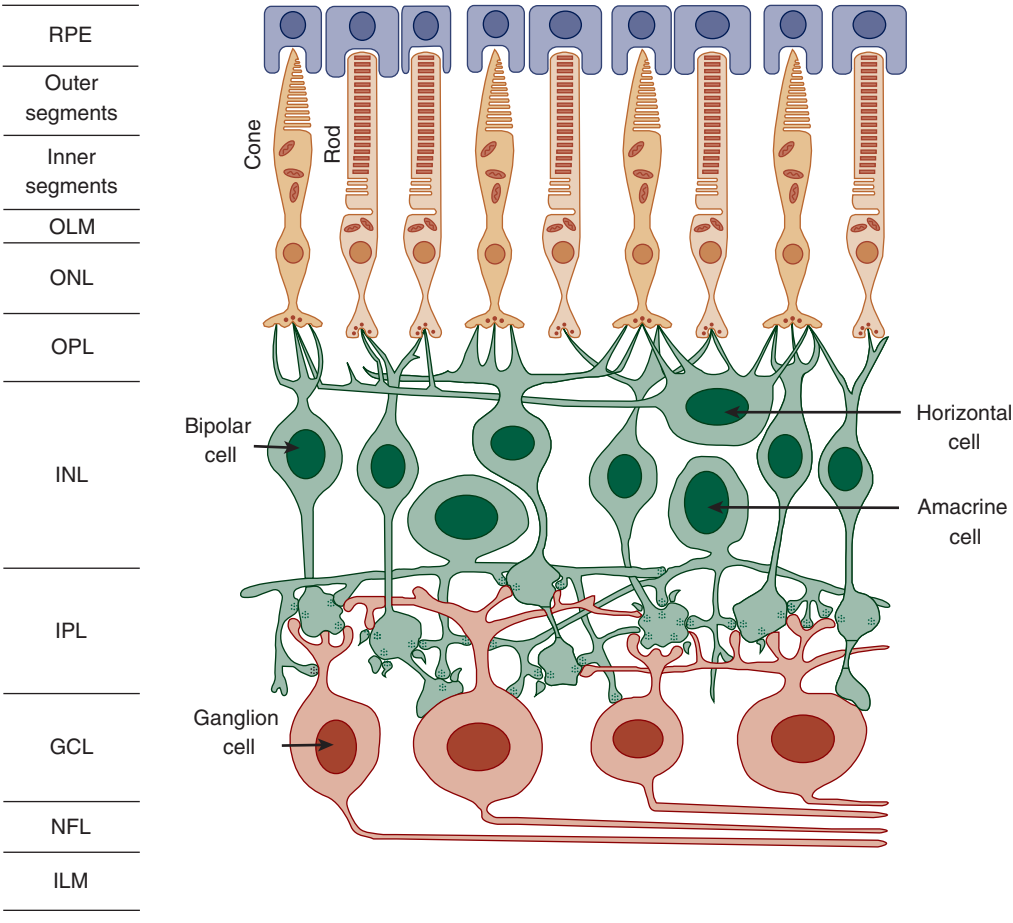

Figure 2–4. Schematic of retinal organization based on Polyak (1941) and Dowling and Boycott (1966). Beginning at the outer retina, the layers are as follows: retinal pigment epithelium (RPE); outer segments of the photoreceptors; inner segments of the photoreceptors; outer limiting membrane (OLM); outer nuclear layer (ONL); outer plexiform layer (OPL); inner nuclear layer (INL); inner plexiform layer (IPL); ganglion cell layer (GCL); nerve fiber layer (NFL); and internal limiting membrane (ILM). Light would come from the bottom of the diagram and pass through the inner retina before reaching the photoreceptors.

information is transmitted from the ganglion cell region back toward the photoreceptors by **interplexiform** cells (Lindberg and Fisher, 1986).

Figures 2–3B, 2–4, and 2–5 show cross sections of the primate retina. Note that light passes through the vitreous and inner layers of the retina, and then hits the photoreceptors, which are located in the outer retina. The inner retinal elements do little to degrade the retinal image because they are somewhat transparent and, as we will learn, laterally displaced in the region of the retina that is associated with the best vision, the fovea.

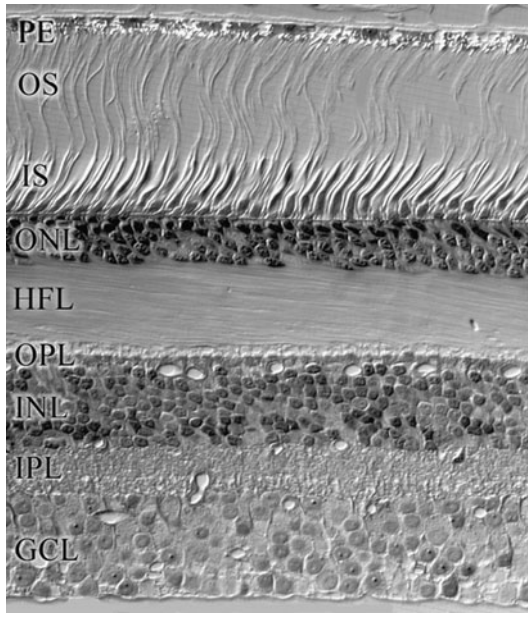

Figure 2–5. Cross section of the monkey retina. The labeled layers are the pigment epithelium (PE), outer segments (OS), inner segments (IS), outer nuclear layer (ONL), Henle nerve fiber layer (HFL), outer plexiform layer (OPL), inner nuclear layer (INL), inner plexiform layer (IPL), and ganglion cell layer (GCL). The Henle fiber layer is constituted of the photoreceptor synaptic processes that extend radially from the foveola. (*Photomicrograph courtesy of Dr. Heinz Waessle.*)

In the discussion that follows, we examine retinal anatomy going from the outer to the inner layers. The outer retina is composed of those elements proximal to the choroid, whereas the inner retina is composed of those elements proximal to the vitreous.

The outermost layer of the retina, the **retinal pigment epithelium (RPE),** is not responsive to radiant energy and does not participate in the encoding of visual information. It provides crucial metabolic support, phagocytizing the continuously shed photoreceptor outer segments (Chapter 3) (Young, 1970, 1971). In addition, the darkly pigmented RPE absorbs light photons that are not absorbed by the photoreceptors, thereby reducing light scatter within the eye.

Clinical Highlight

Figure 2–6 is a photograph of a normal fundus, showing the appearance of the posterior pole as observed during ophthalmoscopy.[3] The reddish appearance is due largely to pigment in the choroid and RPE. Absence of pigment, as occurs in albinism, increases the visibility of the choroidal vasculature (Fig. 2–7).[4]

3. The retina and other ocular structures, as seen during ophthalmoscopy, are referred to as the **fundus.**
4. Patients with albinism have a poorly developed fovea and manifest reduced visual acuity in addition to nystagmus, strabismus, and photophobia.

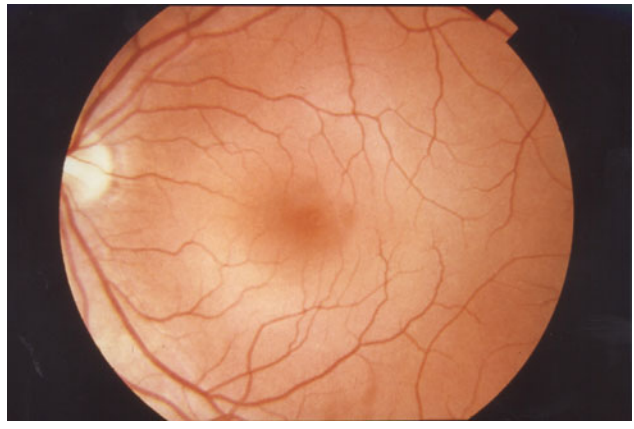

Figure 2–6. Fundus photograph of a left human eye. Vessels that supply the inner retina emerge from the optic nerve head. The avascular fovea is temporal to the optic nerve head. (*Image from National Eye Institute, National Institutes of Health, Bethesda, MD*)

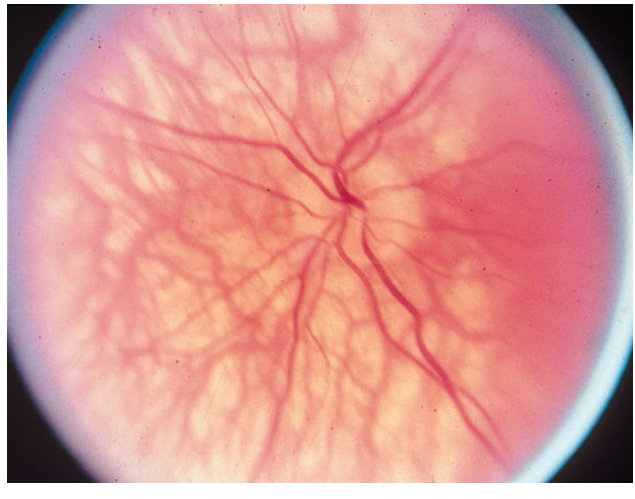

Figure 2–7. Fundus photograph of an albinotic fundus. Note the choroidal vasculature that is highly visible against the white sclera. (*Reproduced with permission from Alexander LJ.* Primary Care of the Posterior Segment. *3rd ed. New York: McGraw-Hill, Inc; 2002.*)

Inner to the RPE are the **photoreceptors.** These cells manifest a very high level of metabolic activity, among the highest in the body. This necessitates their location in the outer retina, close to the choroidal blood supply.

Photoreceptors fall into two groups: **rods,** which are the foundation for nighttime vision, and **cones,** which provide the underpinning for daytime vision. The outermost aspect of a photoreceptor, the **outer segment,** contains a photopigment that absorbs light, converting it into electrical activity. Outer segments form a distinct retinal layer. Photoreceptor **inner segments,** which contain many of the organelles of these cells, excluding their nuclei, also constitute a distinct retinal layer.

The **outer limiting membrane,** formed by interconnecting processes of Müller cells (retinal glial cells), separates the inner segments of the photoreceptors from their nuclei. Photoreceptor nuclei form the **outer nuclear layer.**

The first retinal synapses occur within the **outer plexiform layer (OPL),** which consists of the dendrites of the bipolar and horizontal cells, the synaptic endings of the photoreceptors, and the various synapses among these structures. Inner to the OPL is the **inner nuclear layer (INL).** This layer consists of the cell bodies of the bipolar, horizontal, and amacrine cells.

Clinical Highlight

A splitting between the OPL and INL can be seen in degenerative retinoschisis. As indicated in Fig. 2–8, the region of retinal splitting can appear as a relatively large dome-shaped elevation.

The second stage of synapses is in the **inner plexiform layer.** Contained within this layer are the various synapses among the bipolar, amacrine, and ganglion cells.

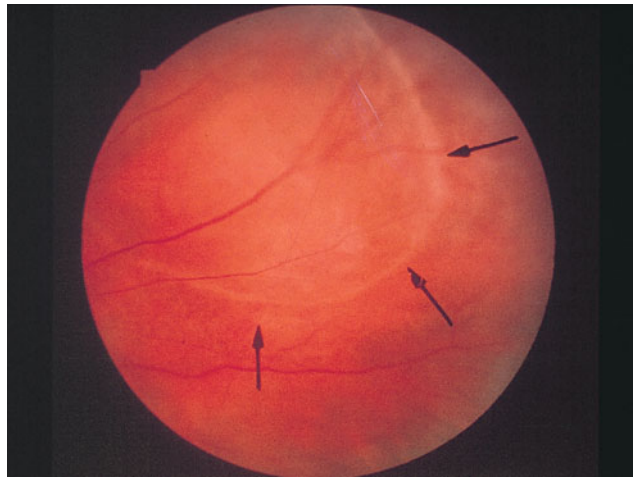

Figure 2–8. Degenerative retinoschisis. The arrows demark the boundaries of the visible splitting within the sensory retina. (*Reproduced with permission from Alexander LJ.* Primary Care of the Posterior Segment. *3rd ed. New York: McGraw-Hill, Inc; 2002.*)

The **ganglion cell layer** is constituted of at least three major classes of neurons. The smaller **midget** ganglion cells comprise approximately 80% of these neurons, and the larger **parasol** ganglion cells approximately 10% (Lennie et al., 1990b). Additionally, there are the less studied **small bistratified** ganglion cells.

A newly discovered category of ganglion cells contains the photosensitive pigment melanopsin (Hattar et al., 2002). As we will discuss in Chapter 12, these neurons appear to play a role in regulating the circadian rhythm (Berson et al., 2002; Provencio et al., 2002).

The axons of the ganglion cells constitute the **nerve fiber layer.** Exiting the eye at the optic disc, these axons form the **optic nerve** (the second cranial nerve) and synapse in the midbrain.

The innermost retinal layer is the **internal limiting membrane.** It acts as an interface between the retina and the vitreous humor, with the vitreous strongly attached to this structure in certain regions (e.g., optic nerve head, vitreous base).

Clinical Highlight

As the vitreous ages, it shrinks and tugs on the retina. This traction mechanically stimulates the retina, producing phosphenes that often appear as flashing lights. As the vitreous continues to shrink, it can tear away from the retina, resulting in a vitreous detachment. In certain cases, the retina itself may be ruptured, resulting in a retinal hole; a rhegmatogenous retinal detachment occurs when fluid enters this hole and seeps into potential space between the sensory retina and RPE, causing the two to separate (Fig. 2–9).

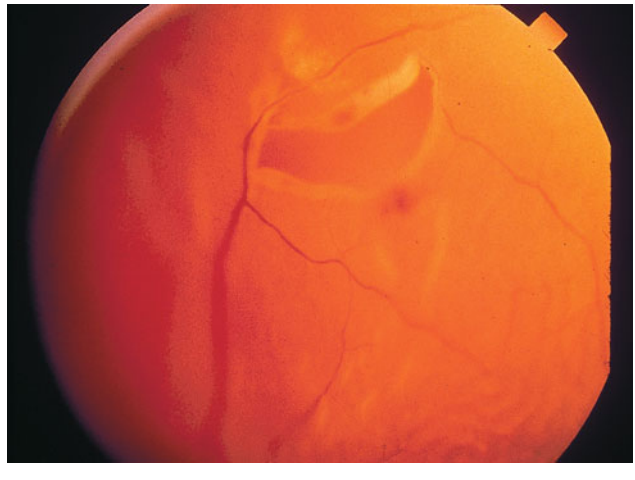

Figure 2–9. Retinal detachment accompanying a tear in the sensory retina. Because of traction at the vitreous–retina interface, the tear assumes a horseshoe shape. (*Reproduced with permission from Alexander LJ.* Primary Care of the Posterior Segment. *3rd ed. New York: McGraw-Hill, Inc; 2002.*)

The preceding description of retinal anatomy is basic and omits many details of both scientific and clinical importance. For instance, there are approximately 20 different types of amacrine cells. It should be apparent, however, that the complex cellular and synaptic arrangement of the retina points to a high degree of information processing within this structure.

A key feature of retinal organization is lateral interaction. Horizontal and amacrine cells integrate information laterally within the retina, allowing for the processing of visual information across space. This important issue is discussed in detail in Chapters 7 and 12.

Since the diameter of the optic nerve and the number of ganglion cell axons it contains are limited by the structure of the skull, not all information that falls upon the retina is transmitted to the brain proper. Although there are more than 100 million photoreceptors within the retina, there are only 1 million ganglion cells, revealing an extensive degree of neural convergence (Østerberg, 1935; Curcio and Allen, 1990). As information is transmitted through the retina, some is highlighted and encoded, whereas other information is lost.

Optic Disc and Fovea

The **optic nerve head** (or **optic disc**)—a prominent clinical landmark of the fundus—is constituted of the ganglion cell axons as they leave the eye to form the optic nerve. The whitish appearance of the optic nerve head is due to the myelin sheath that covers these axons as they leave the eye. Normally, the ganglion cell axons do not acquire a myelin sheath before they reach the optic nerve head.

Clinical Highlight

Myelinated nerve fibers are occasionally seen as a normal clinical variant, appearing as soft, feathery tufts that follow the course of the ganglion cell axons (Fig. 2–10). Although striking when observed by the clinician during ophthalmoscopy, myelinated nerve fibers do not significantly interfere with vision.

There are no photoreceptors in the optic disc, resulting in a **physiological blind spot** in each eye, located approximately 15 degrees temporal to the point of fixation. The right eye's physiological blind spot is demonstrated in Fig. 2–11.

Temporal to the optic disc is the **fovea,** a specialized retinal region of highly developed visual acuity (visual resolution) that allows you to read these words. When looking at the E in Fig. 2–12, its image falls upon the fovea, allowing it to be resolved. Since the surrounding letters fall on more peripheral regions of the retina, where resolution is less acute, they are not easily read.

A number of anatomical features distinguish the fovea. To maximize vision, neural elements of the inner retina are pushed aside to allow light to fall directly on the photopigment-containing outer segments of cones. This creates a depression or pit with gently sloping borders that is approximately 5 degrees in diameter,

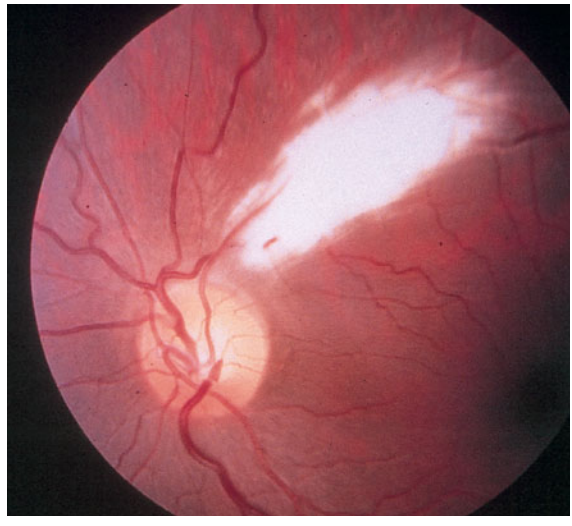

Figure 2–10. Myelinated nerve fibers have a feathery appearance and follow the course of the optic nerve fibers. There may be a slight elevation of visual field thresholds in the affected area. The condition is stable and poses no threat to vision. (*Reproduced with permission from Alexander LJ.* Primary Care of the Posterior Segment, *3rd ed. New York: McGraw-Hill, Inc; 2002.*)

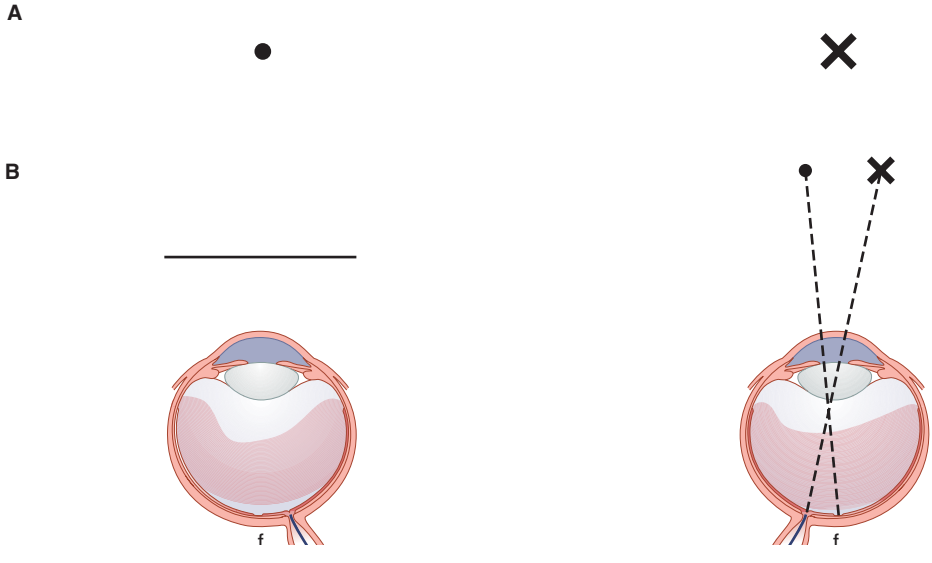

Figure 2–11. **A.** Demonstration of the physiologic blind spot. Close your left eye and view the dot at a distance of 10 to 12 in. Note that the X disappears. This is because the image of the X falls on the optic disc. **B.** Looking down onto the eyes, it can be seen that the optic disc is nasal to the fovea. This results in the physiologic blind spot being temporal to the fixation point.

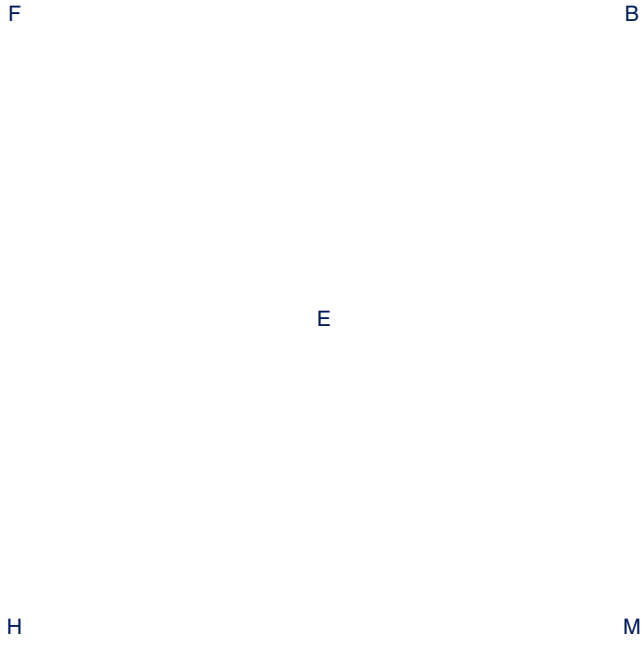

Figure 2–12. While fixating the letter E, note that the other letters are not easily resolvable. Visual resolution is most acute in the fovea and less developed in the peripheral retina.

approximately the same size as the optic disc (Fig. 2–13 and Table 2–1). The bottom of this pit, the **foveola,** subtends a visual angle of approximately 1.2 degrees, twice the angular subtense of the moon (Pirenne, 1967).[5] Cones are the only photoreceptors found in the foveola, where they have a density greater than in any other region of the retina (Fig. 3–8).

A vascular network covers the retina, except in what is referred to as the foveal avascular zone—a region that is larger than the foveola, but smaller than the fovea (see Fig. 2–6). This adaptation prevents the scattering of light by retinal vessels, maximizing the visual resolution provided by the fovea. Metabolic nourishment for foveal (and nonfoveal) cones is provided by the choroid.

Clinical Highlight

In a central retinal artery occlusion, blood flow to the inner retina is disrupted, leading to cell death and edema. The retina appears whitish and hazy except in the fovea, which is nourished by the choroidal blood supply. This cherry-red spot appearance, illustrated in Fig. 2–14, is characteristic of a central retinal artery occlusion.

5. It is handy to know that the moon and sun subtend approximately 0.5 degrees at the eye, compared to 1.5 to 2.0 degrees for your thumb held at arm's length.

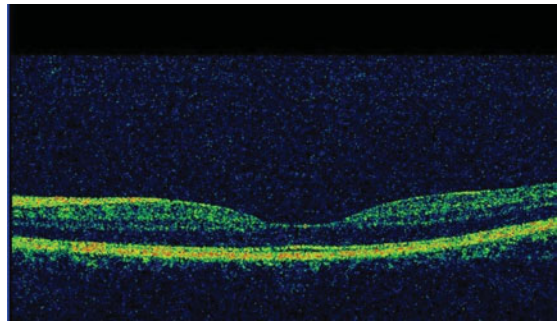

Figure 2–13. Foveal region as seen in ocular coherence tomography (OCT). Note the gradual change in slope that forms the foveal depression. The bottom of this depression is the foveola. (*Image courtesy of Dr. Scott Richter.*)

These adaptations—absence of rods, maximal density of cones, pushing aside of inner retinal elements to expose the cone outer segments to light, and absence of retinal vasculature—all contribute to the excellent resolution provided by the fovea. The fovea, although physically small (approximately 0.01% of the retinal area), plays an exceedingly large role in visual perception. As discussed in Chapter 14, a disproportionate area of the striate visual cortex (approximately 8%) is devoted to processing foveal information, a phenomenon referred to the **cortical magnification** of foveal vision (Azzopardi and Cowey, 1993).

Surrounding the fovea is a region of the retina referred to as the **macula lutea,** which contains a nonphotosensitive yellow pigment located in the inner retina. This pigment absorbs blue light (maximal absorption is in the region of 460 nm) and may aid vision by reducing light scatter or minimizing the effects of chromatic aberration (Wald, 1945). By absorbing high-energy ultraviolet radiation, it may also serve to protect the underlying retinal tissue. Studies are underway to determine if dietary supplements that include lutein and zeaxanthin, which are found in the macular pigment, are useful for prophylaxis and/or treatment of age-related macular degeneration (ARMD), a leading cause of blindness in the elderly (Gale et al., 2003).

TABLE 2–1. DIMENSIONS OF VARIOUS RETINAL LANDMARKS

Structure	Diameter (mm)	Diameter (degrees)
Optic nerve head	1.8	5.0
Macula lutea	5.8	18.5
Fovea	1.8	5.0
Foveal avascular zone	0.7	2.5
Foveola	0.3	1.2

Data from Polyak SL. *The Retina.* Chicago, IL: University of Chicago Press; 1941; Bradley A, Applegate RA, Zeffren BS, van Heuven WAJ. Psychophysical measurement of the size and shape of the human foveal avascular zone. *Ophthalmic Physiol Opt.* 1992;12:18–23.

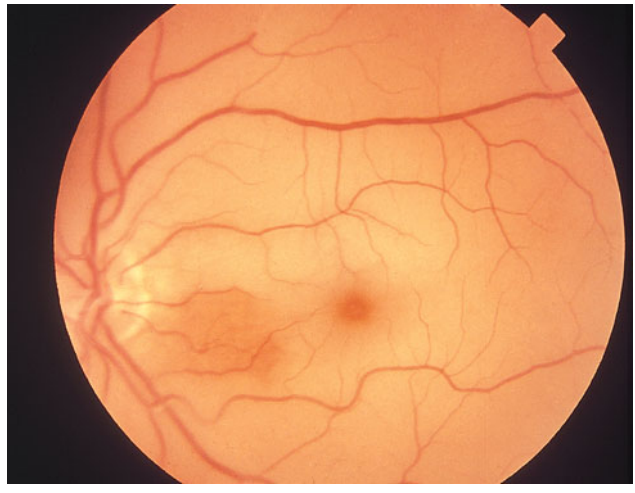

Figure 2–14. In a central retinal occlusion, the fovea takes on the appearance of a "cherry red spot" because it is seen in contrast to the whitish edematous retina that surrounds it. Note that in this case, the tissue temporally adjacent to the disc is also reddish. An intact cilioretinal artery, a normal anatomical variation, continues to nourish this region of the retina. (*Reproduced with permission from Alexander LJ.* Primary Care of the Posterior Segment. *3rd ed. New York: McGraw-Hill, Inc; 2002.*)

Postretinal Pathways

The axons of the retinal ganglion cells leave the eye via the second cranial nerve, the **optic nerve.** At the **optic chiasm,** ganglion cell fibers from the nasal retina of each eye cross over to join the temporal fibers of the fellow eye to form the **optic tract** (Fig. 2–15). As a result, the fibers constituting the left optic tract carry information regarding the right visual field, and fibers in the right optic tract encode the left visual field.

A general scheme of postretinal organization is given in Fig. 2–16. The primary target of the optic tract is the **lateral geniculate nucleus (LGN),** a laminated thalamic nucleus. Most, but not all, retinal ganglion cells synapse in this six-layered structure. Layers 2, 3, and 5 receive input from the ipsilateral eye, whereas layers 1, 4, and 6 receive input from the contralateral eye (see Fig. 13–1).

The LGN is composed of three distinct regions. The ventral two **magnocellular** layers are constituted of comparatively large neurons called magno or M-cells. Smaller neurons, commonly called parvo or P-cells, comprise the four dorsal **parvocellular** layers. The areas between these six layers (interlaminar or intercalated regions) contain yet smaller neurons called **konio** cells.

Axons from midget ganglion cells synapse on P-cells in the LGN to form the **parvo retinogeniculate pathway,** while axons from parasol cells synapse on LGN M-cells to form the **magno retinogeniculate pathway.** The konio cells

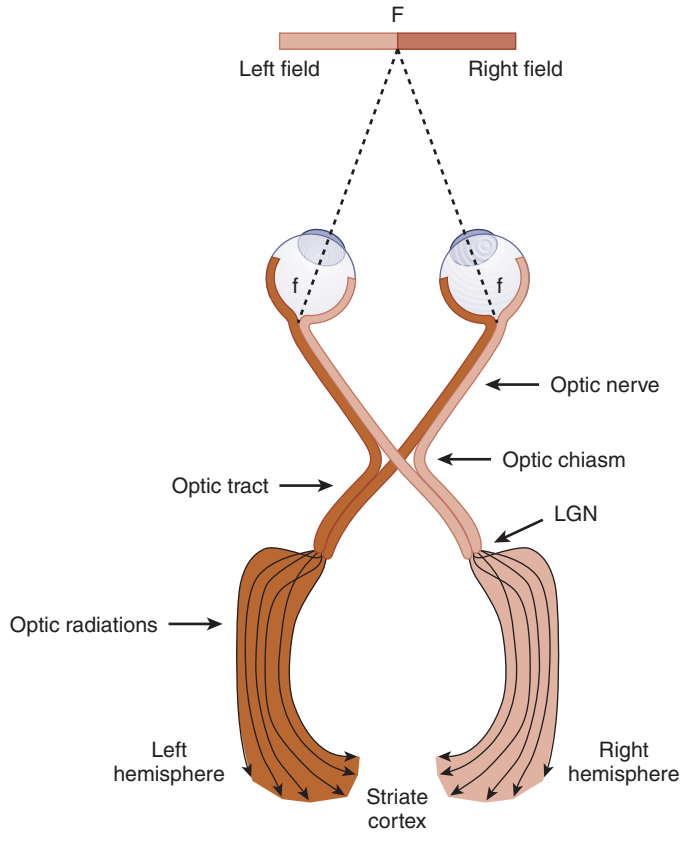

Figure 2–15. Nerve fibers that originate from the nasal half of the retina join fibers from the temporal retina of the fellow eye at the optic chiasm. Consequently, objects in the right half of the visual field are processed in the left cortical hemisphere and objects in the left half of the visual field are processed in the right cortical hemisphere. In this schematic, the foveas (f) are aligned with the fixation point (F).

receive projections from the retinal small bistratified ganglion cells, forming the **konio retinogeniculate pathway.** The parvo, magno, and konio systems are referred to as parallel pathways because they each apparently process different aspects of the image that falls upon the retina. As discussed in Chapter 13, the parvo pathway encodes detail and red–green color information, while the magno pathway encodes fast movement. The konio system plays a role in blue–yellow color vision.

The cells of the LGN send most of their axons to the cerebral cortex, the most highly evolved portion of the brain. This structure consists of two hemispheres, connected by the corpus callosum. The cortical area in which most LGN axons synapse is **striate visual cortex.** This region is also referred to as visual area 1 (V1), primary

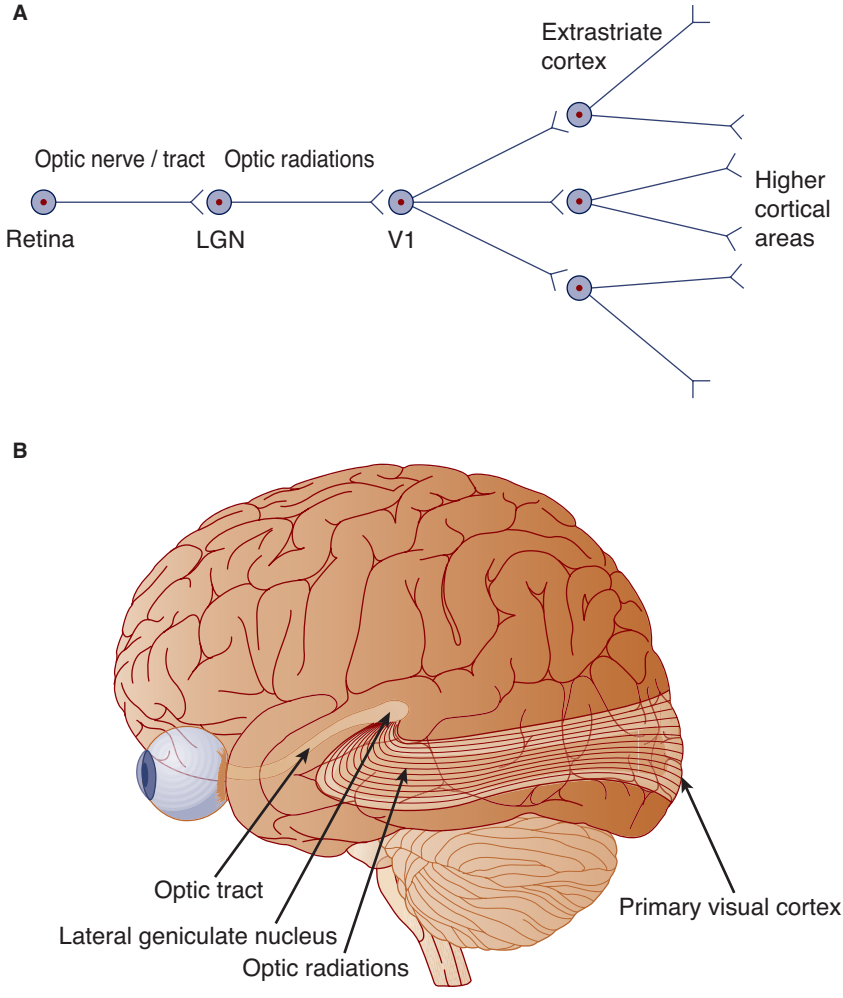

Figure 2–16. **A.** Schematic flow diagram of the retinocortical visual pathway. There is a divergence of information within the cortex. **B.** Sketch of the human brain showing the retinocortical visual pathway. The first postretinal synapse is at the lateral geniculate nucleus (LGN). The LGN projects to striate cortex. (*Reprinted with permission from Hubel DH.* Eye, Brain, and Vision. *New York: Scientific American Library; 1988.*)

visual cortex, and Brodmann area 17. Striate cortex is dominated by foveal input, a phenomenon referred to as the cortical magnification of foveal vision.

Cells in striate cortex send axons to nearby visual cortical areas, which are collectively called **extrastriate visual cortex.** From this point, axons are sent to a great diversity of higher cortical areas that are involved in the integration of visual information with other senses and memory. Importantly, striate cortex also sends a major projection back to the LGN. This feedback loop, which in some

ways is similar to the retinal centrifugal pathway, may be involved in the gating of information.

The anatomical organization of the cortex is, in certain respects, the opposite of that of the retina. Whereas the retina manifests convergence from the photoreceptors to the ganglion cells, there is a divergence within the cortex, with information broadly distributed to a very large number of neurons throughout this structure (see Fig. 2–16A). Information is sent first to areas of extrastriate cortex that are specialized for analyzing attributes such as motion and color, and then to higher centers, which combine visual information with memory and other senses. Higher visual centers, in turn, send information back to striate cortex via backward projections.

The **retinocortical** projection (retina to LGN to striate visual cortex) is constituted of the parvo, magno, and konio retinocortical pathways. While the great majority of retinal ganglion cells contribute to this projection, a smaller percentage synapse in the superior colliculus (tectum), a subcortical area that plays a role in encoding eye movements, and the pulvinar region, a thalamic nucleus associated with visual attention, motion processing, and visually guided movement (Merabet et al., 1998). As discussed in Chapter 14, these pathways, which project to extrastriate, but not striate, cortex may play a role in the phenomenon of blind sight (Rodman et al., 1989; Weiskrantz, 1986).

What are the central projections of the recently discovered melanopsin-containing ganglion cells? In the rat, these photosensitive ganglion cells project to the suprachiasmic nucleus of the hypothalamus, while in the macaque retina they receive rod and cone input and project to the LGN (Berson et al., 2002; Dacey et al., 2005). The functional significance of this later arrangement is not clear.

This book is concerned with the mechanisms by which visual information is analyzed by the retina and the brain proper. Before we begin this discussion, some basic characteristics of light are reviewed.

ELECTROMAGNETIC SPECTRUM

Humans are capable of detecting only a small portion of the electromagnetic (EM) spectrum (Fig. 2–17). Light, or visible radiation, ranges in wavelength from approximately 380 to 700 nm (1 nm = 10^{-9} m). Other wavelengths are not visible, either because the ocular media does not transmit them or because they are not absorbed by the retinal photopigments.

Wavelength and Frequency

The EM spectrum ranges from short-wavelength radiation, such as gamma rays, to long-wavelength radiation, such as AM transmission. Wavelength and frequency of

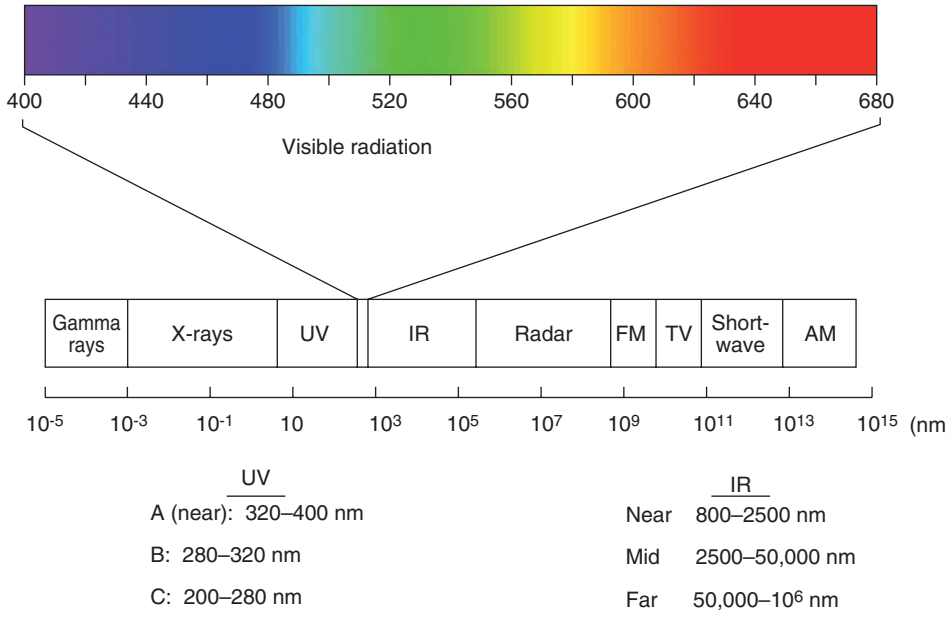

Figure 2–17. Electromagnetic (EM) spectrum. Note that visible radiation (light) takes up a very small portion of the EM spectrum. Below are common designations for ultraviolet (UV) and infrared (IR) radiation. (*Color spectrum courtesy of Dr. Jay Neitz.*)

EM radiation are inversely proportional, as indicated by the following relationship (Fig. 2–18):

$$v = c/\lambda$$

where

v = frequency of light
c = speed of light (3×10^8 m/s)
λ = wavelength of light

The color of light is determined by its wavelength composition. This can be demonstrated by directing white light, which is a mixture of the various wavelengths of light, onto a prism (Fig. 2–19). Because index of refraction is inversely proportional to wavelength, a spectrum of colors is produced. Students traditionally remember the sequence of colors with the acronym **ROY G BIV** (red, orange, yellow, green, blue, indigo, violet).

Dual Nature of Light

Up to now, we discussed EM radiation only in terms of its wave nature. It is, however, often convenient to conceptualize it in terms of its quantal nature. In this

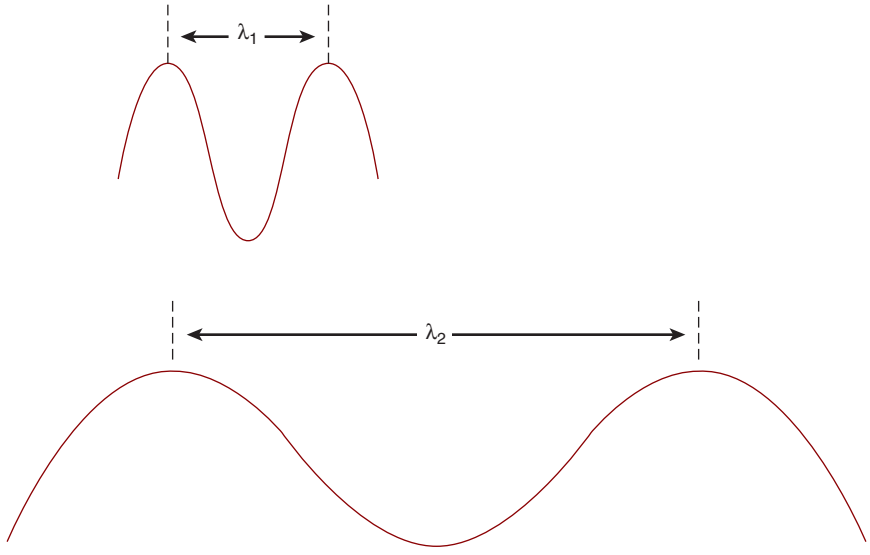

Figure 2–18. λ_1 has a shorter wavelength and a greater frequency than λ_2.

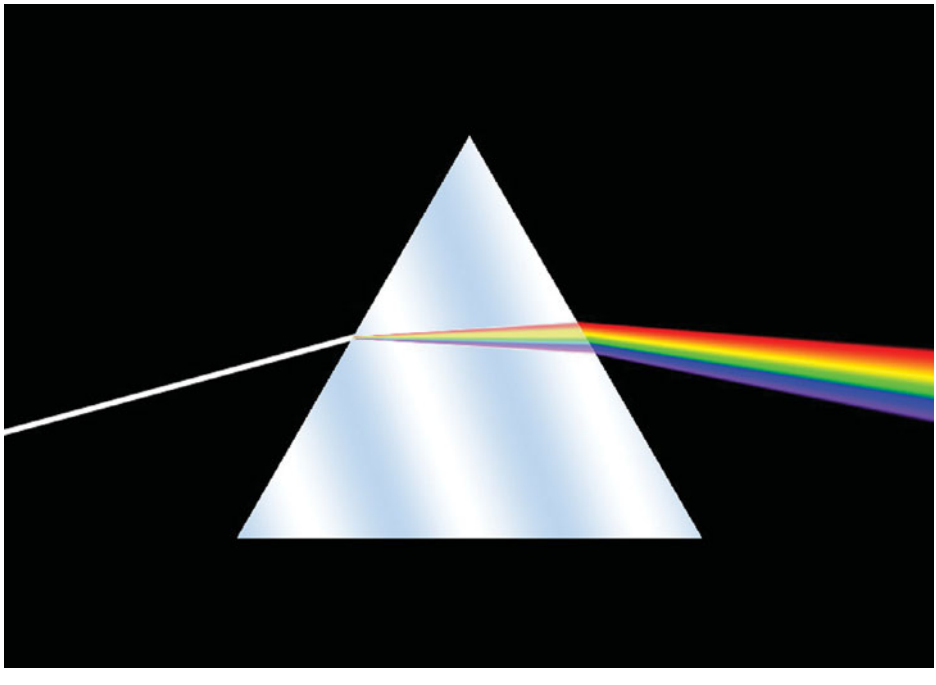

Figure 2–19. A prism breaks up white light into its various components. (*Source:* Wikimedia, Creative Commons ShareAlike 1.0 license, http://creativecommons.org/licenses/sa/1.0/.)

Figure 2–20. Light can be considered as consisting of packets of energy referred to as quanta or photons.

conceptualization, EM radiation consists of discrete packages of energy called **quanta** or **photons** (Fig. 2–20).

The amount of energy in a quantum of light is given by the following relationship:

$$E = hv$$

where

E = energy per quantum
h = Planck's constant (6.626×10^{-37} J/Hz)
v = frequency

or

$$E = hc/\lambda$$

where

c = speed of light (3×10^8 m/s)
λ = wavelength

These relationships show that quanta of short wavelengths have more energy than do quanta of longer wavelengths. This is clinically important because high-energy quanta produce more tissue damage when absorbed than do low-energy quanta.

Because of its short wavelength, ultraviolet (UV) radiation contains much energy per quantum. Consequently, when absorbed by the skin, this radiation can produce substantial cellular damage, including mutations that lead to malignancy. Excessive exposure to UV radiation, as occurs in sunbathing, is a preventable cause of skin carcinoma.

Ultraviolet exposure can damage ocular tissues. Cataract, pinguecula, and pterygium formation are promoted by exposure to UV radiation, and this radiation may also play a role in the development of ARMD. For this reason, it is common for eye care practitioners to recommend spectacles that block UV rays.

TRANSMISSION CHARACTERISTICS OF THE EYE

Atmospheric scatter (for short wavelengths) and absorption eliminate much of the sun's radiation. To protect the sensitive retina upon which EM radiation is focused, the remaining short-wavelength radiation is largely blocked by those ocular

elements that precede the retina. Because long-wavelength radiation contains relatively less energy, its blockage is less critical.

Clinical Highlight

The cornea absorbs much of the very short wavelength UVC radiation (<280 nm; see Fig. 2–17) (Pitts, 1974; Lerman, 1980). Consequently, excess ocular exposure to UVC, as may occur when snow skiing without appropriate sunglasses, can lead to solar keratitis (i.e., corneal inflammation).

The crystalline lens provides most of the protection against UVA and UVB. It can be thought of as a filter that absorbs UV radiation and, thereby, protects the retina. However, this absorption of UV radiation, over many years, damages the lens and can result in cataract formation (Weale, 1983).

During cataract surgery, the crystalline lens is typically replaced with an artificial lens (intraocular lens implant) that contains a UV filter to protect the retina. In those instances where an intraocular lens is not implanted, it is critical that UV protection be provided to the patient. This can be accomplished by including a UV filter in the patient's spectacle lenses.

Because longer wavelengths (>700 nm) contain little energy (compared to shorter wavelengths), their blockage by the ocular media is less critical. Nonetheless, excessive exposure to near-infrared radiation (~1450 nm) can produce a so-called glass blower's cataract (Knowles, 1982). Longer wavelength radiation is not visible because it is not absorbed by the retinal photopigments.

SUMMARY

Electromagnetic radiation incident on the eye is focused on the retina. Those wavelengths that may damage the retina are, for the most part, filtered out by the ocular media.

The cornea provides two-thirds of the refractive power of the eye, with the crystalline lens providing the remaining power. These tissues are nourished by a complex metabolic system that is dependent on the production of aqueous by the ciliary body and its drainage by the canal of Schlemm.

From a teleologic perspective, the purpose of the eye is to focus an image of the world on the retina, a multilayered neural structure, approximately 0.2 mm thick, rich in both the varieties of neurons it contains and the various synaptic connections between these neurons. The retina begins the process of analyzing the image that falls upon it. This analysis is an active process whereby visual information is encoded such that it is useful to higher visual centers. In a very real sense, visual perception begins in the retina, a component of the brain.