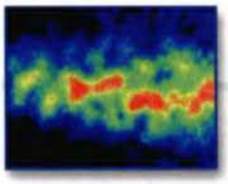


Chapter 11

Vision: The Eye

Overview

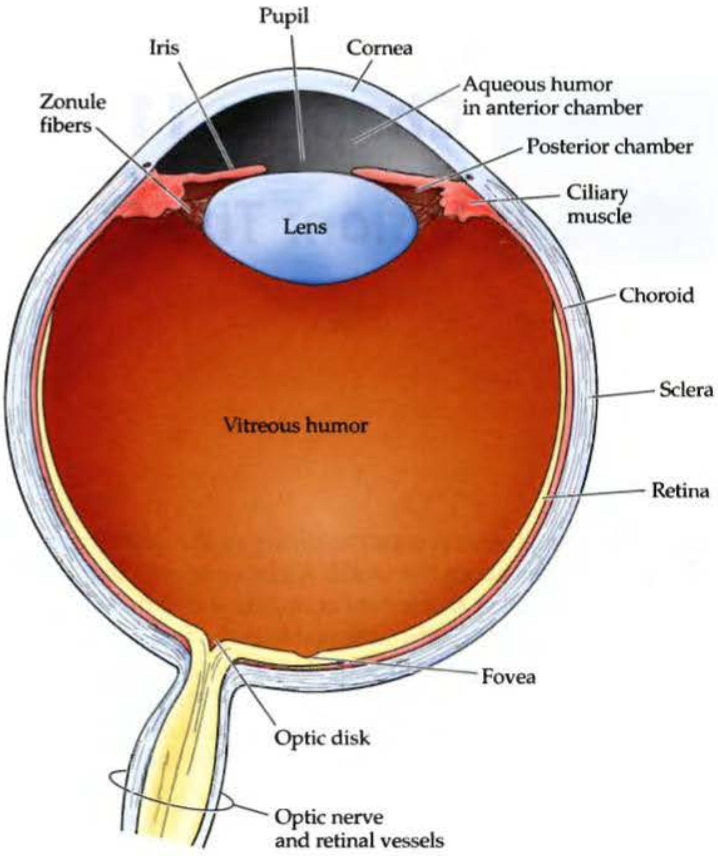
The human visual system is extraordinary in the quantity and quality of information it supplies about the world. A glance is sufficient to describe the location, size, shape, color, and texture of objects and, if the objects are moving, their direction and speed. Equally remarkable is the fact that visual information can be discerned over a wide range of stimulus intensities, from the faint light of stars at night to bright sunlight. The next two chapters describe the molecular, cellular, and higher order mechanisms that allow us to see. The first steps in the process of seeing involve transmission and refraction of light by the optics of the eye, the transduction of light energy into electrical signals by photoreceptors, and the refinement of these signals by synaptic interactions within the neural circuits of the retina.

Anatomy of the Eye

The eye is a fluid-filled sphere enclosed by three layers of tissue (Figure 11.1). Only the innermost layer of the eye, the **retina**, contains neurons that are sensitive to light and are capable of transmitting visual signals to central targets. The immediately adjacent layer of tissue includes three distinct but continuous structures collectively referred to as the **uveal tract**. The largest component of the uveal tract is the **choroid**, which is composed of a rich capillary bed (important for nourishing the photoreceptors of the retina) as well as a high concentration of the light absorbing pigment melanin. Extending from the choroid near the front of the eye is the **ciliary body**, a ring of tissue that encircles the **lens** and consists of a muscular component that is important for adjusting the refractive power of the lens, and a vascular component (the so-called ciliary processes) that produces the fluid that fills the front of the eye. The most anterior component of the uveal tract is the **iris**, the colored portion of the eye that can be seen through the cornea. It contains two sets of muscles with opposing actions, which allow the size of the **pupil** (the opening in its center) to be adjusted under neural control. The **sclera** forms the outermost tissue layer of the eye and is composed of a tough white fibrous tissue. At the front of the eye, however, this opaque outer layer is transformed into the **cornea**, a specialized transparent tissue that permits light rays to enter the eye.

Beyond the cornea, light rays pass through two distinct fluid environments before striking the retina. In the **anterior chamber**, just behind the cornea and in front of the lens, lies **aqueous humor**, a clear, watery liquid that supplies nutrients to both of these structures. Aqueous humor is produced by the ciliary processes in the **posterior chamber** (the region between the lens and the iris) and flows into the anterior chamber through the pupil. The amount of fluid produced by the ciliary processes is substantial: it is estimated that the entire volume of fluid in the anterior chamber is replaced 12 times a day. Thus the rates of

Figure 11.1 Anatomy of the human eye.



aqueous humor production must be balanced by comparable rates of drainage from the anterior chamber in order to ensure a constant intraocular pressure. A specialized meshwork of cells that lies at the junction of the iris and the cornea—a region called the **limbus**—is responsible for aqueous drainage. Failure of adequate drainage results in a disorder known as **glaucoma**, in which high levels of intraocular pressure can reduce the blood supply to the eye and eventually damage retinal neurons.

The space between the back of the lens and the surface of the retina is filled with a thick, gelatinous substance called the **vitreous humor**, which accounts for about 80% of the volume of the eye. In addition to maintaining the shape of the eye, the vitreous humor contains phagocytic cells that remove blood and other debris that might otherwise interfere with light transmission. The housekeeping abilities of the vitreous humor are limited, however, as a large number of middle-aged and elderly individuals with vitreal "floaters" will attest. Floaters are collections of debris too large for phagocytic consumption that therefore remain to cast annoying shadows on the retina; they typically arise when the aging vitreous membrane pulls away from the overly long eyeball of myopic individuals (Box 11A).

The Formation of Images on the Retina

Normal vision requires that the optical media of the eye be transparent, and both the cornea and the lens are remarkable examples of tissue specialization, achieving a level of transparency that rivals that found in inorganic materials such as glass. Not surprisingly, alterations in the composition of the cornea or the lens can significantly reduce their transparency and have serious consequences for visual perception. Indeed, opacities in the lens known as **cataracts** account for

BOX 11A Myopia and Other Refractive Errors

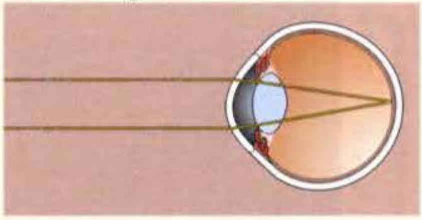
Discrepancies of the various physical components of the eye cause a majority of the human population to have some form of refractive error, called **ametropia**. People who are unable to bring distant objects into clear focus are said to be nearsighted, or myopic (Figure B). **Myopia** can be caused by the corneal surface being too curved, or by the eyeball being too long. In either case, with the lens as flat as it can be, the image of distant objects focuses in front of, rather than on, the retina.

People who are unable to focus on near objects are said to be farsighted, or hyperopic. **Hyperopia** can be caused by the eyeball being too short or the refracting system too weak (Figure C). Even with the lens in its most rounded-up state, the image is out of focus on the retinal surface (focusing at some point behind it). Both myopia and hyperopia are correctable by appropriate lenses—concave (minus) and convex (plus), respectively—or by the increasingly popular technique of corneal surgery.

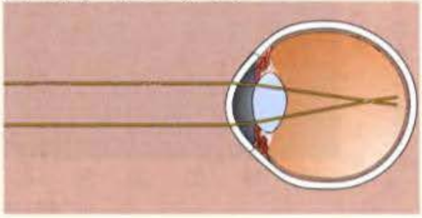
Myopia is by far the most common ametropia; an estimated 50 percent of the U.S. population is affected. Given the large number of people who need glasses, contact lenses, or surgery to correct this refractive error, one naturally wonders how nearsighted people coped before spectacles were invented only a few centuries ago. From what is now known about myopia, most people's vision may have been considerably better in ancient times. The basis for this assertion is the surprising finding that the growth of the eyeball is strongly influenced by focused light falling on the retina. This phenomenon was first described in 1977 by Torsten Wiesel and Elio Raviola at Harvard Medical School, who studied monkeys reared with their lids sutured (the same approach used to demonstrate the effects of visual deprivation on cortical connections in the visual system; see Chapter 24), a procedure that deprives the eye of focused retinal images. They found that animals growing to maturity under these conditions show an elongation of the eyeball. The effect of focused light deprivation appears to be a local one, since the abnormal growth of the eye occurs in experimental animals even if the optic nerve is cut. Indeed, if only a portion of the retinal surface is deprived of focused light, then only that region of the eyeball grows abnormally.

Although the mechanism of light-mediated control of eye growth is not fully understood, many experts now believe that the modern prevalence of myopia may be due to some aspect of modern civilization—perhaps learning to read and write at an early age—that interferes with the normal feedback control of vision on eye development, leading to abnormal elongation of the eyeball. A corollary of this hypothesis is that if children (or, more likely, their parents) wanted to improve their vision, they might be able to do so by practicing far vision to counterbalance the near-work "overload." Practically, of course, most people would probably choose wearing glasses or contacts or having corneal surgery rather than indulging in the onerous daily practice that would presumably be required. Furthermore, not everyone agrees that such a remedy would be effective, and a number of investigators (and drug companies) are exploring the possibility of pharmacological intervention during the period of childhood when abnormal eye growth is presumed to occur. In any event, it is a remarkable fact that deprivation of focused light on the retina causes a compensatory growth of the eye and that this feedback loop is so easily perturbed.

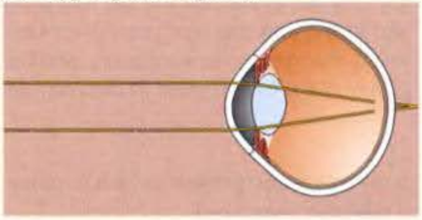
(A) Emmetropia (normal)



(B) Myopia (nearsighted)



(C) Hyperopia (farsighted)



Refractive errors. (A) In the normal eye, with ciliary muscles relaxed, an image of a distant object is focused on the retina. (B) In myopia, light rays are focused in front of the retina. (C) In hyperopia, images are focused at a point beyond the retina.

Even people with normal (**emmetropic**) vision as young adults eventually experience difficulty focusing on near objects. One of the many consequences of aging is that the lens loses its elasticity; as a result, the maximum curvature the lens can achieve when the ciliary muscle contracts is gradually reduced. The near point (the closest point that can be brought into clear focus) thus recedes, and objects (such as this book) must be farther and farther away from the eye in order to focus them on the retina. At some point, usually during early middle age, the accommodative ability of the eye is so reduced that near vision tasks like reading become difficult or impossible (Figure D). This condition is referred to as **presbyopia**. Presbyopia can be corrected by convex lenses for near-vision tasks, or by bifocal lenses

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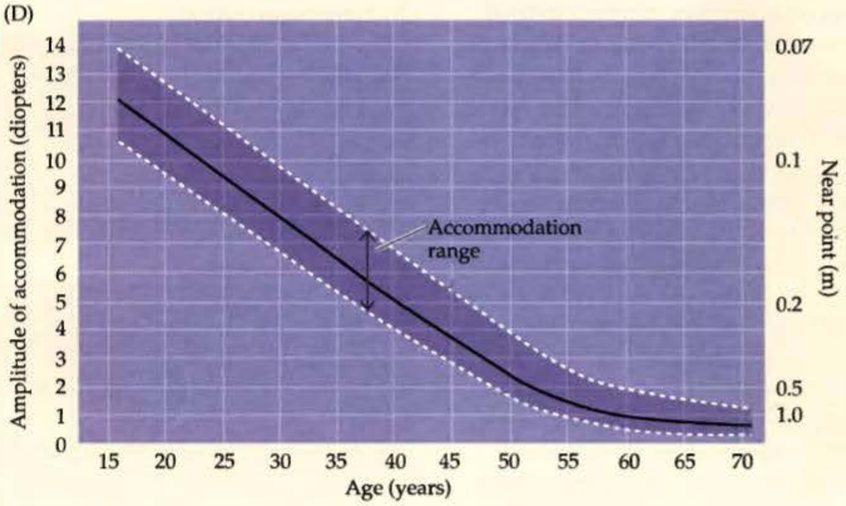
BOX 11A *(Continued)*



(D) Changes in the ability of the lens to round up (accommodate) with age. The graph also shows how the near point (the closest point to the eye that can be brought into focus) changes. Accommodation, which is an optical measurement of the refractive power of the lens, is given in diopters. (After Westheimer, 1974.)

if myopia is also present (which requires a negative correction).

Bifocal correction presents a particular problem for those who prefer contact lenses. Because contact lenses float on the surface of the cornea, having the distance correction above and the near correction below (as in conventional bifocal glasses) doesn't work (although "omnifocal" contact lenses have recently been used with some success). A surprisingly effective solution to this problem for some contact lens wearers has been to put a near correcting lens in one eye and a distance correcting lens in the other! The success of this approach is another testament to the remarkable ability of the visual system to adjust to a wide variety of unusual demands.

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roughly half the cases of blindness in the world, and almost everyone over the age of 70 will experience some loss of transparency in the lens that ultimately degrades the quality of visual experience. Fortunately, successful surgical treatments for cataracts can restore vision in most cases. Furthermore, the recognition that a major factor in the production of cataracts is exposure to ultraviolet (UV) solar radiation has heightened public awareness of the need to protect the lens (and the retina) by reducing UV exposure through the use of sunglasses.

Beyond efficiently transmitting light energy, the primary function of the optical components of the eye is to achieve a focused image on the surface of the retina. The cornea and lens are primarily responsible for the refraction (bending) of light necessary for the formation of focused images on the photoreceptors of the retina (Figure 11.2). The cornea contributes most of the necessary refraction, as can be appreciated by considering the hazy, out-of-focus images experienced when swimming underwater. Water, unlike air, has a refractive index close to that of the cornea; as a result, immersion in water virtually eliminates the refraction that normally occurs at the air/cornea interface; thus the image is no longer focused on the retina. The lens has considerably less refractive power than the cornea; however, the refraction supplied by the lens is adjustable, allowing objects at various distances from the observer to be brought into sharp focus.

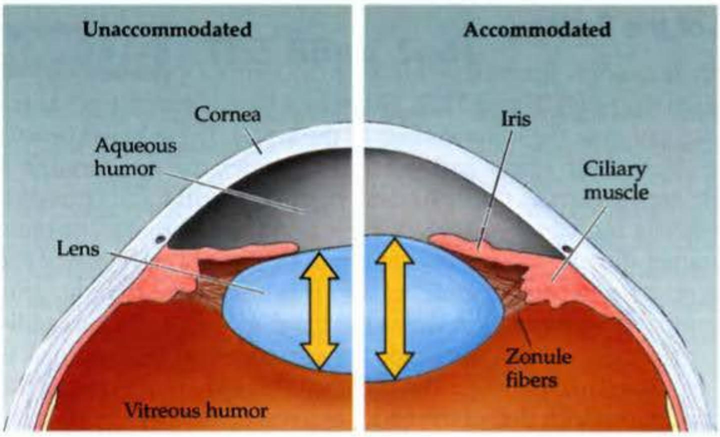

Figure 11.2 Diagram showing the anterior part of the human eye in the unaccommodated (left) and accommodated (right) state. Accommodation for focusing on near objects involves the contraction of the ciliary muscle, which reduces the tension in the zonule fibers and allows the elasticity of the lens to increase its curvature.

Dynamic changes in the refractive power of the lens are referred to as **accommodation**. When viewing distant objects, the lens is made relatively thin and flat and has the least refractive power. For near vision, the lens becomes thicker and rounder and has the most refractive power (see Figure 11.2). These changes result from the activity of the **ciliary muscle** that surrounds the lens. The lens is held in place by radially arranged connective tissue bands called **zonule fibers** that are attached to the ciliary muscle. The shape of the lens is thus determined by two opposing forces: the elasticity of the lens, which tends to keep it rounded up (removed from the eye, the lens becomes spheroidal); and the tension exerted by the zonule fibers, which tends to flatten it. When viewing distant objects, the force from the zonule fibers is greater than the elasticity of the lens, and the lens assumes the flatter shape appropriate for distance viewing. Focusing on closer objects requires relaxing the tension in the zonule fibers, allowing the inherent elasticity of the lens to increase its curvature. This relaxation is accomplished by the sphincter-like contraction of the ciliary muscle. Because the ciliary muscle forms a ring around the lens, when the muscle contracts, the attachment points of the zonule fibers move toward the central axis of the eye, thus reducing the tension on the lens. Unfortunately, changes in the shape of the lens are not always able to produce a focused image on the retina, in which case a sharp image can be focused only with the help of additional corrective lenses (see Box 11A).

Adjustments in the size of the pupil also contribute to the clarity of images formed on the retina. Like the images formed by other optical instruments, those generated by the eye are affected by spherical and chromatic aberrations, which tend to blur the retinal image. Since these aberrations are greatest for light rays that pass farthest from the center of the lens, narrowing the pupil reduces both spherical and chromatic aberration, just as closing the iris diaphragm on a camera lens improves the sharpness of a photographic image. Reducing the size of the pupil also increases the depth of field—that is, the distance within which objects are seen without blurring. However, a small pupil also limits the amount of light that reaches the retina, and, under conditions of dim illumination, visual acuity becomes limited by the number of available photons rather than by optical aberrations. An adjustable pupil thus provides an effective means of reducing optical aberrations, while maximizing depth of field to the extent that different levels of illumination permit. The size of the pupil is controlled by innervation from both sympathetic and parasympathetic divisions of the visceral motor system, which in turn are modulated by several brainstem centers (see Chapters 20 and 21).

The Surface of the Retina

Using an ophthalmoscope, the inner surface of the retina, or **fundus**, can be visualized through the pupil (Figure 11.3). Numerous blood vessels, both arteries and veins, fan out over the inner surface of the retina. These blood vessels arise from the ophthalmic artery and vein, which enter the eye through a whiteish circular area known as the **optic disk** or **optic papilla**. The optic disk is also the site where retinal axons leave the eye and travel through the optic nerve to reach target structures in the thalamus and midbrain. This region of the retina contains no photoreceptors and, because it is insensitive to light, produces the perceptual phenomena known as the blind spot (Box 11B). In addition to being a conspicuous retinal landmark, the appearance of the optic disk is a useful gauge of intracranial pressure. The subarachnoid space surrounding the optic nerve is continuous with that of the brain; as a result, increases in intracranial pressure—a sign of serious neurological problems such as space-occupying lesions—can be detected as a swelling of the optic disk.

Another prominent feature of the fundus is the **macula lutea**, an oval spot containing yellow pigment (xanthophyll), roughly 1.5 millimeters in diameter and located near the center of the retina. The macula is the region of the retina that supports high visual acuity (the ability to resolve fine details). Acuity is greatest at the center of the macula, a small depression or pit in the retina called the **fovea**. The pigment xanthophyll has a protective role, filtering ultraviolet wavelengths that could be harmful to the photoreceptors. Damage to this region of the retina, as occurs in age-related macular degeneration has a devastating impact on visual perception (Box 11C).

Retinal Circuitry

Despite its peripheral location, the retina, which is the neural portion of the eye, is actually part of the central nervous system. During development, the retina forms as an outpocketing of the diencephalon called the optic vesicle. The optic

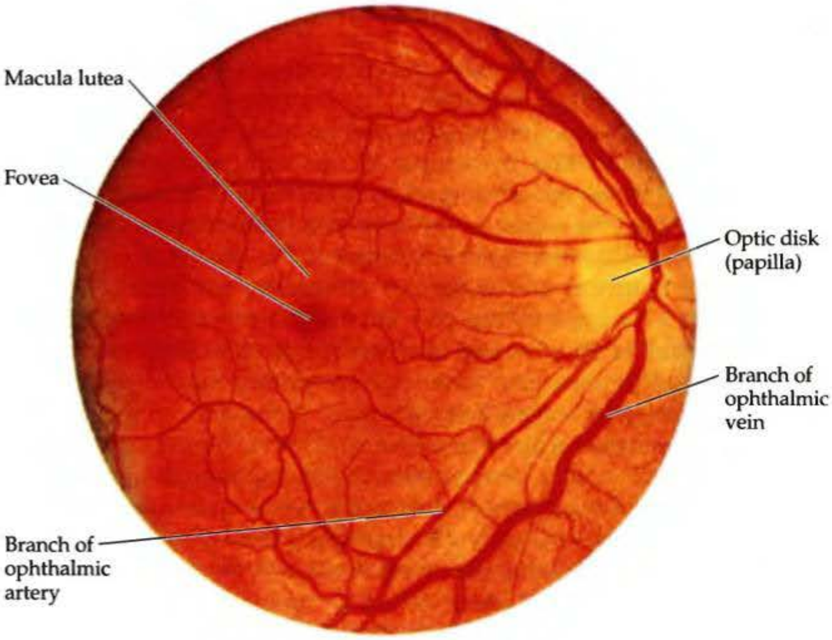

Figure 11.3 The inner surface of the retina, viewed with an ophthalmoscope. The optic disk is the region where the ganglion cell axons leave the retina to form the optic nerve; it is also characterized by the entrance and exit, respectively, of the ophthalmic arteries and veins that supply the retina. The macula lutea can be seen as a distinct area at the center of the optical axis (the optic disk lies nasally); the macula is the region of the retina that has the highest visual acuity. The fovea is a depression or pit about 1.5 mm in diameter that lies at the center of the macula.