PART I

THE EYE AND VISUAL PATHWAYS

CHAPTER 1

INTRODUCTION

The physicist Richard Feynman once illustrated the extraordinary nature of vision as follows: We are immersed in a sea of electromagnetic waves whose lengths vary over a huge range (Figure 1.1). These waves interact with each other and with objects around us to present a cacophony of electromagnetic signals to our eyes. Through a tiny aperture, about 2 mm in diameter, the eye selects a small fraction of these wavelengths and, together with the brain, reconstructs the position, shape, color, and motion of each object we see around us. Feynman compared the situation to that of a water bug floating on the surface at one corner of a swimming pool. The only information available to the bug comes from the movements of its body caused by the waves that reach it. Were the bug able to reconstruct from these waves the positions and motions of all the people entering, leaving, and swimming in the pool, it would be doing something similar to what the eye and brain do with the minuscule electromagnetic disturbances passing through the pupil.

Why does the eye normally respond only to electromagnetic energy with wavelengths in the range 400–700 nm (1 nm = 10^{-9} m)? To answer this question, one must ask what electromagnetic energy was available to the earliest living forms that developed vision. The major source of such energy reaching the surface of the earth is the sun, which emits radiation with the spectrum shown in Figure 1.2. Note that the energy peaks near 500 nm, within the visual range, but it also extends to longer and shorter

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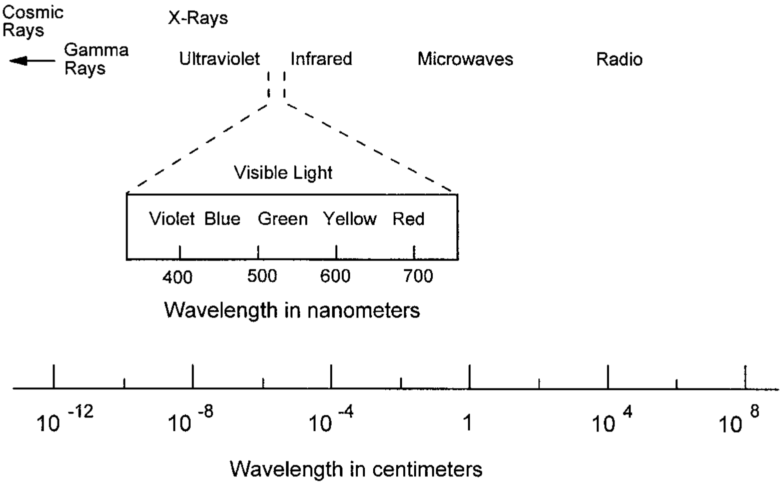

Figure 1.1. The electromagnetic spectrum.

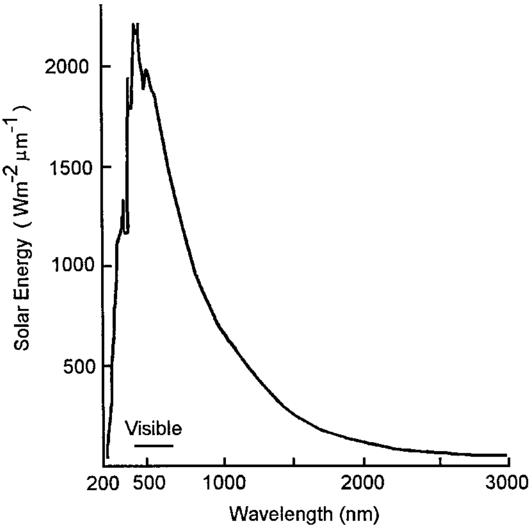

Figure 1.2. Solar-energy spectrum outside the atmosphere. (Reprinted, with permission, from D. M. Gates: Spectral distribution of solar radiation at the earth's surface. *Science* 151:523–8. Copyright 1966, American Association for the Advancement of Science.)

wavelengths. As this solar radiation passes through the atmosphere, the intensity of ultraviolet rays is reduced by the ozone layer, and that of infrared rays by water vapor, narrowing the effective range of wavelengths reaching the earth's surface. Further filtering occurs in sea water, which exhibits a window of minimal attenuation at those wavelengths we call light.

Figure 1.3 compares the spectral content of light above and below the ocean's surface with the spectral sensitivities of the rod and cone systems of human vision. (Differences between the two types of photoreceptors subserving these systems will be discussed later.) Our eyes, like those of many other animals, detect that narrow range of wavelengths available beneath the surface of the sea, where the earliest visual systems emerged. Some animals, such as certain species of birds and insects, can see ultraviolet light, but even this sensitivity is restricted to the so-called near-ultraviolet, wavelengths not much shorter than those sensed by our own eyes. Pit vipers can sense infrared radiation, but they do this with specialized somatic sensory receptors, not with their eyes.

In order to use the energy available from the sun, the earliest living organisms required molecules with very special properties. First, these molecules had to absorb the available electromagnetic energy without being destroyed, and then they had to divert the energy in some way to useful biological processes. Several molecules emerged to accomplish this, perhaps the most important of which is chlorophyll. Virtually all living creatures depend directly or indirectly on the ability of chlorophyll-containing cells to synthesize carbohydrates from carbon dioxide and water and release oxygen into the environment. In fact, the development of the ozone layer required the evolution of photosynthesis in microorganisms of the sea, a process that made terrestrial life possible by shielding nucleic acids and other vital cellular elements from destructive ultraviolet radiation.

Phototropism in plants and vision in animals depend largely on another group of compounds, the carotenoids. A special class of these, the retinoids, play important roles in development and cell metabolism through actions that are still imperfectly understood. They may act as cofactors in important biochemical reactions and may also regulate gene expression. One of these retinoids, the 11-*cis* isomer of retinal, is the aldehyde of vitamin A and has the important property of changing shape when it absorbs light within the band of wavelengths available from the sun. The visual photopigments in all multicellular animals are formed by combining 11-*cis* retinal, the chromophore, with a large, membrane-bound protein called an opsin. The opsins of visual photopigments are members of a large family of membrane-spanning molecules, most of which sense chemical stimuli outside the cell and regulate critical biochemical processes within the cell.

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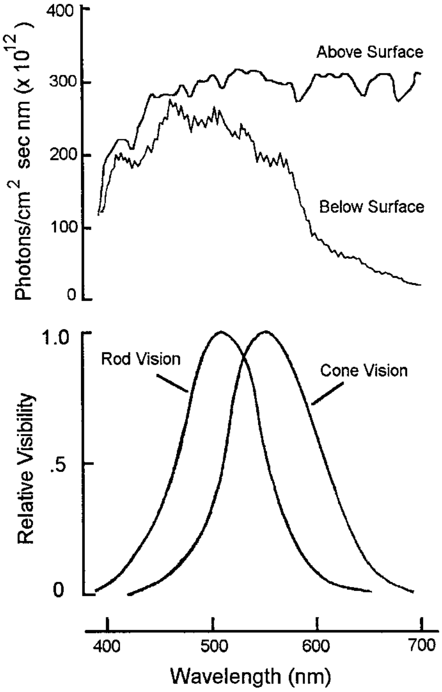

Figure 1.3. Top panel: Comparison of solar spectra measured just above and 3 m below the surface of the clear tropical sea at Eniwetok. (Reprinted from W. N. McFarland and F. W. Munz: The photic environment of clear tropical seas during the day. *Vision Research* 15:1063–70. Copyright 1975, with kind permission from Elsevier Science, Ltd., The Boulevard, Langford Lane, Kidlington OX5 1GB, United Kingdom.) Bottom panel: Spectral sensitivities of human rod and cone vision. (Reprinted from S. Hecht and R. E. Williams: The visibility of monochromatic radiation and the absorption spectrum of visual purple. *Journal of General Physiology* 5:1–34. Copyright 1922, with permission of the Rockefeller University Press.)

Figure 1.4 illustrates schematically the family resemblance of some of the better known of these membrane receptors.

Just as the cow's opsin of Figure 1.4 is related structurally to various membrane receptors of humans, hamsters, turkeys, and pigs, the photopigment opsins of various species bear striking similarities in their amino acid sequences, indicating that they are derived from an ancient common ancestor. The diagram of Figure 1.5 illustrates schematically the resemblances among several opsins from species as evolutionarily divergent as fruit flies and humans: The greater the sequence similarity of any two opsins, the shorter the distances along the line segments connecting them.

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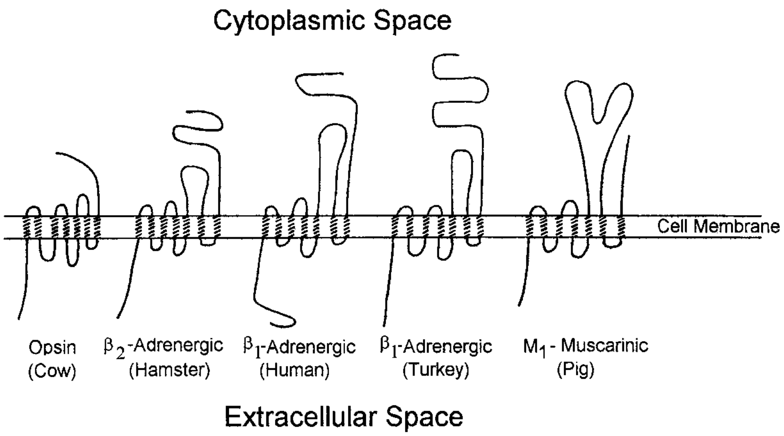

Figure 1.4. Examples from a family of membrane-spanning proteins serving photoreception (far left) and receptors for adrenergic and muscarinic cholinergic neurotransmitters. All have seven transmembrane segments, but their intracellular and extracellular domains differ in length. (Adapted from E. R. Weiss, D. J. Kelleher, C. W. Woon, S. Soparkar, S. Osawa, L. E. Heasley, and G. L. Johnson: Receptor activation of G proteins. *FASEB Journal* 2:2841–8, 1994, with permission of the Federation of American Societies for Experimental Biology.)

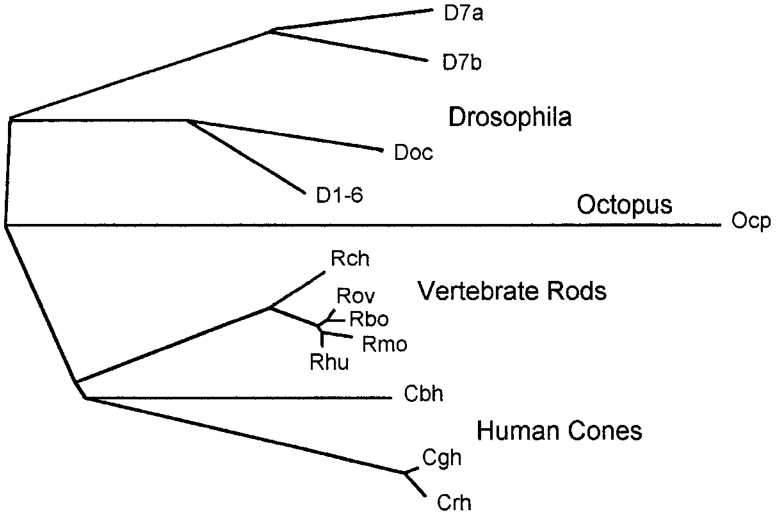

Figure 1.5. Evolutionary distances between various opsins. The distance along a line connecting two opsins reflects the difference in their amino acid compositions. D, *Drosophila* rhodopsins; Ocp, octopus rhodopsin. Vertebrate rod opsins: Rch, chicken; Rbo, cow; Rov, sheep; Rmo, mouse; Rhu, human. Human cone opsins: Cbh, Cgh, and Crh are human short-, medium-, and long-wavelength cones, respectively. (Adapted from T. H. Goldsmith: Optimization, constraint, and history in the evolution of eyes. *Quarterly Review of Biology* 65:281–322, 1990, with permission of The University of Chicago Press.)

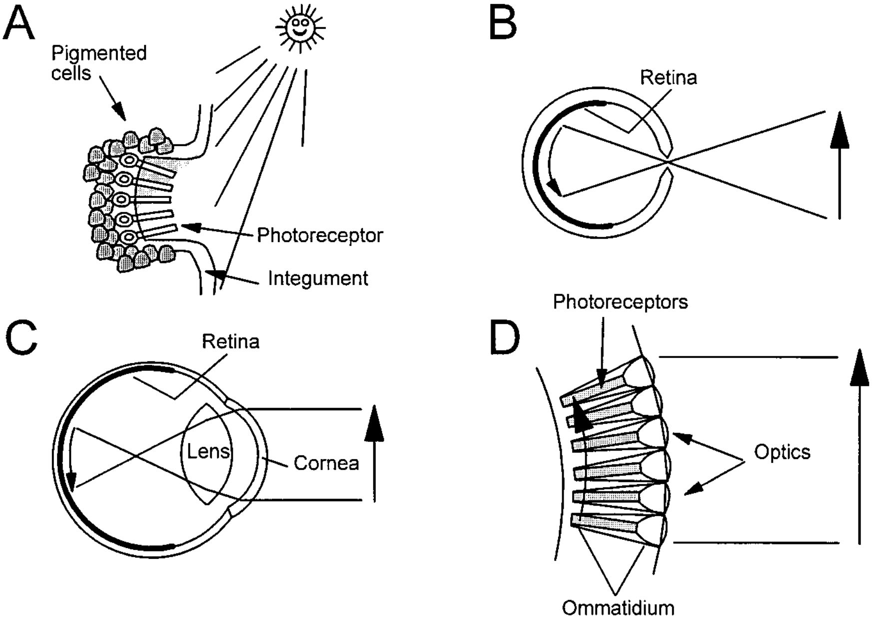

Figure 1.6. Varieties of eyes. (A) An eye spot, such as that found in *Planaria*. (B) An eye that uses a pin-hole aperture to form images. Such an eye occurs in *Nautilus*. (C) Vertebrate-type camera eye using a lens and cornea for image formation. (D) Compound eye, such as that of the horseshoe crab, *Limulus polyphemus*.

Even though the photopigments of all animals share a common ancestor, this is not true of their eyes. Vertebrate and invertebrate eyes differ in many important ways, and no definite ancestral link has been established between them. The same can be said for various forms of eyes among invertebrates. The most primitive eyes probably were clusters of photosensitive cells gathered together in pigmented pits called eye spots (Figure 1.6A). Eye spots serve to signal relative degrees of light and darkness and appear to have evolved independently many times. The pigmented cells lining the pit bestow some directional sensitivity on the eye spot by preventing light from reaching the photoreceptors through the often transparent bodies of the small invertebrate animals. If the pits are deep enough, shadows cast by the walls of the pit on different parts of the receptor array provide additional directional information, which can serve an animal well when it needs to escape at the sudden appearance of a predator's shadow.

A great advance in vision came with the development of eyes capable of collecting light and forming images on the array of photoreceptors. Although these eyes take many shapes throughout the animal kingdom,

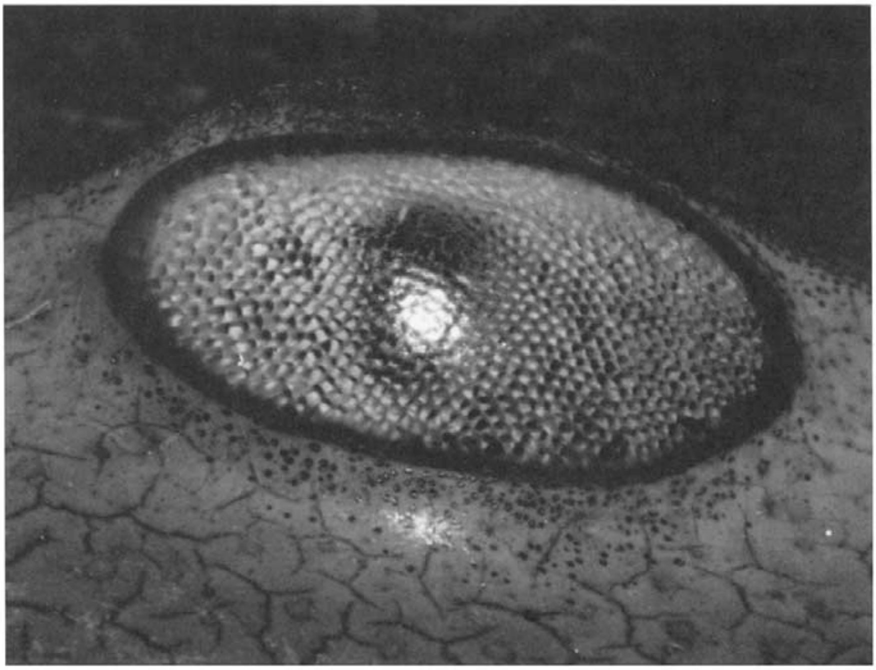

Figure 1.7. Lateral eye of *Limulus polyphemus*. The multiple facets of this compound eye are evident in the photograph. The central dark pseudopupil is caused by absorption of incident light within the ommatidia. (Reprinted, with permission, from W. W. Weiner and S. C. Chamberlain: The visual fields of American horseshoe crabs: two different eye shapes in *Limulus polyphemus*. *Visual Neuroscience* 11: 333–46, 1994.)

they can conveniently be divided into camera eyes and compound eyes. Camera eyes resemble photographic cameras in having a single chamber and an optical mechanism for forming an image of the outside world on a photosensitive surface, the retina. The camera eyes of invertebrates are often referred to as ocelli (singular, ocellus) and, sometimes, as simple eyes. The image-forming apparatus may be a tiny hole in the eyecup, resembling that of a pin-hole camera (Figure 1.6B), or some combination of a cornea and lens, such as occurs in vertebrates (Figure 1.6C). Compound eyes are found only in invertebrates and are composed of repeating modules called ommatidia, each with its own photoreceptors and imaging apparatus (Figures 1.6D and 1.7). In some compound eyes the adjacent ommatidia are optically isolated by pigment-containing cells; in others, an image is formed cooperatively by neighboring ommatidia.

Whereas vertebrates have only camera eyes, invertebrates can have both camera eyes and compound eyes. In addition to its two lateral compound eyes, *Limulus polyphemus*, the horseshoe crab, has four ocelli located in various places. Spiders and scorpions have 6–8 ocellar eyes, but no compound eyes. The scallop *Pecten* has about 60 simple eyes located along the edge of its mantle, which are of additional interest because they form images by reflection from a mirror-like structure behind the photoreceptors.

Eyes are composed of a variety of different tissues, brought together during development by a sequence of genetic signals that are still poorly understood. Important components of the vertebrate eye actually have their origin in the developing central nervous system and are incorporated into the peripheral organ of sight by a process of great complexity. In Chapter 2, we explore the basic components of the human eye and the processes that lead to its formation.

Further Reading

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CHAPTER 2

STRUCTURE AND DEVELOPMENT OF THE HUMAN EYE

Major Anatomic Features of the Eye

Figure 2.1 illustrates schematically the major components of the human eye, which resembles that of most other primates. The sclera is a tough outer coat that is fibrous in humans but contains bone or cartilage in some other vertebrate species. The cornea is continuous with the sclera and provides the first element of the refracting media that bend the light to form an image on the retina. The lens lies behind the iris and in front of the vitreous humor, which fills the greater part of the globe. Aqueous humor fills the posterior chamber (the space between the lens and iris) and the anterior chamber (the space between the iris and the cornea). The posterior and anterior chambers are continuous through the pupil, the aperture formed by the iris.

The general features of the retina, the multilayered neural structure lining the back of the eyeball, can be visualized in the living eye with an ophthalmoscope or special camera (Figure 2.2). Axons leave the retina through the optic disc or optic papilla and enter the optic nerve to reach the brain. At the posterior pole of the eye, the retina thins to form the fovea, an area specialized for high-acuity vision. The visual axis is an imaginary line from the fovea through the center of the pupil (Figure 2.1). Behind the retina is the pigment epithelium, which is separated from the sclera by the vascular choroid. This vascular coat is continuous with similar