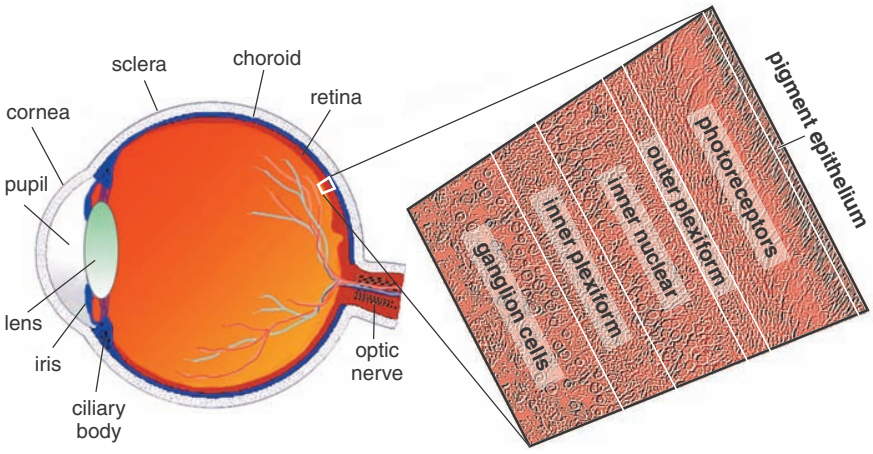

Figure 2. Diagram of a human eye shows its various structures *(left)*. A thin piece of retina is enlarged in a photomicrograph *(right)*, revealing its layers. The photoreceptors lie against a dark row of cells called the pigment epithelium. (Drawing by the author. Except where noted, photographs by Nicolas Cuenca and the author.)

the light continues to shine on them and do not release a neurotransmitter.

Although both rods and cones respond to light with a slow hyperpolarizing response, they report quite different image properties. Rods, detecting dim light, usually respond to relatively slow changes. Cones, dealing with bright signals, can detect rapid light fluctuations. In both cases, photoreceptors begin the process of decomposing images into separate parts. Both rods and cones respond to light directly over them. Thus, their *receptive fields* are very narrow.

An image continues to be broken into component elements at the first synapses of the visual pathway, those between photoreceptors and bipolar cells. Different bipolar cells have different types of receptors for the neurotransmitter glutamate, allowing the cells to respond to photoreceptor input differently *(Figure 7)*. Some bipolar cells are tuned to faster and some to slower fluctuations in the visual signal; some glutamate receptors resensitize rapidly and others more gradually. The cells thus fire either quickly in succession or relatively slowly in response to the same amount of stimulation. These receptors respond to glutamate by activating what's known as an OFF pathway in the visual process, detecting dark images against a lighter background. (Recall that photoreceptors constantly release glutamate unless exposed to light.) Other bipolar cells have inhibitory glutamate receptors; in other words, they prevent the bipolar cell from firing when the cell is exposed to the neurotransmitter. These receptors activate the ON pathway, detecting light images against a darker background.

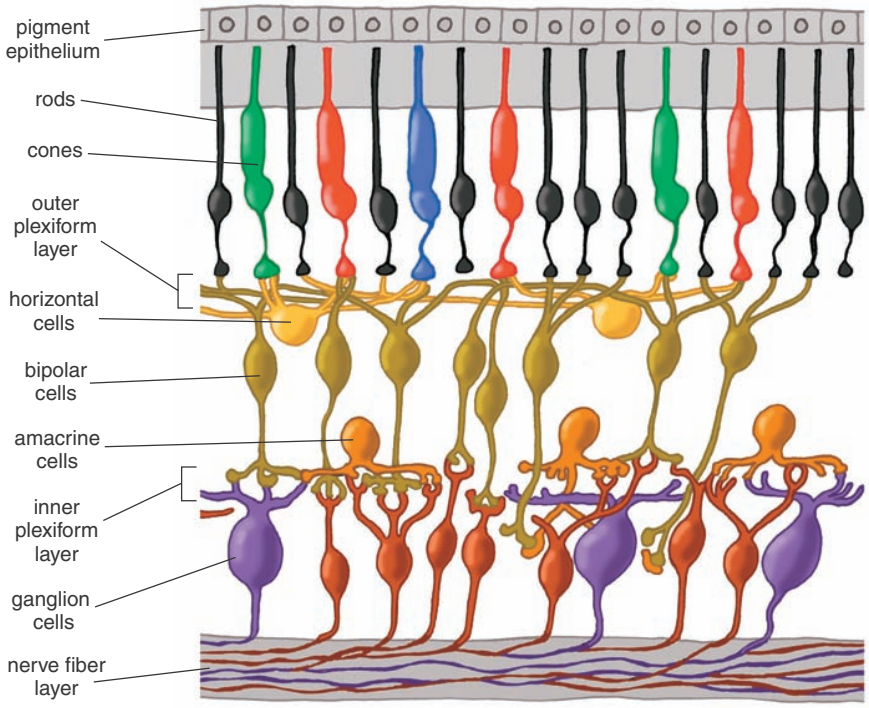

Figure 3. Cells in the retina are arrayed in discrete layers. The photoreceptors are at the top of this rendering, close to the pigment epithelium. The bodies of horizontal cells and bipolar cells compose the inner nuclear layer. Amacrine cells lie close to ganglion cells near the surface of the retina. Axon-to-dendrite neural connections make up the plexiform layers separating rows of cell bodies.

Parallel Processing

The parallel sets of visual channels for ON (detecting light areas on dark backgrounds) and OFF (detecting dark areas on light backgrounds) qualities of an image are fundamental to our seeing. Vertebrate vision depends on perceiving the contrast between images and their backgrounds. For example, we read black letters against a white background using the OFF channels that start in the retina. Parallel bipolar channels transmit inputs to ganglion cells. Early in development the architecture of the inner plexiform layer, full of synapses between bipolar and ganglion cells, shows that synaptic connections become segregated in distinct, parallel pathways. Connections occur between ON bipolar cells and ON ganglion cells and also between OFF bipolar cells and OFF ganglion cells in demarcated portions of the inner plexiform layer.

If the retina were simply to transmit opposite-contrast images directly from the photoreceptors to the brain, the resulting vision would probably be coarse-grained and blurry. Further processing in the retina defines precise edges to images and allows us to focus on fine details. The honing of the image starts at the first synaptic level in the retina, where horizontal cells receive input from cones. Each horizontal cell actually receives input from many cones, so its collection area or *receptive field* is large. Horizontal cells' receptive fields become even broader because