Figure 21–16 Long-range horizontal connections in each layer of the visual cortex integrate information from different parts of the visual field.

A. The axons of pyramidal cells extend for many millimeters parallel to the cortical surface. Axon collaterals form connections with other pyramidal cells as well as with inhibitory interneurons. This arrangement enables neurons to integrate information over large parts of the visual field. An important characteristic of these connections is their relationship to the functional columns. The axon collaterals are found in clusters (**arrows**) at distances greater than 0.5 mm from the cell body. (Reproduced, with permission, from Gilbert and Wiesel 1983. Copyright © 1983 Society for Neuroscience.)

B. Horizontal connections link columns of cells with similar orientation specificity.

C. The pattern of horizontal connections is visualized by injecting an adenoviral vector containing the gene encoding green fluorescent protein into one orientation column and superimposing the labeled image (**black**) on an optically imaged map of the orientation columns in the vicinity of the injection. (Diameter of white circle is 1 mm.) (Reproduced, with permission, from Stettler et al. 2002.)

Visual Information Is Represented by a Variety of Neural Codes

Individual neurons in a sensory pathway respond to a range of stimulus values. For example, a neuron in a color-detection pathway is not limited to responding to one wavelength but is instead tuned to a range of wavelengths. A neuron's response peaks at a particular value and tails off on either side of that value, forming a bell-shaped tuning curve with a particular bandwidth. Thus, a neuron with a peak response at 650 nm and a bandwidth of 100 nm might give identical responses at 600 nm and 700 nm.

To be able to determine the wavelength from neuronal signals, one needs at least two neurons representing filters centered at different wavelengths. Each neuron can be thought of as a *labeled line* in which activity signals a stimulus with a given value. When more than one such neuron fires, the convergent signals at the postsynaptic relay represent a stimulus with a wavelength that is the weighted average of the values represented by all the inputs.

A single visual percept is the product of the activity of a number of neurons operating in a specific combinatorial and interactive fashion called a *population code.* Population coding has been modeled in various ways. The most prevalent model is called *vector averaging.*

We can illustrate population coding with a population of orientation-selective cells, each of which responds optimally to a line with a specific orientation. Each neuron responds not just to the preferred stimulus but rather to any line that falls within a range of orientations described by a Gaussian tuning curve with a particular bandwidth. A stimulus of a particular orientation most strongly activates cells with tuning curves centered at that orientation; cells with tuning curves centered away from but overlapping that orientation are excited less strongly.

Each cell's preferred orientation, the line label, is represented as a vector pointing in the direction of that orientation. Each cell's firing is a "vote" for the cell's line label, and the cell's firing rate represents the weighting of the vote. The cell's signal can thus be represented by a vector pointing in the direction of the cell's preferred orientation with a length proportional to the strength of the cell's response. For all the activated cells, one can calculate a vector sum with a direction that represents the value of the stimulus (Figure 21–17).
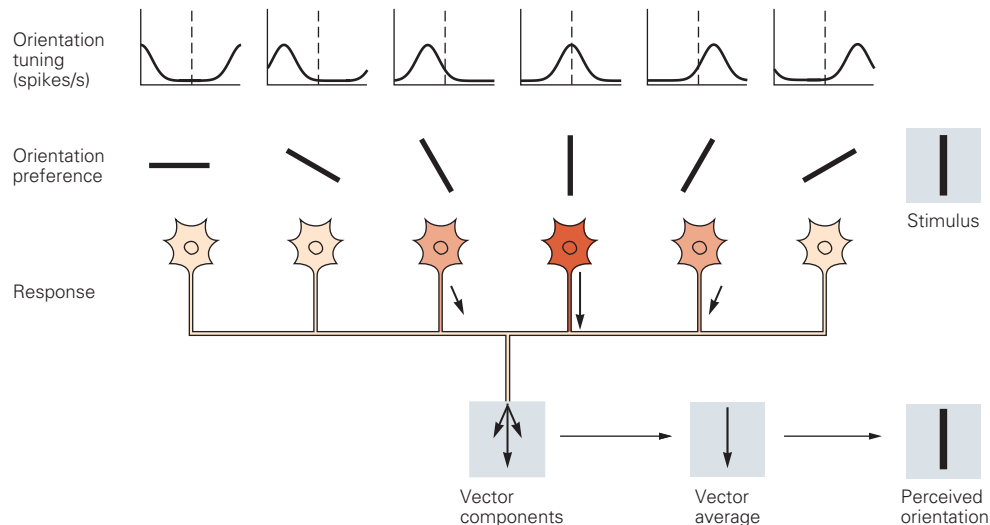

Figure 21–17 Vector averaging is one model for population coding in neural circuits. Vector averages describe the possible relationship between the responses in an ensemble of neurons, the tuning characteristics of individual neurons in the ensemble, and the resultant percept. Individual neurons respond optimally to a particular orientation of a stimulus in the visual field, but also respond at varying rates to a range of orientations. The stimulus orientation to which a neuron fires best can be thought of as a line label—when the cell fires briskly, its activity signifies the presence of a stimulus with that orientation. A number of neurons with different orientation preferences will respond to the same stimulus. Each neuron's response can be represented as a vector whose length indicates the strength of its response and whose direction represents its preferred orientation, or line label. (Adapted, with permission, from Kapadia, Westheimer, and Gilbert 2000.)

Another aspect of the population code is the variability of a neuron's response to the same stimulus. Repeated presentation of a stimulus to a neuron sensitive to that stimulus will elicit a range of responses. The most sensitive part of a neuron's tuning curve lies not at the peak but along the flanks, where the tuning curve is steepest. Here, small changes in the value of a stimulus produce the strongest change in response. Changes in stimulus value must, however, be sufficient to elicit a change in response that significantly exceeds the normal variability in the response of the neuron. One can compare that amount of change to the perceptual discrimination threshold. When many neurons contribute to the discrimination, the signal-to-noise ratio increases, a process known as probability summation, and the critical difference in stimulus value required for a significant change in neuronal response is less.

When the brain represents a piece of information, an important consideration is the number of neurons that participate in that representation. Although all information about a visual stimulus is present in the retina, the retinal representation is not sufficient for object recognition. At the other end of the visual pathway, some neurons in the temporal lobe are selective for complex objects, such as faces. Can an individual cell represent something as complex as a particular face? Such a hypothetical neuron has been dubbed a "grandmother cell" because it would represent exclusively a person's grandmother, or a "pontifical cell" because it would represent the apex of a hierarchical cognitive pathway.

The nervous system does not, however, represent entire objects by the activity of single neurons. Instead, some cells represent parts of an object, and an ensemble of neurons represents an entire object. Each member of the ensemble may participate in different ensembles that are activated by different objects. This arrangement is known as a *distributed code.* Distributed codes can involve a few neurons or many. In any case, a distributed code requires complex connectivity between the cells representing a face and those representing the name and experiences associated with that person.

The foregoing discussion assumes that neurons signal information by their firing rate and their line labels. An alternative hypothesis is that the timing of action potentials itself carries information, analogous to Morse code. The code might be read from the synchronous firing of different sets of neurons over time. At one instant, one group of cells might fire together followed by the synchronous firing of another group. Over a single train of action potentials, a single cell could participate in many such ensembles. Whether

sensory information is represented this way and whether the nervous system carries more information than that represented by firing rate alone are not known.

Highlights

1. Vision is a constructive process fundamentally different from the mere recording of visual input as in a camera. Rather, the brain uses visual input to infer information about the world around it, including information about objects, such as their sizes, shapes, distances, and identities and how rapidly they are moving.

2. The tuning of neural circuits for visual features such as contrast, orientation, and motion often matches the distribution of the feature in the natural environment. This suggests an evolutionary, ethologically driven origin for the neural circuitry.

3. Visual circuitry, and thus vision, are modulated by individual visual experience.

4. Vision makes extensive use of parallel processing. The higher visual centers form two distinct pathways. The dorsal pathway, located in parietal cortex, is involved in motion perception, attention, and visually guided action. The ventral pathway, located in temporal cortex, processes form and objects. Further subdivisions of the ventral pathway are specialized, for example, for recognizing faces. These pathways, although distinct, communicate with each other; this is likely important for the perception of objects as coherent wholes.

5. Parallel processing starts at the retina. Distinct retinal circuits analyze each point of the visual input for different local features including local contrasts of achromatic bright versus dark, red versus green, and blue versus yellow. The information is sent out through distinct classes of retinal ganglion cells (magnocelluar, parvocelluar, and koniocellular, respectively, for the three features noted) whose axons form the optic nerves.

6. The optic nerves from the two eyes regroup at the optic chiasm such that all fibers from the left visual hemifield project to the right hemisphere of the brain, and vice versa. However, the parallel retinal channels remain anatomically segregated by eye and by visual feature, past a thalamic relay station, the lateral geniculate nucleus (LGN), up to primary visual cortex (V1).

7. The different channels enter V1 at different layers, although primarily they enter at the major input layers 4 and 6. The visual input is recombined to extract new sets of features. These include tuning for orientation, motion, and object depth (obtained by combining left- and right-eye inputs).

8. V1 neurons sharing basic properties such as spatial location or orientation preference form columns extending vertically from the pia to the white matter.

9. V1 neurons also form systematic horizontal maps of their response properties over cortex. The tuning for location forms a smooth "visuotopic" map of visual space, which changes gradually with distance, and is most finely resolved at the fovea, growing progressively coarser toward the periphery. Superimposed on the spatial map are locally smooth maps of orientation preference and left-versus right-eye preference, with interspersed columns that preferentially process color. These visual response features cycle over relatively short cortical distances, in effect completing one full cycle over each partial shift of the spatial map. Thus, V1 circuits effectively analyze each visual location, in parallel, for the full set of V1 visual features.

10. Neural processing in V1 reflects its architecture, with local vertical processing along columns and lateral processing across columns. In addition, there is long-range processing that spans multiple columns.

11. The output of V1 feeds into progressively higher visual areas comprising more than 30 centers distributed along the dorsal and ventral pathways. The connectivity is reciprocal, with higher loci sending dense feedback targeting lower areas including the LGN.

12. A useful measure of visual processing is provided by changes in neuronal "receptive fields" along the visual pathway. The receptive field is the region of visual space from which the neuron receives input; it is further characterized by the neuron's optimal visual stimulus. Receptive fields grow larger and more complex at successive stages along the visual pathway. Their optimal stimuli also increase in complexity from simple pixel-like dots for photoreceptors, to oriented lines for V1, to faces in higher face-selective centers of the ventral pathway.

13. Looking forward, one of the most important unsolved questions is the interaction between feedforward visual processing through progressively "higher" neural computations and feedback mediated via the dense plexus of connections from higher to lower levels. Understanding this interaction may be the key to understanding how the brain effortlessly forms complex visual percepts.

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Aniruddha Das

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22

Low-Level Visual Processing: The Retina

THE RETINA IS THE BRAIN'S WINDOW on the world. All visual experience is based on information processed by this neural circuit in the eye. The retina's output is conveyed to the brain by just one million optic nerve fibers, and yet almost half of the cerebral cortex is used to process these signals. Visual information lost in the retina—by design or deficiency—can never be recovered. Because retinal processing sets fundamental limits on what can be seen, there is great interest in understanding how the retina functions.

On the surface, the vertebrate eye appears to act much like a camera. The pupil forms a variable aperture, and the cornea and lens provide the refractive optics that project a small image of the outside world onto the light-sensitive retina lining the back of the eyeball (Figure 22–1). But this is where the analogy ends. The retina is a thin sheet of neurons, a few hundred micrometers thick, composed of five major cell types that are arranged in three cellular layers separated by two synaptic layers (Figure 22–2).

The photoreceptor cells, in the outermost layer, absorb light and convert it into a neural signal, a process known as phototransduction. These signals are
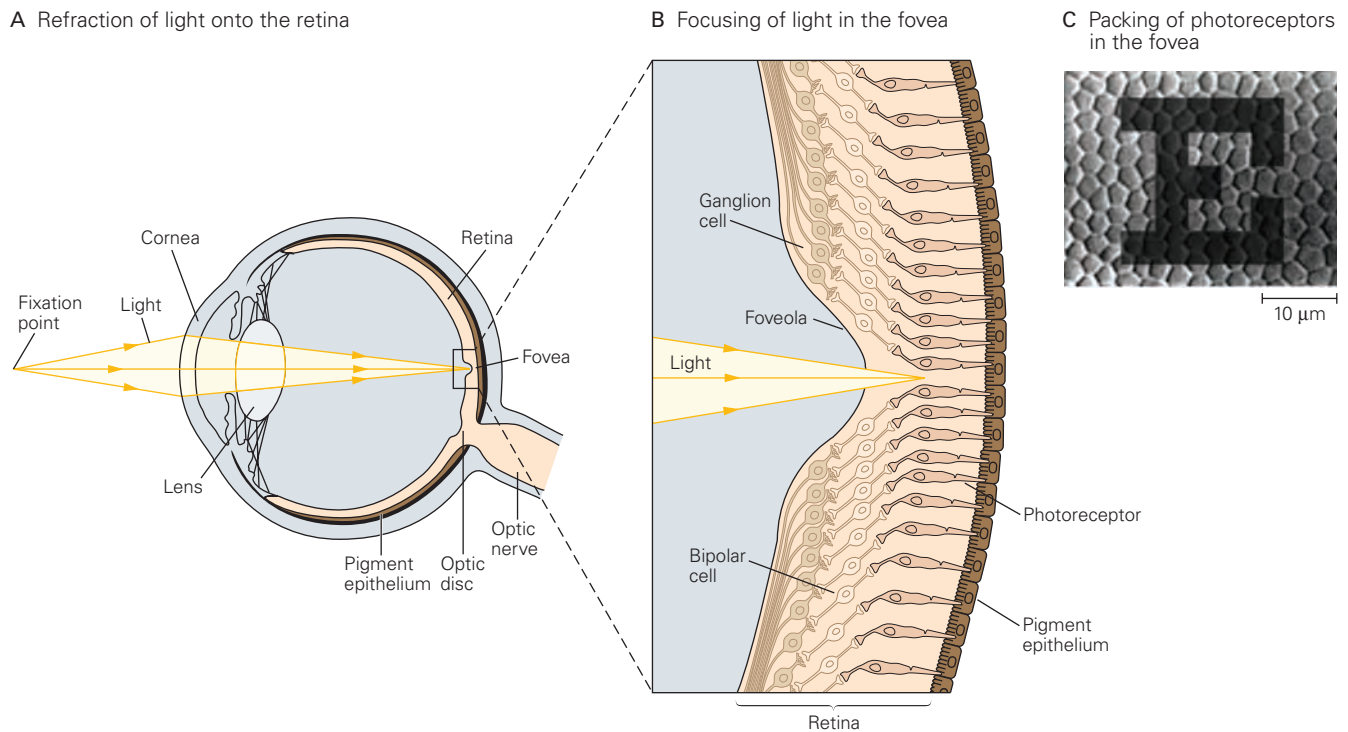
A Refraction of light onto the retina

B Focusing of light in the fovea

C Packing of photoreceptors in the fovea

10 μm

Figure 22–1 The eye projects the visual scene onto the retina's photoreceptors.

A. Light from an object in the visual field is refracted by the cornea and lens and focused onto the retina.

B. In the foveola, corresponding to the very center of gaze, the proximal neurons of the retina are shifted aside so light has direct access to the photoreceptors.

C. A letter from the eye chart used to assess normal visual acuity is projected onto the densely packed photoreceptors in the fovea. Although less sharply focused than shown here as a result of diffraction by the eye's optics, the smallest discernible strokes of the letter are approximately one cone diameter in width. (Adapted, with permission, from Curcio and Hendrickson 1991. Copyright © 1991 Elsevier Ltd.)

passed synaptically to bipolar cells, which in turn connect to retinal ganglion cells in the innermost layer. Retinal ganglion cells are the output neurons of the retina, and their axons form the optic nerve. In addition to this direct pathway from sensory to output neurons, the retinal circuit includes many lateral connections provided by horizontal cells in the outer synaptic layer and amacrine cells in the inner synaptic layer (Figure 22–3).

The retinal circuit performs low-level visual processing, the initial stage in the analysis of visual images. It extracts from the raw images in the eyes certain spatial and temporal features and conveys them to higher visual centers. The rules of this processing are adapted to changes in environmental conditions. In particular, the retina must adjust its sensitivity to ever-changing conditions of illumination. This adaptation allows our vision to remain more or less stable despite the vast range of light intensities encountered during the course of each day.
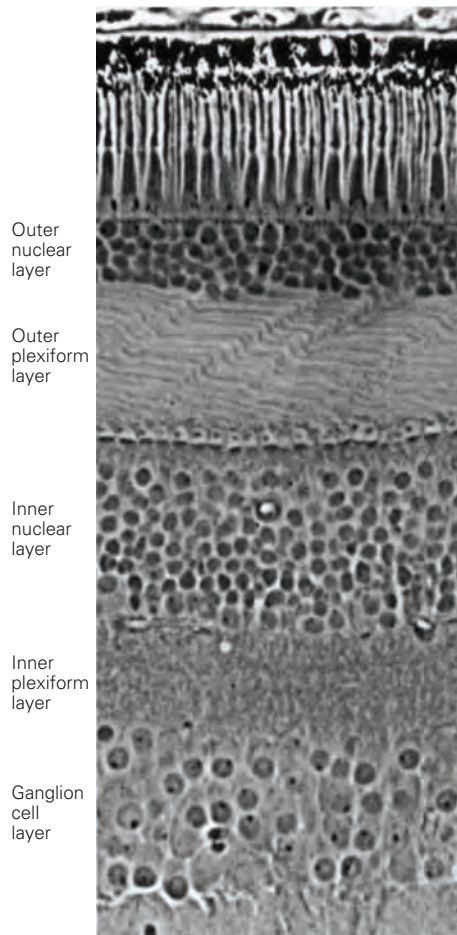
In this chapter, we discuss in turn the three important aspects of retinal function: phototransduction, preprocessing, and adaptation. We will illustrate both the neural mechanisms by which they are achieved and their consequences for visual perception.

The Photoreceptor Layer Samples the Visual Image

Ocular Optics Limit the Quality of the Retinal Image

The sharpness of the retinal image is determined by several factors: diffraction at the pupil's aperture, refractive errors in the cornea and lens, and scattering due to material in the light path. A point in the outside world is generally focused into a small blurred circle on the retina. As in other optical devices, this blur is smallest near the optical axis, where the image quality
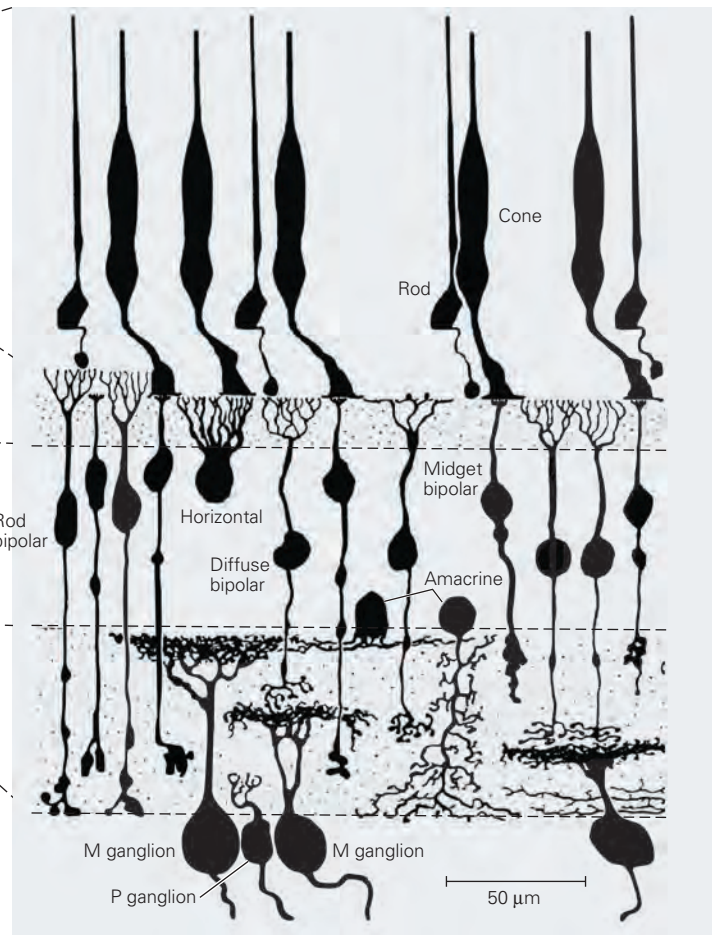
A Section of retina

B Neurons in the retina

Outer
nuclear
layer

Outer
plexiform
layer

Inner
nuclear
layer

Inner
plexiform
layer

Ganglion
cell
layer

Cone

Rod

Rod
bipolar

Horizontal

Midget
bipolar

Diffuse
bipolar

Amacrine

M ganglion

M ganglion

P ganglion

50 µm

Figure 22–2 The retina comprises five distinct layers of neurons and synapses.

A. A perpendicular section of the human retina seen through the light microscope. Three layers of cell bodies are evident. The outer nuclear layer contains cell bodies of photoreceptors; the inner nuclear layer includes horizontal, bipolar, and amacrine cells; and the ganglion cell layer contains ganglion cells and some displaced amacrine cells. Two layers of fibers and synapses separate these:

the outer plexiform layer and the inner plexiform layer. (Reproduced, with permission, from Boycott and Dowling 1969. Permission conveyed through Copyright Clearance Center.)

B. Neurons in the retina of the macaque monkey based on Golgi staining. The cellular and synaptic layers are aligned with the image in part **A**. (Abbreviations: **M ganglion**, magnocellular ganglion cell; **P ganglion**, parvocellular ganglion cell.) (Reproduced, with permission, from Polyak 1941.)

approaches the limit imposed by diffraction at the pupil. Away from the axis, the image is degraded significantly owing to aberrations in the cornea and lens and may be degraded further by abnormal conditions such as light-scattering cataracts or refractive errors such as myopia.

The area of retina near the optical axis, the *fovea*, is where vision is sharpest and corresponds to the center of gaze that we direct toward the objects of our attention. The density of photoreceptors, bipolar cells, and ganglion cells is highest at the fovea (Figure 22–1B). The spacing between photoreceptors there is well matched to the size of the optical blur circle, and thus

the image is sampled in an ideal fashion. Light must generally traverse several layers of cells before reaching the photoreceptors, but in the center of the fovea, called the *foveola*, the other cellular layers are pushed aside to reduce additional blur from light scattering (Figure 22–1B). Finally, the back of the eye is lined by a black pigment epithelium that absorbs light and keeps it from scattering back into the eye.

The retina contains another special site, the *optic disc*, where the axons of retinal ganglion cells converge and extend through the retina to emerge from the back of the eye as the optic nerve (Figure 22–1A). By necessity, this area is devoid of photoreceptors and thus

A Cone signal circuitry
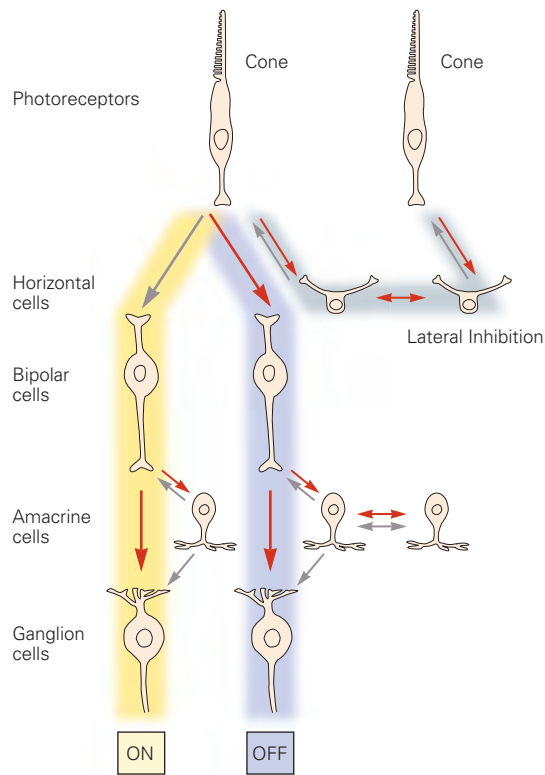
B Rod signal circuitry
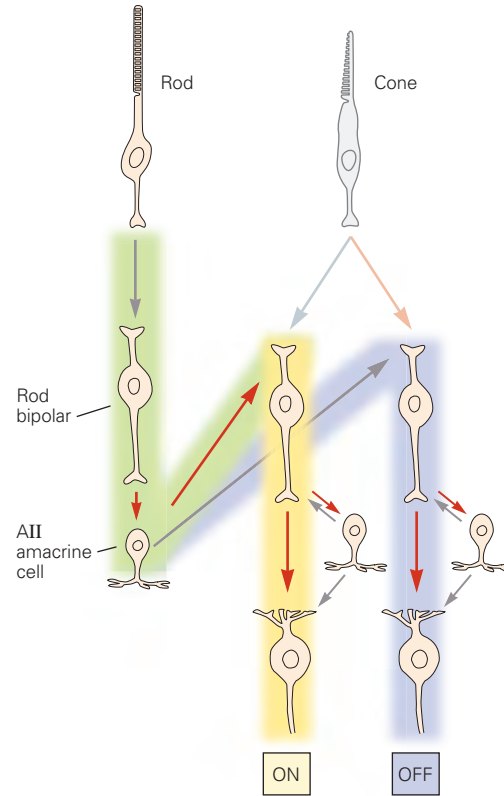
Figure 22–3 The retinal circuitry.

A. The circuitry for cone signals, showing the split into ON cell and OFF cell pathways (see Figure 22–10) as well as the pathway for lateral inhibition in the outer layer. **Red arrows** indicate sign-preserving connections through electrical or glutamatergic synapses. **Gray arrows** represent sign-inverting connections through GABAergic, glycinergic, or glutamatergic synapses.

B. Rod signals feed into the cone circuitry through AII amacrine cells, where the ON and OFF cell pathways diverge.

corresponds to a blind spot in the visual field of each eye. Because the disc lies nasal to the fovea of each eye, light coming from a single point never falls on both blind spots simultaneously, so that normally we are unaware of them. We can experience the blind spot by using only one eye (Figure 22–4). The blind spot demonstrates what blind people experience—not blackness, but simply nothing. This explains why damage to the peripheral retina often goes unnoticed. It is usually through accidents, such as bumping into an unnoticed object, or through clinical testing that a deficit of sight is revealed.

The blind spot is a necessary consequence of the inside-out design of the retina, which has puzzled and amused biologists for generations. The purpose of this organization may be to enable the tight apposition of photoreceptors with the retinal pigment epithelium, which plays an essential role in the turnover of retinal pigment and recycles photoreceptor membranes by phagocytosis.

There Are Two Types of Photoreceptors: Rods and Cones

All photoreceptor cells have a common structure with four functional regions: the outer segment, located at the distal surface of the neural retina; the inner segment, located more proximally; the cell body; and the synaptic terminal (Figure 22–5A).

Most vertebrates have two types of photoreceptors, rods and cones, distinguished by their morphology. A rod has a long, cylindrical outer segment within which the stacks of discs are separated from the plasma membrane, whereas a cone often has a shorter, tapered outer segment, and the discs are continuous with the outer membrane (Figure 22–5B).