CHAPTER 13
INFORMATION PROCESSING IN THE RETINA

13.1 ORGANIZATION OF THE RETINA

13.1.1. Types of neurons and circuits in the retina.

13.1.1.1. Through (sequential) connections. The obvious direction in which information travels is from the photoreceptors through to the brain, via the optic nerve. However, before information reaches the optic nerve, it passes through synapses between several different cell types. These through connections, or sequential connections, include the following synapses:

**E Bipolar cells.** The rods and cones contact bipolar cells. Rods and cones release glutamate in a graded fashion, in an amount proportional to their degree of depolarization. (Remember that rods and cones become hyperpolarized by light, causing glutamate release to decrease). Glutamate binds to specific receptor sites on the bipolar cells, associated with specific types of ion channels. Depending on the kinds of ion channels present, the bipolar cell may become depolarized (as do most neurons when glutamate is released), or it may become hyperpolarized. The bipolar cells produce only graded potentials, not action potentials. Like the rods and cones, they release glutamate in proportion to their degree of depolarization.

![Figure 13-1](image-url)

**Figure 13-1.** Straight-through connections in the retina. Light or darkness causes changes in the membrane potential of the photoreceptors, and consequent changes in neurotransmitter release onto bipolar cells. Some bipolar cells are depolarized by glutamate (off-center, left) while others are hyperpolarized (on-center, right).

**Ganglion cells.** The bipolar cells contact ganglion cells. Ganglion cells are the only cells in the retina that produce action potentials. A ganglion cell only produces action potentials, however, when the release of glutamate by the bipolar cell(s) that contact it is sufficient to
depolarize it to threshold. These action potentials are transmitted to the brain via the fibers of the optic nerve.

**Figure 13-2.** Straight-through connections in the retina. Light or darkness cause changes in neurotransmitter release in photoreceptors and bipolar cells which become either hyperpolarized or depolarized by light. Changes in glutamate release by the bipolar cells cause changes in the membrane potential of ganglion cells. If the ganglion cell is depolarized to threshold, it produces action potentials that are then conducted to the brain via axons that run in the optic nerve.

### 13.1.1.2. Lateral connections.

The retina not only has straight-through connections, it has lateral connections via the *horizontal cells* and *amacrine cells*. The lateral connections allow cells in one part of the retina to influence the activity of cells in another part of the retina.

**Horizontal cells.** The horizontal cells receive input from one or more photoreceptors and contact bipolar cells that are innervated directly by other photoreceptors. They release an inhibitory neurotransmitter, GABA, in a graded fashion in response to depolarization by the photoreceptor(s). GABA hyperpolarizes the bipolar cells onto which it is released, causing them, in turn, to release less glutamate onto the ganglion cell(s) which they contact.

**Amacrine cells.** The amacrine cells receive input from one or more bipolar cells and contact ganglion cells that receive input from other bipolar cells. Just like the horizontal cells, the amacrine cells release inhibitory neurotransmitter in a graded fashion, hyperpolarizing the ganglion cells that they contact, making them less likely to fire an action potential.

### 13.1.1.3. Different classes of bipolar and ganglion cells.

The end result of the various stages of retinal processing is different classes of ganglion cells. Some ganglion cells are "turned on" by light (i.e., fire an increased number of action potentials) and "turned off" by darkness (i.e., fire a decreased number of action potentials). Conversely, other ganglion cells are "turned on" by darkness" and "turned off" by light.
13.2. INFORMATION PROCESSING IN THE PERIPHERAL VISUAL SYSTEM.

It should be apparent by now that the retina does not just collect and transduce information about light. The signal that is transmitted to the brain has already gone through multiple stages of processing before it even enters the optic nerve.

13.2.1. Information processing by rods and cones.

The rods and cones have different functional roles in transforming patterns of light energy into patterns of electrochemical energy.

![Diagram of lateral connections and straight-through connections in the retina.](image)

**Figure 13-3.** Lateral connections (horizontal information flow) added to the straight-through connections (vertical information flow) in the retina. Horizontal cells are contacted by photoreceptors and they, in turn, contact bipolar cells. Amacrine cells are contacted by bipolar cells and they, in turn, contact ganglion cells. Both classes of lateral connections are inhibitory at the postsynaptic neuron.

**13.2.1.1. The rod pathway.** The rods provide convergent input to bipolar cells and thence to a population of large ganglion cells. This arrangement means that the rod pathway amplifies the visual signal in ganglion cells under low-light conditions by adding together the activity of multiple photoreceptors. However, by its very nature, the amplification of a signal through convergence results in a loss of acuity.

In the retinal periphery, the rods predominate. This is why acuity in the peripheral visual field is not as good as in the foveal field, where only cones are present. However, under very low-light conditions it is sometimes easiest to see using peripheral (rod) vision.

**13.2.1.2. The cone pathway.** The cones provide one-to-one input to bipolar cells, and thence to a population of small ganglion cells. This arrangement means that information about the fine structure of the visual image is preserved, or even enhanced. In addition to high acuity, the cone pathway also provides information about color.
13.2.2. Receptive fields.

Because light from different parts of the visual field falls on different parts of the retina, each retina contains a two-dimensional representation of visual space. The best comparison would be to think of the retina as the film in the back of a camera.

The region of space (e.g., the visual field) within which a stimulus will affect the response of a sensory receptor or neuron (e.g., cone, bipolar cell, or ganglion cell) is called the receptive field of that photoreceptor or neuron. The receptive field is always determined relative to the receptor or neuron under consideration. In other words, "what stimulus affects the activity or state of the neuron whose activity we are observing?"

If we measure the receptive fields of individual photoreceptors, they will all be similar in that they are determined by whether or not light reaches the receptor. However, because there is convergence from many rods onto their bipolars and ganglion cells while cones project in a 1:1 fashion, the receptive fields of rods will be larger than those of cones, comprising the sum of the receptive fields of all the rods that provide input.

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Thought question: What is the advantage of having different sizes of receptive fields in a sensory system?
The receptive field of a retinal neuron is the part of the visual field that, when stimulated, evokes a change in the activity or state of that particular neuron. For example, in this hypothetical array, the receptive field of each photoreceptor corresponds to the portion of the visual field with the same letter (e.g., photoreceptor A "sees" the snake's head and photoreceptor J sees the rattles on its tail. The receptive fields of the ganglion cells are determined by the pattern of input from the photoreceptors. For example, if we recorded from ganglion cell 1, its receptive field would include portions A and B of the visual field (the snake's head and upper body). Ganglion cell 3 only gets input from photoreceptor E, so its receptive field is E (the last diamond-patterned segment of the snake's body). Ganglion cell 5 gets input from G, H, I and J, so it "sees" most of the black portion of the tail plus the rattles.

Stimuli within the receptive field of a bipolar cell, ganglion cell or neuron may either excite or inhibit the cell. For example, retinal ganglion cells typically increase their response when a light is present in some parts of their receptive field but decrease it when the light is in other parts.

An “on-center” retinal ganglion cell increases its response rate when there is light at the center of its receptive field. An “off-center” ganglion cell increases its response when there is darkness at the center of its receptive field (off-center) and decreases its firing rate when the darkness is in the surrounding area (on-surround). If the light doesn't fill the whole center or surround portion of the receptive field, or if it overlaps both, the result will be a combination, or algebraic sum, of the "on" and "off" effects.

In a real visual situation, the firing rate of every retinal ganglion cell is constantly being modulated up and down as lighter and darker portions of the visual scene pass through the different regions of its receptive field.

Thought question: If all of the ganglion cells in your retina increased their firing rate in response to light and were completely inactive in darkness, would this change your perception of the world? Why or why not? If you answered "yes", how do you think your perception would change?
Figure 13-6. The effect of a dark spot of different sizes in a light field on the responses of a retinal ganglion cell with an off-center/on-surround receptive field organization. The solid line indicates the receptive field center, the dotted line the receptive field surround. The shaded area represents the dark spot and its location relative to the cell's receptive field. The traces at the bottom represent the action potentials fired by the cell in response to the dark stimulus.

Figure 13-7. A hypothetical neural circuit that would create a center-surround receptive field (on center-off surround). The neurons in the center (+) all cause depolarization of the neuron from which responses are recorded. The neurons in the surround (-) all cause hyperpolarization of the cell from which responses are recorded.

13.2.3. Lateral inhibition.

The center-surround organization of receptive fields of ganglion cells and bipolar cells is created by the lateral inhibitory connections provided by the horizontal and amacrine cells. Lateral inhibition is not peculiar to the visual system. It is present in other sensory systems as well, as you may recall from the section on the somatosensory system.

13.2.3.1. Receptive fields, lateral inhibition and perception of contrast. The center-surround organization of receptive fields makes retinal bipolar cells and ganglion cells very sensitive to contrast. For example, the response of a given cell to light will be stronger if the light portion of the visual field is adjacent to a dark portion. As a result, the retinal mechanisms for contrast enhancement make our visual systems very sensitive to edges or borders and allow us to perceive even weak contrasts.

Sometimes the retinal mechanisms that produce such great sensitivity to contrast cause us to perceive contrast that is not really there - an optical illusion. One such illusion is called Mach bands. This illusion consists of a series of adjacent bands of different shades of grey. Within each band there appears to be a gradient from lighter to darker, running from the darker flanking band to the lighter flanking band.
Figure 13-8. Mach bands illustrate perceived contrast enhancement at borders between bands of different shades of grey. (a) illustrates the border between two bands (a photocopy doesn't do it justice, but you get the idea) (b) is a plot of the actual brightness profile, with equal brightness at points A and B and at points C and D. (c) shows the perceived brightness profile, in which B seems brighter than A and C seems darker than D.

Another related optical illusion is called the Hermann grid. In this case, you will perceive a grey area at what would be the intersection of the white horizontal and vertical lines separating the black squares.

Figure 13-9. The Hermann grid. Fixate on the tiny black dot at the center, and you will see grey blotches at all of the intersections except the one on which you are fixating. After a minute or so of fixation, move your eye to the lower left to fixate on the small white dot. You should see an after-image of the grid, which will move slightly with respect to the actual image.

13.2.4. Adaptation.

The Hermann grid not only illustrates how we perceive contrasts, it also illustrates some points having to do with retinal adaptation. As discussed in the previous chapter, if you look at something long enough (e.g., the Hermann grid), then look away, you will see an after-image. The after-image is due to bleaching of photopigments on the retina, as well as some other processes that cause neural activity to settle to a level that signifies "no change" - therefore no stimulus. When a change does occur, the perception of the new stimulus is enhanced so that the areas that previously corresponded to the black parts of the figure now appear lighter than a light background.

The most powerful visual stimulus is not light per se, but rather changes in light across the visual field, and/or over time. Because we need change in order to see, our eyes are constantly moving in microsaccades even when we thing we are fixating on a visual stimulus.
The fact that you can't keep your eyes perfectly still is illustrated by fixating on the dot at the center of the Hermann grid for a minute or so, then moving your eye slightly away and watching the jitter between the real image and the after-image.

Thought question: Given what you know about the organization of different types of receptive fields in the retina, think of a possible explanation for why we see the grey patches at the intersections of the white lines on the Hermann grid.