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looks much more similar, yet they're physically identical to patches a_1 and a_2. Your perception of these patches is being strongly influenced by the three-dimensional appearance of the image. In the configuration on the left, patch a_1 appears to be a dark gray patch that is brightly illuminated, whereas patch a_2 is a light gray patch that is dimly illuminated. In the configuration on the right, however, both patches appear to receive the same level of illumination and, therefore, appear about equal in lightness. Retinal ganglion cells know nothing about the three-dimensional layout of objects. Thus, these cells should be insensitive to the global context in which the patches appear. Evidently, then, retinal mechanisms cannot fully account for illusions of surface lightness. We must look beyond the eye to the brain for a complete account of these illusions (for clues about brain areas that might be involved in perception of surface lightness, see Rossi, Rittenhouse, and Paradiso, 1996).

Despite what these demonstrations may seem to indicate, the retina does play a role in signaling lightness levels within local regions of the image. Even with his compelling demonstrations, Adelson (1993) acknowledges that retinal processes contribute to illusions of lightness and brightness. No one would deny that retinal signals are crucially involved in registering information about surface perception. To the contrary, retinal ganglion cells are the *only* vehicles for communicating visual information from the eye to the brain. Everything that we see—whether veridical or illusory—must be represented in the neural activity among the 1.25 million ganglion cells of each eye. Without a doubt, their receptive field properties help shape the world that we see.

In this section we have focused on possible perceptual consequences of center/surround antagonism. Now let's turn to another aspect of retinal ganglion cell organization, a feature that governs how well those cells perform on two seemingly incompatible visual tasks.

Sensitivity versus Resolution

Aspects of Convergence

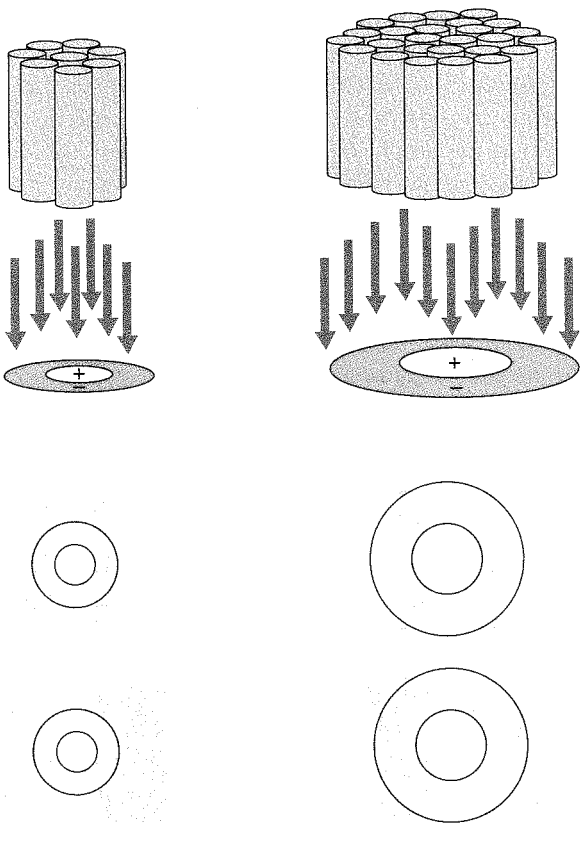
Earlier we noted that over the entire retina, signals from 100 million photoreceptors converge on about 1.25 million retinal ganglion cells. This suggests an average convergence, over the entire retina, of about 80 photoreceptors to 1 ganglion cell. But this summary statistic is misleading.

Suppose we examine the number of receptors and the corresponding number of ganglion cells locally in different small patches throughout the retina, ranging from the macula to the periphery. For each patch of retina, we can calculate the degree of convergence by taking the ratio of receptors to retinal ganglion cells. This calculation reveals two important facts. First, the convergence ratio varies widely and systematically from one part of the retina to another. Second, near the center of the macula, the convergence ratio approaches unity—about one photoreceptor per ganglion cell—whereas in the periphery of the retina, the ratio is several hundred to one. In other words, there is a strong connection between retinal eccentricity and the amount of convergence. The connection is so strong that it suggests the operation of some grand plan. What might that plan be? To answer this question, we need to explain what is gained and what is lost by this neural convergence. As we proceed, keep in mind that the extent of receptor to ganglion cell convergence is directly related to the ganglion cell's receptive field size. The greater the number of receptors contributing to the receptive field of a given ganglion cell, the larger that cell's receptive field. This principle is illustrated schematically in Figure 3.23. Two ganglion cell receptive fields are shown schematically in the top panel, one small (*left*) and one large (*right*). Note that fewer photoreceptors contribute input to the small receptive field compared to the larger receptive field. We'll get to the bottom part of the drawing in a moment.

To picture the consequences of convergence, consider an extreme example. Suppose your eye had only a single retinal ganglion cell—a convergence ratio of 100 million to 1. In effect, your entire retina would be the receptive field for this solitary cell. How would your vision differ from its present form? It's certain that your vision would be changed in two ways, one for the good, one for the bad.

We'll start with the bad. With only one retinal ganglion cell to tell your brain what the eye saw, you would not be able to read or watch television. In fact, you would be virtually blind. Imagine the problem the brain faces with this solitary retinal ganglion cell as its only link to the visual world. The brain would be unable to distinguish different distributions of light falling on the back of the eye; all distributions would have the same effect on the cell. You would confuse letters of the alphabet and be unable to recognize your friends by sight. In brief, your resolution would be awful—not a good situation.

FIGURE 3.23 | A ganglion cell receiving input from just a few receptors (left-hand example) has a smaller receptive field and thus responds well to a smaller stimulus and responds poorly, if at all, to larger stimulus. A ganglion cell receiving input from a larger array of neighboring receptors (right-hand example) has a larger receptive field and responds poorly to a small stimulus but vigorously to large one. The larger receptive field, because it pools signals over a larger area, can also register the presence of weak levels of light.



Resolution refers to the ability to distinguish differences in the spatial distribution of light in an image. The best-known measure of resolution is **visual acuity,** which we will discuss in a moment. With only one retinal ganglion cell to "describe" the image on the retina, your resolution would be nil. Regardless of the total light falling on the retina, you wouldn't be able to distinguish one letter of the alphabet from another—even with extremely large, headline type. You don't need to go to the extremes of our single-ganglion-cell example to discover that convergence is incompatible with good resolution. Generally, greater degrees of convergence lead to poorer resolution. That's because when visual information from a large region of space converges onto a single ganglion cell, the visual system inevitably loses track of exactly where within that region of space the information originated. That is why *convergence is the enemy of resolution.*

To see this enemy in action, look at the patterns of light within the ON and OFF regions of the two receptive fields shown in the bottom panel of Figure 3.23; one pattern consists of narrow, small contours and the other consists of broader, larger contours. Although the cell with the larger receptive field receives input from a larger number of receptors, responses to the narrow dark and light contours would cancel one another. As a result, this cell would fail to respond to the smaller contours. In contrast, the cell with the smaller receptive field, receiving input from fewer receptors, would give a vigorous response to the narrow pattern because the light and dark portions of the pattern "fit" within this cell's receptive field profile. The smaller receptive field thereby has superior visual acuity because convergence—the enemy of resolution—is more limited for this cell. To activate the cell with the larger receptive field, the pattern would have to consist of broader contours; those broad contours would not activate the cell with the smaller receptive field.

Now for the good news about convergence. Let's begin with two hypothetical ganglion cells, *A* and *B*. Suppose *A* receives input from a relatively small cluster of neighboring receptors (such as the ganglion cell in the upper left of Figure 3.23) while *B* received input from a larger array of neighboring receptors (such as the ganglion cell in the upper right of Figure 3.23). How well are these two different ganglion cells able to signal the presence of dim light? In other words, how sensitive to light are the two cells? You've learned that for a ganglion cell's activity to change, it must receive a sufficient amount of transmitter substance from the bipolar cells. In effect, a retinal ganglion cell weighs all the neurochemical evidence it receives and decides whether the cumulative evidence exceeds some minimum threshold. If that threshold is exceeded, the ganglion cell's activity level is altered, signaling the brain that a visual event is occurring. In weighing the cumulative evidence, the ganglion cell disregards which particular

bipolar cells (and, hence, which photoreceptors) provide the individual pieces of evidence. From the ganglion cell's perspective, only the total is important. With this in mind, let's compare the abilities of ganglion cells *A* and *B* to inform the brain about the presence of dim light imaged on the retina.

For this comparison, we'll use a large but dim spot of light that can be centered on either ganglion cell's receptive field. Let's start with ganglion cell *A*, the one receiving input from a small cluster of photoreceptors. Even though the image of the dim spot fills this cell's receptive field, the receptors would give a weak response to the light. Some of these weak photoreceptor messages get passed along to cells in the intermediate layers of the retina, but those cells, too, will generate weak messages at best. As a result, ganglion cell *A* may well receive too little transmitter substance to disturb its spontaneous activity. So this ganglion cell will fail to inform the brain that a dim spot of light is present.

What about ganglion cell *B*, the one receiving input from a larger array of photoreceptors? These photoreceptors will also give a weak response because the light is dim. But there will be substantially more photoreceptors contributing weak signals to the ganglion cell via the bipolars. The ganglion cell, therefore, will receive more transmitter substance ("evidence"), thereby increasing its chances of being activated. Consequently, the brain is much more likely to receive messages about the dim spot of light.

The principle is simple: Increasing the number of receptors contributing input to a retinal ganglion cell allows weak signals to be summed, yielding a total input strong enough to change the activity of that ganglion cell. A retinal ganglion cell sums weak signals originating from an array of retinal locations, an ability known as **spatial summation.** Spatial summation enables you to see very dim light. In other words, it enhances the sensitivity of your eyes. Because summation depends on convergence, one can say that *convergence is the ally of sensitivity.*

Now you can appreciate the conflict. On the one hand, convergence is a prerequisite for high sensitivity; on the other, convergence interferes with good resolution. To design an eye that detects very dim lights *and* possesses good spatial resolution represents a real challenge.

The Duplex Solution So how do your eyes manage to resolve these two conflicting demands—resolution and sensitivity? To answer this question, let's return to an analogy we've already used, the analogy between the eye and a camera.

Photographers face the same kinds of problems we've been discussing. Some types of film, such as those used for nighttime surveillance, have extremely large grains of photosensitive material and, thereby, a high sensitivity to light. This makes such film usable at very low light levels. (As you may know, a film's light sensitivity is indexed by its ISO or ASA rating.) Highly sensitive films usually have relatively poor resolution, and so they don't produce very sharp photographs.

Other types of film, such as the microfilm used by librarians, have exceedingly small grains of photosensitive material and therefore produce very sharp photographs (even in huge enlargements). However, these types of film work properly only at relatively high light levels. With film, then, as with the eye, there is a trade-off between resolution and sensitivity. The photographer can solve this dilemma by simply changing the film in the camera, matching the film to the available light. The eye, however, doesn't allow the capability of loading and unloading different types of film as needed. In fact, this is unnecessary because the "film" in the eye is **duplex,** meaning that the eye contains two types of photosensitive elements (or films). One—associated with the rod photoreceptors—provides high sensitivity to light; the other—associated with the cone photoreceptors—provides high resolution. In the human eye, the two types of film occupy somewhat different locations along the back of the eye.

To see how this duplex arrangement works, think back to the convergence of receptors onto ganglion cells. Recall that the central region of the eye (where cones predominate) has very little convergence. Hence, it has excellent resolution but only average sensitivity to light. Peripheral regions of the retina (where rods predominate) have high degrees of convergence, hence poor resolution but good light sensitivity. (For further discussion of high sensitivity, see Box 3.4.)

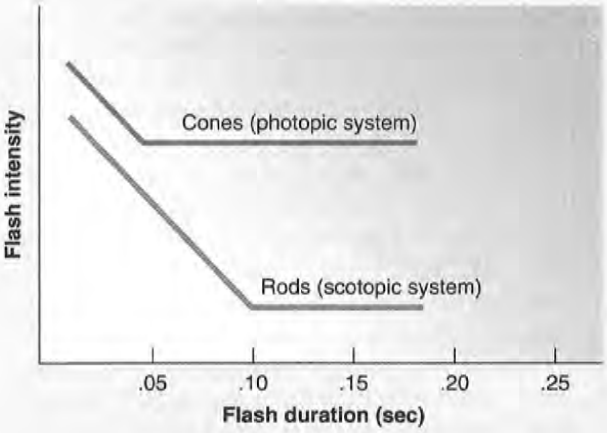
The preceding chapter pointed out that the center of the primate retina contains mainly cones and very few rods. As a result, activity of retinal ganglion cells with receptive fields near the center of the retina reflects mainly the responses of cones. Because of the predominance of rods in the retinal periphery, the activity of ganglion cells with receptive fields in that region reflects mainly the influence of rods. As you are about to learn, rods and cones differ in numerous ways important to vision. This means that ganglion cells in the rod-dominated periphery make different contributions to

BOX 3.4 Adding Photons Over Time and Space

Multiple factors govern the eye's sensitivity. Some have already been discussed—the wavelength of light, its intensity and spatial pattern, and where on the retina the stimulus falls. But there are two other, very important variables: its duration and its size.

To understand the importance of duration and size, we must consider exactly what events need to occur before one can detect a very weak stimulus. Suppose that seeing the stimulus requires that the photoreceptors absorb some small number of photons—a **photon** being the smallest unit of light energy. (The actual number of photons doesn't matter so long as it is greater than 1.) Imagine that we split the stimulus into two installments, both intense enough to cause the receptors to absorb exactly one-half the total number of photons needed for seeing. Now let's introduce one condition: allow one hour to elapse between delivery of the first and second installments of photons. Will you see the stimulus? No, because by the time the second installment of photons arrives, the effects of the first installment will have long since disappeared.

Granting that an hour's delay is unreasonable, how much time can elapse between installments of photons before the effects of the first installment completely dissipate? Photoreceptors have a limited memory—called **temporal summation**—with the rods' "memory" being somewhat longer than that of the cones. But whichever system is stimulated, the shorter the interval between the two installments, the greater the chances that the residue of the first installment will be available to add to the effects of the second. Delivering all the photons within a very short time period guarantees that effects



produced by the earliest photons will add to those of the later ones. If the stimulus is stretched out in time, a greater *total* number of photons must be delivered to the eye, since losing the advantage of temporal summation makes each photon less efficient.

This fact has been formalized as **Bloch's law,** which states that a constant product of light intensity and time will be equally detectable. Sometimes Bloch's law is expressed as

$$I \times T = C$$

where I stands for intensity, T for time, and C for constant visual effect. Bloch's law says that time can be traded for intensity. Lengthening the presentation of some relatively weak light makes it just as visible as another, more in-

vision than do ganglion cells in the cone-dominated central region of the retina. Many ganglion cells receive inputs from both rods and cones (Enroth-Cugell, Hertz, and Lennie, 1977), so that both classes of photoreceptors share communication pathways to the brain. However, rod and cone signals to these mixed input ganglion cells get switched from all-cone to all-rod inputs depending on the overall level of light. As pointed out previously, this switching function is thought to be accomplished by the amacrine cells.

Rod-dominated ganglion cells support vision even when light levels are several hundred times less than that required by their cone-dominated counterparts. This results partly from the rods' own greater sensitivity (Detwiler, Hodgkin, and McNaughton, 1980), as well as greater convergence on rod-dominated retinal ganglion cells. Vision under dimly lit conditions is termed **scotopic** (from the Greek words *skotos,* meaning "darkness," and *opsis,* meaning "sight"). We'll use the term *scotopic vision* to signify vision that depends on rod photoreceptors. You must keep in mind that these rod signals are still passed through the intermediate retinal layers to ganglion cells, which send those rod-mediated messages to the brain.

The cones require somewhat higher light levels in order to function properly. Thus, vision using this class of photoreceptors is described as **photopic** (from the

tense light that is presented only briefly. So long as each has the same product (of intensity and time), the two stimuli contain the same total energy and will be equally detectable. These relationships are depicted in the figure at the end of this box. There, the vertical axis represents the stimulus intensity that is just barely detectable (I), and the horizontal axis represents the stimulus's duration (T). Two lines are shown on the graph, one representing the behavior of the scotopic system, the other representing the behavior of the photopic system. Bloch's law predicts that data should fall on an oblique line, a 45-degree slope. Note that in both lines this prediction holds when the durations are relatively short.

For the rods, Bloch's law breaks down at about one-tenth of a second. For cones, it breaks down much earlier, at about one-twentieth of a second or less (Hood and Finkelstein, 1986). These values reflect the temporal memories—temporal summation—of the two systems. Incidentally, Bloch's law also pertains to contrast, not just luminance: It is possible to interchange exposure duration with stimulus contrast to yield constant visual effects, within limits (Harley, Dillon, and Loftus, 2004).

There is a *spatial* analog to the *temporal* law just discussed. We mentioned previously that many photoreceptors will share a single ganglion cell. In other words, the ganglion cell adds together signals from spatially separate sources—two or more photoreceptors—a capacity referred to in the text as spatial summation.

Suppose we take a very small stimulus and by trial and error determine how intense it must be in order to be just detectable. This stimulus causes the absorption of a minimum, or threshold, number of photons. If we distribute that same number of photons widely over the retina, seeing will not result. The spatially dispersed photons stimulate photoreceptors that do not contribute to the same ganglion cells. As a result, the opportunity for cooperative effect is reduced.

Within certain limits, all stimuli having the same product of intensity *and* area will be equally detectable. This is not completely surprising since any two stimuli having the same product of area and intensity contain identical amounts of total light. This trade-off between intensity and area is known as **Ricco's law**. Ricco's law holds only in the fovea, and even there, it holds only for very small stimuli.

We don't want to leave you with the idea that the visual system responds *solely* to the number of photons gathered over time and space. If it did respond that way, you'd confuse long, weak flashes with brief, intense ones. This confusion would be particularly strong when flashes of different durations contained the same total number of photons, since according to Bloch's law, they would be equally detectable. However, even when two flashes contain the same total number of photons (and hence, are equally detectable), people can still discriminate between a long, weak flash and a brief, intense one (Zacks, 1970). In other words, the visual system registers more than just the total number of photons. It also discriminates how those photons are distributed over time. At present, though, it is not known how the visual system manages this discrimination.

Greek word *photos*, meaning "light"). Figure 3.24 indicates the light levels considered photopic and those considered scotopic. This is an important distinction because, as you'll see later, photopic and scotopic vision differ in a number of significant ways. There is a narrow, intermediate range of light levels where both rods and cones operate, and vision in this very limited range is termed **mesopic** (from the Greek word *mesos*, meaning "middle"). In this chapter, we shall concentrate on vision in the much larger photopic and scotopic ranges.

As noted earlier, the eye must satisfy two competing goals: good resolution and good sensitivity. We now discuss each of these goals in turn.

Resolution

Since convergence is the enemy of resolution, the photopic system, having less convergence, should have better resolution. It is estimated that 33 percent of all the retina's ganglion cells receive input from cones occupying the fovea, which itself accounts for only 2 percent of the retina's total area. Thus, we expect resolution to be best in the center of the macula, where the ratio of cones to ganglion cells is about 1 to 1. We do not yet know precisely how the convergence of the cone system changes across the retina (the extensive physiological measurements required to answer that question have yet to be performed). Instead, we must infer the answer using related information: the density of cones at various places on the

FIGURE 3.27 | The photographs on the left and the right simulate the degraded spatial detail present when you fixate on the middle picture.

FIGURE 3.28 | All letters in this chart should be equally legible when you fixate on the small dot in the center of the chart.

Acuity also decreases appreciably as the level of illumination drops (you probably already know this from your own difficulty reading a menu in a dimly lit restaurant). Yet it's obviously not the number of cones or the density of ganglion cells that changes with light level. The reduction in acuity with decreasing illumination is probably caused by changes in the spatial layout of receptive fields of the ganglion cells. As the overall level of illumination drops, the surrounding portions of ganglion cell receptive fields become less effective and, consequently, the center regions become larger (Barlow, Fitzhugh, and Kuffler, 1957; Maffei and Fiorentini, 1973). Box 3.5 completes the story by describing additional influences on visual acuity.

Sensitivity

Scotopic Vision Under ideal conditions, rod photoreceptors operate at the theoretical limit of their sensitivity, generating measurable electrical signals when only a single photon is absorbed by a given rod's photopigment (Lewis and Del Priore, 1988; Hecht, Shlaer, and Pirenne, 1942; Rodieck, 1998). But the capture of a single photon does not constitute seeing. In order for light to generate a visual sensation, more than one rod, though not many more, must

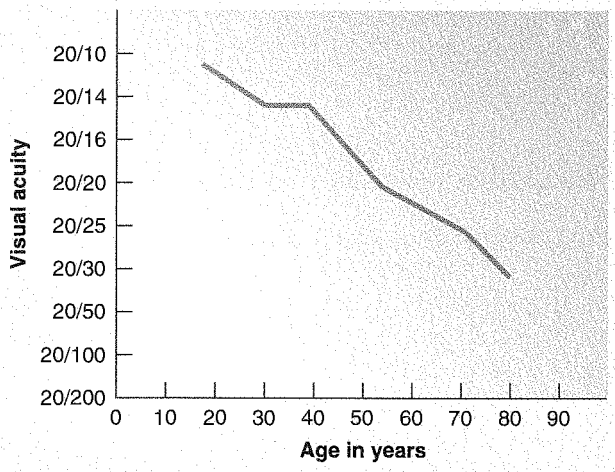
Visual Acuity: The Meaning of 20/20 Vision BOX 3.5

Visual acuity can be defined in several different ways. One common definition relates acuity to the smallest target, such as a letter, that can be correctly recognized. A person able to recognize smaller letters is said to have better acuity. You may have heard someone comment with pride about having 20/20 visual acuity. What exactly do these numbers mean?

When optometrists and ophthalmologists began quantifying acuity more than a century ago, they created eye charts containing letters of various sizes. Patients tried to read ever smaller letters, until they came to letters so small that reading was impossible. One Dutch doctor, Hermann Snellen, tested hundreds of people who had no eye diseases (so-called "normals") and found that half these people were unable to see details smaller than a certain size. He designated this size—details whose images on the retina were about 0.005 millimeters high—as "normal." For any given detail, the viewing distance is crucial. If you move far enough away, even headlines become impossible to read. So visual acuity is expressed in relation to the distance at which the eye chart is read, usually 20 feet. Someone is said to have normal visual acuity if, while standing 20 feet from the chart, that individual can read the same letters that the average healthy person can read at 20 feet. Hence, the notation "20/20." The metric equivalent of 20/20 is 6/6, since testing is carried out at a viewing distance of 6 meters.

Acuity can be either better or worse than 20/20. If you cannot see small print, your acuity may be only 20/60. This means that you must get as close as 20 feet in order to read what the average person can read from 60 feet. Likewise, if you have really sharp eyes, your vision may be 20/15 or even 20/10. This means that you can read letters at a distance of 20 feet that the average person cannot. He or she has to move closer to the letters in order to read them: within 15 feet in the first case, 10 feet in the second.

But 20/20 is not good enough. A normal, healthy young person should have vision *better* than 20/20. The graph shown in the right-hand column shows that for young people, visual acuity is on average better than 20/20. Acuity declines as we get older. Part of this decline is owing to the reduced size of an older person's pupils, which allows less light to reach the retina (Owsley, Sekuler, and Siemsen, 1983). Older people also have particular difficulty with eye charts whose letters are of low contrast. On such charts the test letters are printed in various shades of gray rather than in black. Tony Adams of the University of California's School of Optometry used a low-contrast eye chart to



measure the acuities of young and old people, all of whom had 20/20 acuity when tested with the normal, high-contrast eye charts. Adams and his colleagues (1988) found that the older observers showed a far greater decline in acuity at low contrast. This result bears on the design of work and home environments in which older persons have to function.

Visual acuity varies with factors other than age and light level. Some people have particular trouble reading eye charts composed of letters bunched together. They'll be able to read smaller letters on a less crowded line of the eye chart, even though they fail with a line of larger letters that are crowded together. You can see this **crowding effect** in an eye chart prepared by Stuart Anstis. Compare the legibility of this crowded chart to the legibility of the chart shown in Figure 3.28. They are almost the same, except that Anstis has added many extra letters to the chart in this box.

Visual acuity scores may also be affected by cognitive factors, including memorization of the eye chart (by someone who is particularly anxious to "pass" an eye test). Sometimes these cognitive factors play a role even though neither patient nor doctor intend them to. Erica, the youngest daughter of one of the authors (R.S.), was having her eyes examined by a well-meaning though inexperienced ophthalmologist who, to make matters worse, was in a hurry. Wanting to measure acuity separately for each eye, the ophthalmologist asked Erica to close her left eye

(continued)

Blinking, Winking, and Flickering BOX 9.2

In modern industrialized societies, people are immersed in lights that blink and flicker. Some of these lights, such as the flashing lights atop a police vehicle, try to capture attention. Others, like the flashing light at a railroad crossing, are designed to warn. For a flashing light to be effective, it must flicker at a rate that can be easily seen. If it flickers too rapidly or too slowly, the flicker will be imperceptible.

Much is known about the **critical flicker frequency (CFF)**—the highest rate of flicker that can be perceived as such. When this highest frequency is exceeded, the separate flashes of light blend together to yield the illusion of continuous light. Under the best conditions, the human CFF is around 60 Hz. (*Hz*, the abbreviation for "hertz," is a unit of flicker rate equivalent to one on/off cycle per second.) In fact, this is why you cannot see the flicker from a typical fluorescent lamp. Although the lamp actually does flicker on and off at a rate of 60 Hz, you can't see the flicker because its rate exceeds your CFF. However, a bee looking at the same lamp could perceive the 60-Hz flicker, as a bee's CFF is far higher than yours, around 300 Hz (Lythgoe, 1979). To put these values into context, consider that standard television sets in North America refresh their screens at 60 hz, painting 60 images each second on their screens. Movies as shown in a movie theater are filmed at a rate of 24 images per second, but in the theater each image is actually projected twice in succession, producing an effective refresh rate of 48 Hz. Early movies, in contrast, were projected at a much more leisurely rate, only 16 frames per second. Because this value is far below the human CFF, early movies seemed to flicker, and the motion portrayed in those movies often seemed jerky.

The CFF depends on many variables, including the light's intensity and size. In addition, CFF varies with location in the visual field. The rate of flicker of a large stimulus, such as a television set or a bank of fluorescent lights, may be too fast to be seen when you look at the stimulus directly, but may be highly visible when you look slightly away from it. You may have experienced this annoying peripheral flicker if you've been in a room where the fluorescent ceiling lights were functioning improperly.

In some individuals, seizures can be brought on by exposure to a flickering light. Individuals with this condition, called photoconvulsive epilepsy, have to be aware that seizures can be triggered by a strobe light in a disco, a malfunctioning television set or the flashing lights of video games (Ferrie et al., 1994). With a television, the likelihood of a seizure is enhanced by low-frequency (50-Hz) television systems (like the standard sets used in Europe), by very bright images, or by close viewing (Badinand-Hubert et al., 1998).

Warning lights flicker at rates well below the CFF. Just how sensitive is the human visual system at these lower rates of flicker? Recall from Chapter 5 that human vision has an optimal spatial frequency—there is an object size that can be seen most easily. The same holds for temporal frequency—there is a rate of flicker that can be seen most easily, typically around 10 Hz.

TABLE 9.1 | Perceptual Consequences of Eye Movements

Test Conditions	Command Signals (C)	Eyes Move	Retina Image Motion (R)	Experience (E) [C − R = E]
Normal; stable environment	Left (+1)	Left	Left (+1)	No motion [1 −1 = 0]
Normal; stable environment	Right (−1)	Right	Right (−1)	No motion [(−1) − (−1) = 0]
Eye passively displaced left	None (0)	Left	Left (+1)	Right [0 − 1 = −1]
Eye paralyzed; person *wills* movement left	Left (+1)	None	None (0)	Left [1 − 0 = 1]
Environment translates left	None (0)	None	Right (−1)	Environment moves left [0 − (−1) = 1]

cerning the perceived direction of motion should develop from a comparison between two quantities—the command signals to the extraocular muscles and the accompanying retinal image motion. To derive perceived direction, subtract the retinal image motion from the command signal (remembering to respect signs).

In the first two test conditions (normal) of Table 9.1, the observer decides to move the eyes leftward, across a stationary visual environment, and the eyes do as they're instructed. Subtracting the retinal image motion from the command signal yields zero (no perceived motion) in both cases. Now we come to a more interesting condition.