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CHAPTER 1

Introduction to Perception

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Some Questions We Will Consider:

- Why should you read this book? (p. 4)
- What is the sequence of steps from looking at a stimulus like a tree to perceiving the tree? (p. 5)
- What is the difference between perceiving something and recognizing it? (p. 8)
- How do perceptual psychologists go about measuring the varied ways that we perceive the environment. (p. 13)

Imagine that you have been given the following hypothetical science project.

Project: Design a device that can *locate*, *describe*, and *identify* all objects in the environment, including their distance from the device and their relationships to each other. In addition, make the device capable of traveling from one point to another, avoiding obstacles along the way.

Extra credit: Make the device capable of having *conscious experience*, such as what *people* experience when they look out at a scene.

Warning: This project, should you decide to accept it, is extremely difficult. It has not yet been solved by the best computer scientists, even though they have access to the world’s most powerful computers.

Hint: Humans and animals have solved these problems in a number of elegant ways. They use (1) two spherical sensors called “eyes,” which contain a light-sensitive chemical, to sense light; (2) two detectors on the sides of the head, called “ears,” which are fitted with tiny vibrating hairs to sense pressure changes in the air; (3) small pressure detectors of various shapes imbedded under the skin to sense stimuli on the skin; and (4) two types of chemical detectors to detect gases that are inhaled and solids and liquids that are ingested.

Additional note: Designing the detectors is just the first step in creating the system. An information processing system is also needed. In the case of the human, this information processing system is a “computer” called the brain, with 100 billion active units and interconnections so complex that they have still not been completely deciphered. Although the detectors are an important part of the project, the design of the computer is crucial, because the information that is picked up by the detectors needs to be analyzed. Note that the operation of the human system is still not completely understood and that the best scientific minds in the world have made little progress with the extra credit part of the problem. Focus on the main problem first, and leave conscious experience until later.

The “science project” just described is about **perception**—conscious experience that results from stimulation of the senses. Our goal in this book is to understand how humans and animals perceive, starting with the detectors—the eyes, ears, skin receptors, and receptors in the nose and mouth—and then moving on to the computer—the brain. We want to understand how we sense things in the environment and interact with them. The paradox we face is that although we still don’t understand perception, perceiving is something that occurs almost effortlessly. In most situations, we simply open our eyes and see what is around us, listen and hear sounds, eat and taste, without expending any particular effort.

Because of the ease with which we perceive, many people see perception as something that “just happens” and don’t see the feats achieved by our senses as complex or amazing. “After all,” the skeptic might say, “for vision, a picture of the environment is focused on the back of my eye, and that picture provides all the information my brain needs to duplicate the environment in my consciousness.” But the idea that perception is not very complex is exactly what misled computer scientists in the 1950s and 1960s to propose that it would take only about a decade or so to create “perceiving machines” that could negotiate the environment with humanlike ease. That prediction, made half a century ago, has yet to come true, even though a computer defeated the world chess champion in 1997 and defeated two *Jeopardy!* champions in 2010. From a computer’s point of view, perceiving a scene is more difficult than playing world championship chess or accessing vast amounts of knowledge to answer quiz questions. In this chapter, we will consider a few practical reasons for studying perception, how perception occurs in a sequence of steps, and how to measure perception.

Why Read This Book?

The most obvious answer to the question “Why read this book?” is that it is required reading for a course you are taking. Thus, it is probably an important thing to do if you want to get a good grade. But beyond that, there are a number of other reasons for reading this book. For one thing, it will provide you with information that may be helpful in other courses and perhaps even your future career. If you plan to go to graduate school to become a researcher or teacher in perception or a related area, this book will provide you with a solid background to build on. In fact, many of the research studies you will read about were carried out by researchers who read earlier editions of this book when they were undergraduates.

The material in this book is also relevant to future studies in medicine or related fields, because much of our discussion is about how the body operates. Medical applications that depend on an understanding of perception include devices to restore perception to people who have lost vision or hearing and treatments for pain. Other applications include robotic vehicles that can find their way through unfamiliar environments, face recognition systems that can identify people as

they pass through airport security, speech recognition systems that can understand what someone is saying, and highway signs that are visible to drivers under a variety of conditions.

But reasons to study perception extend beyond the possibility of useful applications. Studying perception can help you become more aware of the nature of your own perceptual experiences. Many of the everyday experiences that you take for granted—such as tasting food, looking at a painting in a museum, or listening to someone talking—can be appreciated at a deeper level by considering questions such as “Why do I lose my sense of taste when I have a cold?” “How do artists create an impression of depth in a picture?” and “Why does an unfamiliar language sound as if it is one continuous stream of sound, without breaks between words?” This book will not only answer these questions but will answer other questions that you may not have thought of, such as “Why don’t I see colors at dusk?” and “How come the scene around me doesn’t appear to move as I walk through it?” Thus, even if you aren’t planning to become a physician or a robotic vehicle designer, you will come away from reading this book with a heightened appreciation of both the complexity and the beauty of the mechanisms responsible for your perceptual experiences, and perhaps even with an enhanced awareness of the world around you.

Because perception is something you experience constantly, knowing about how it works is interesting in its own right. To appreciate why, consider what you are experiencing right now. If you touch the page of this book, or look out at what’s around you, you might get the feeling that you are perceiving exactly what is “out there” in the environment. After all, touching this page puts you in direct contact with it, and it seems likely that what you are seeing is what is actually there. But one of the things you will learn as you study perception is that everything you see, hear, taste, feel, or smell is the result of the activity in your nervous system and your knowledge gained from past experience.

Think about what this means. There are things out there that you want to see, hear, taste, smell, and feel. But the only way to achieve this is by activating *sensory receptors* in your body designed to respond to light energy, sound energy, chemical stimuli, and pressure on the skin. When you run your fingers over the pages of this book, you feel the page and its texture because the pressure and movement are activating small receptors just below the skin. Thus, whatever you are feeling depends on the activation of these receptors. If the receptors weren’t there, you would feel nothing, or if they had different properties, you might feel something different from what you feel now. This idea that *perception depends on the properties of the sensory receptors* is one of the themes of this book.

A few years ago, I received an email from a student (not one of my own, but from another university) who was using an earlier edition of this book.¹ In her email, “Jenny” made a

¹Who is “I”? In various places in the book you will see first-person references such as this one (“I received an email”) or others, like “a student in my class,” or “I tell my students,” or “I had an interesting experience.” Because this book has two authors, you may wonder who *I* or *my* is. The answer is that, unless otherwise noted, it is author B. G., because most of the first-person references in this edition are carried over from the 9th edition, which was written by B. G.

number of comments about the book, but the one that struck me as being particularly relevant to the question “Why read this book?” is the following: “By reading your book, I got to know the fascinating processes that take place every second in my brain, that are doing things I don’t even think about.” Your reasons for reading this book may turn out to be totally different from Jenny’s, but hopefully you will find out some things that will be useful, or fascinating, or both.

The Perceptual Process

Perception happens at the end of what can be described, with apologies to the Beatles, as a long and winding road (McCartney, 1970). This road begins outside of you, with stimuli in the environment—trees, buildings, birds chirping, smells in the air—and ends with the behavioral responses of perceiving, recognizing, and taking action. We picture this journey from stimuli to responses by the seven steps in **Figure 1.1**, called the **perceptual process**. The process begins with a stimulus in the environment (a tree in this example) and ends with the conscious experiences of perceiving the tree, recognizing the tree, and taking action with respect to the tree.

Because this process is involved in everything we will be describing in this book, it is important to note that Figure 1.1 is a simplified version of what happens. First, many things happen within each “box.” For example, “neural processing,”

involves understanding not only how cells called neurons work, but how they interact with each other and how they operate within different areas of the brain. Another reason we say the series of boxes in Figure 1.1 is simplified is that steps in the perceptual process do not always unfold in a one-follows-the-other order. For example, research has shown that perception (“I see something”) and recognition (That’s a tree”) may not always happen one after another, but could happen at the same time, or even in reverse order (Gibson & Peterson, 1994). And when perception or recognition leads to action (“Let’s have a closer look at the tree”), that action could change perception and recognition (“Looking closer shows that what I thought was an oak tree turns out to be a maple tree”). This is why there are reverse arrows between perception, recognition, and action. In addition, there is an arrow from “action” back to the stimulus. This turns the perceptual process into a “cycle” in which taking action, for example, walking toward the tree, changes the observer’s view of the tree.

Even though the process is simplified, Figure 1.1 provides a good way to think about how perception occurs and introduces some important principles that will guide our discussion of perception throughout this book. In the first part of this chapter, we will briefly describe each stage of the process; in the second part, we will consider ways of measuring the relationship between stimuli and perception.

But What About “Sensation”?

Before we begin describing the stages of the perceptual process, let’s consider something that may have occurred to you: Why is Figure 1.1 called the *perceptual* process, when the title of this book is *Sensation and Perception*? To answer this question, let’s consider the terms *sensation* and *perception*. When a distinction is made between *sensation* and *perception*, *sensation* is often identified as involving simple “elementary” processes that occur right at the beginning of a sensory system, as when light stimulates receptors in the eye. In contrast, *perception* is identified with complex processes that involve higher-order mechanisms such as interpretation and memory that involve activity in the brain. It is therefore often stated, especially in introductory psychology textbooks, that *sensation* involves detecting elementary properties of a stimulus (Carlson, 2010), and *perception* involves the higher brain functions involved in interpreting events and objects (Myers, 2004).

Keeping this distinction in mind, let’s consider the displays in **Figure 1.2**. **Figure 1.2a** is extremely simple—a single dot. Let’s for the moment assume that this simplicity means that there is no interpretation or higher-order processes, so sensation is involved. Looking at **Figure 1.2b**, with three dots, we might now think that we are dealing with perception, because we interpret the three dots as creating a triangle. Going even further, we can say that **Figure 1.2c**, which is made up of many dots, is a “house.” Surely this must be perception because it involves many dots and our past experience with houses. But let’s return to **Figure 1.2a**, which we called a dot. As it turns out, even a stimulus this simple can be seen in more than one

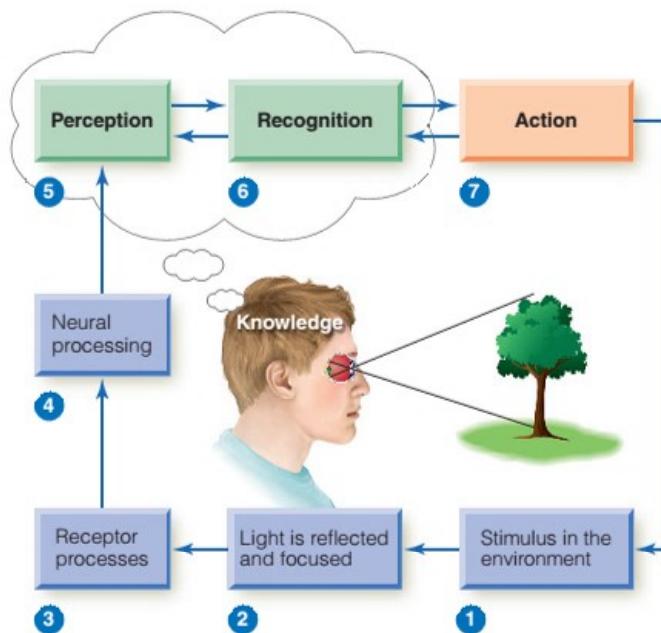


Figure 1.1 The perceptual process. These seven steps, plus “knowledge” inside the person’s brain, summarize the major events that occur between the time a person looks at the stimulus in the environment (the tree in this example) and perceives the tree, recognizes it, and takes action toward it. Figures 1.3–1.6 describe the steps in the perceptual process in more detail.

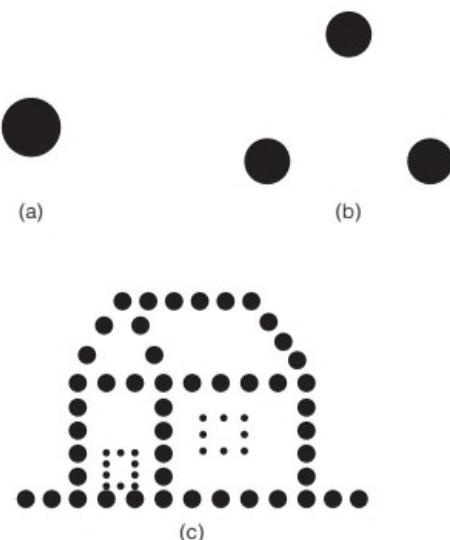


Figure 1.2 (a) One dot, (b) a triangle, (c) a house. What do these stimuli tell us about sensations and perceptions? See text for discussion.

way. Is this a black dot on a white background or a hole in a piece of white paper? Now that interpretation is involved, does our experience with Figure 1.2a become *perception*?

This example illustrates that deciding what is *sensation* and what is *perception* is not always obvious. As we will see in this book, there are experiences that depend heavily on processes that occur right at the beginning of a sensory system, in the sensory receptors or nearby, and there are other experiences that depend on interpretation and past experiences, using information stored in the brain. But this book takes the position that calling some processes *sensation* and others *perception* doesn't add anything to our understanding of how our sensory experiences are created, so the term *perception* is used almost exclusively throughout this book.

Perhaps the main reason not to use the term *sensation* is that, with the exception of papers on the history of perception research (Gilchrist, 2012), the term *sensation* appears only rarely in modern research papers (for example, papers on the sense of taste occasionally refer to taste *sensations*), whereas the term *perception* is extremely common. Despite the fact that introductory psychology books may distinguish between sensation and perception, modern perception researchers don't make this distinction.

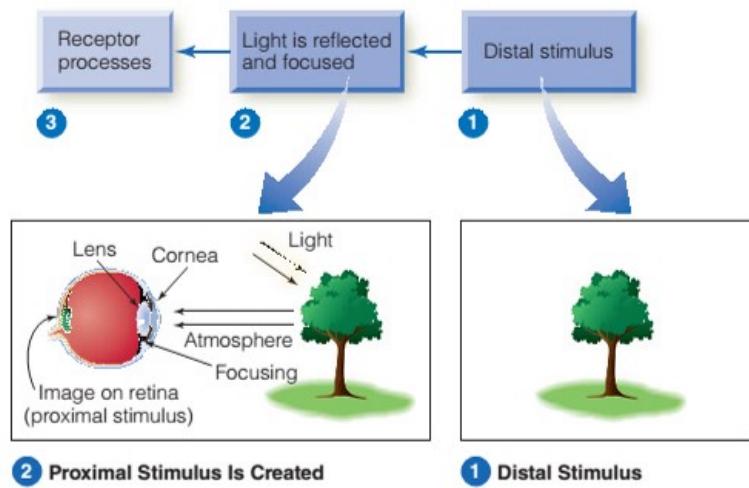
So why is this book called *Sensation and Perception*? Blame history. Sensation was discussed in the early history of perceptual psychology, and courses and textbooks followed suit by including *sensation* in their titles. But while researchers eventually stopped using the term *sensation*, the titles of the courses and books remained the same. So sensations are historically important (we will discuss this briefly in Chapter 5), but as far as we are concerned, everything that involves understanding how we experience the world through our senses comes under the heading of perception. With that bit of terminology out of the way, we are now ready to consider Steps 1 and 2 of the perceptual process, by accompanying someone who is observing a tree in a field.

Distal and Proximal Stimuli (Steps 1 and 2)

There are stimuli within the body that produce internal pain and enable us to sense the positions of our body and limbs. But for the purposes of this discussion, we will focus on stimuli that exist "out there" in the environment, and we will consider what happens to stimuli in the first two steps of the perceptual process in which stimuli in the environment reach receptors in the eye (**Figure 1.3**).

We begin with the tree that the person is observing, which we call the *distal stimulus* (Step 1). It is called distal because it is "distant"—out there in the environment. The person's perception of the tree is based not on the tree getting into his eye (ouch!), but on light reflected from the tree and reaching

Figure 1.3 Steps 1 and 2 of the perceptual process. Step 1: Information about the tree (the *distal stimulus*) is carried by light. Step 2: The light is transformed when it is reflected from the tree, when it travels through the atmosphere, and when it is focused by the eye's optical system. The result is the *proximal stimulus*, the image of the tree on the retina, which is a representation of the tree.



the visual receptors (Step 2). The reflection of light from the tree introduces one of the central principles of perception, the **principle of transformation**, which states that *stimuli and responses created by stimuli are transformed, or changed, between the distal stimulus and perception*.

The first transformation occurs when light hits the tree and is then reflected from the tree to the person's eyes. The nature of the reflected light depends on properties of the light energy hitting the tree (is it the midday sun, light on an overcast day, or a spotlight illuminating the tree from below?), properties of the tree (its textures, shape, the fraction of light hitting it that it reflects), and properties of the atmosphere through which the light is transmitted (is the air clear, dusty, or foggy?).

When this reflected light enters the eye, it is transformed as it is focused by the eye's optical system, which is the *cornea* at the front of the eye and the *lens* directly behind it. If these optics are working properly, they form a sharp image of the tree on the *receptors* of the person's *retina*, a 0.4-mm-thick network of nerve cells that covers the back of the eye and that contains the receptors for vision. This image on the retina is the **proximal stimulus**, so called because it is "in proximity" to the receptors (Step 2). If the eye's optics are not working properly, this proximal stimulus—the image that reaches the retina—may be blurred.

The fact that an image of the tree is focused on the retina introduces another principle of perception, the **principle of representation**, which states that *everything a person perceives is based not on direct contact with stimuli but on representations of stimuli that are formed on the receptors and the resulting activity in the person's nervous system*.

The distinction between the distal stimulus (Step 1) and the proximal stimulus (Step 2) illustrates both transformation and representation. The distal stimulus (the tree) is *transformed* into the proximal stimulus, and this image *represents* the tree in the person's eyes. But this transformation from "tree" to "image of the tree on the retina" is just the first in a series of transformations. The next transformation occurs within the receptors at the back of the eye.

Receptor Processes (Step 3)

Sensory receptors are cells specialized to respond to environmental energy, with each sensory system's receptors specialized to respond to a specific type of energy. Visual receptors respond to light, auditory receptors to pressure changes in the air, touch receptors to pressure transmitted through the skin, and smell and taste receptors to chemicals entering the nose and mouth. When the visual receptors that line the back of the eye receive the light reflected from the tree, they do two things: (1) They transform environmental energy into electrical energy; and (2) they shape perception by the way they respond to different properties of stimuli (**Figure 1.4**).

Visual receptors transform light energy into electrical energy because they contain a light-sensitive chemical called **visual pigment**, which reacts to light. The transformation of one form of energy (light energy in this example) to another form (electrical energy) is called **transduction**. Another

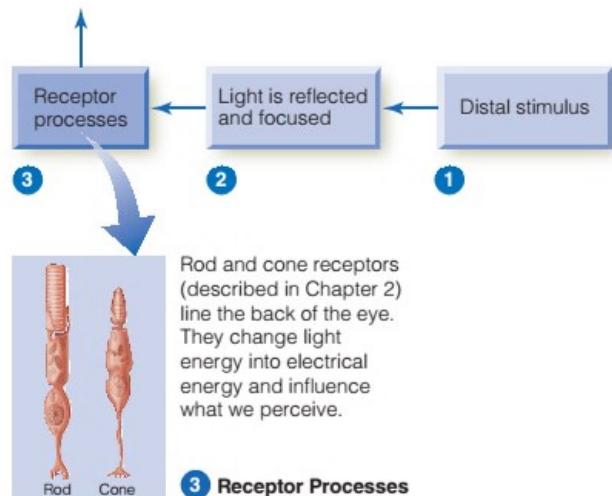


Figure 1.4 Step 3 of the perceptual process. *Receptor processes* include transduction (the transformation of light energy into electrical energy) and the shaping of perception by the properties of visual pigments in the receptor's outer segments. The end result is an electrical representation of the tree.

example of transduction occurs when you touch the "withdrawal" button or icon on an ATM. The pressure exerted by your finger is transduced into electrical energy, which causes a device that uses mechanical energy to dispense your money out of the machine.

Transduction by the visual pigments is crucial for perception, because without it information about the representation of the tree formed on the retina would not reach the brain and perception would not occur. In addition, the visual pigments shape perception in two ways: (1) The ability to see dim light depends on having a high concentration of light-sensitive pigment in the receptors; and (2) there are different types of pigments, which respond best to light in different parts of the visible spectrum. Some pigments respond better to light in the blue-green part of the spectrum; others respond better to the yellow-red part of the spectrum. We will describe both transduction and how the properties of the different pigments influence perception in Chapter 2.

Neural Processing (Step 4)

Once transduction occurs, the tree becomes represented by electrical signals in thousands of visual receptors. But what happens to these signals? As we will see in Chapter 2, they travel through a vast interconnected network of neurons that (1) *transmit* signals from the receptors, through the retina, to the brain, and then within the brain; and (2) *change* (or *process*) these signals as they are transmitted. These changes occur because of interactions between neurons as the signal travels from the receptors to the brain. Because of this processing, some signals become reduced or are prevented from getting through, and others are amplified so they arrive at the brain with added strength. This processing then continues as signals travel to various places in the brain.

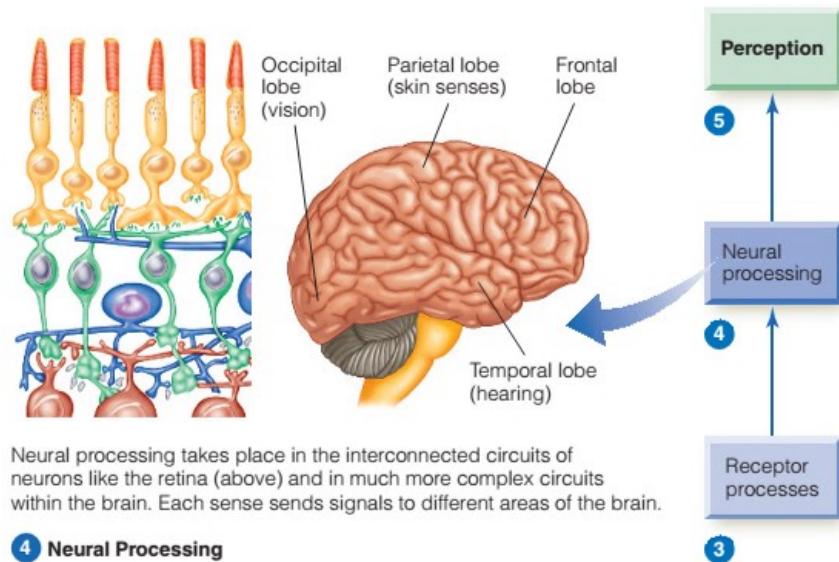


Figure 1.5 Step 4 of the perceptual process. *Neural processing* involves interactions between the electrical signals traveling in networks of neurons early in the system, in the retina; later, on the pathway to the brain; and finally, within the brain.

The changes in these signals that occur as they are transmitted through this maze of neurons is called **neural processing** (**Figure 1.5**). Processing will be described in more detail in Chapters 2 and 3. For now, the main point is that processing continues the process of transformation that began when looking at the tree created an image of the tree inside the eye, which was then changed into electrical signals in the visual receptors. A similar process occurs for other senses as well. For example, sound energy (pressure change in the air) is transformed into electrical signals inside the ear and is transmitted out of the ear along the auditory nerve, then through a series of structures on the way to the brain.

Electrical signals from each sense arrive at the **primary receiving area** for that sense in the cerebral cortex of the brain (as shown in Figure 1.5). The **cerebral cortex** is a 2-mm-thick layer that contains the machinery for creating perceptions, as well as other functions, such as language, memory, and thinking. The primary receiving area for vision occupies most of the **occipital lobe**; the area for hearing is located in part of the **temporal lobe**; and the area for the skin senses—touch, temperature, and pain—is located in an area in the **parietal lobe**. As we study each sense in detail, we will see that once signals reach the primary receiving areas, they are then transmitted to many other structures in the brain. For example, the **frontal lobe** receives signals from all of the senses, and it plays an important role in perceptions that involve the coordination of information received through two or more senses.

The sequence of transformations that occurs between the receptors and the brain, and then within the brain, means that the pattern of electrical signals in the brain is changed compared to the electrical signals that left the receptors. It is important to note, however, that although these signals have changed, they still represent the tree. In fact, the changes that occur as the signals are transmitted and processed are crucial for achieving the next step in the perceptual process, the *behavioral responses*.

Behavioral Responses (Steps 5–7)

Finally, after all that reflection, focusing, transduction, transmission, and processing, we reach the behavioral responses (**Figure 1.6**). This transformation is perhaps the most miraculous of all, because *electrical signals* (Step 4) are transformed into *conscious experience*: The person *perceives* the tree (Step 5) and *recognizes* it (Step 6). We can distinguish between *perception*, which is conscious awareness of the tree, and *recognition*, which is placing an object in a category, such as “tree,” that gives it meaning, by considering the case of Dr. P., a patient described by neurologist Oliver Sacks (1985) in the title story of his book *The Man Who Mistook His Wife for a Hat*.

Dr. P., a well-known musician and music teacher, first noticed a problem when he began having trouble recognizing his students visually, although he could immediately identify them by the sound of their voices. But when Dr. P. began misperceiving common objects, for example addressing a parking meter as if it were a person or expecting a carved knob on a piece of furniture to engage him in conversation, it became clear that his problem was more serious than just a little forgetfulness. Was he blind, or perhaps crazy? It was clear from an eye examination that he could see well, and by many other criteria it was obvious that he was not crazy.

Dr. P.’s problem was eventually diagnosed as **visual form agnosia**—an inability to recognize objects—that was caused by a brain tumor. He perceived the parts of objects but couldn’t identify the whole object, so when Sacks showed him a glove, Dr. P. described it as “a continuous surface unfolded on itself. It appears to have five outpouchings, if this is the word.” When Sacks asked him what it was, Dr. P. hypothesized that it was “a container of some sort. It could be a change purse, for example, for coins of five sizes.” The normally easy process of object recognition had, for Dr. P., been derailed by his brain tumor.

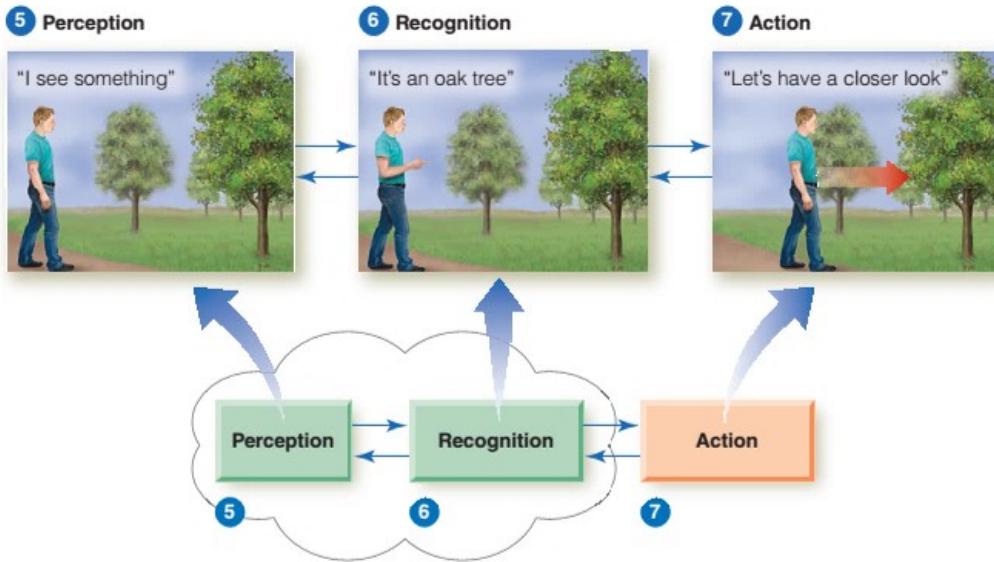


Figure 1.6 Steps 5–7 of the perceptual process. The behavioral responses: *perception*, *recognition*, and *action*.

He could perceive the object and recognize parts of it, but he couldn't perceptually assemble the parts in a way that would enable him to recognize the object as a whole. Cases such as this show that it is important to distinguish between perception and recognition.

The final behavioral response is **action** (Step 7), which involves motor activities. For example, the person might decide to walk toward the tree, have a picnic under it, or climb it. Even if he doesn't decide to interact directly with the tree, he is taking action when he moves his eyes and head to look at different parts of the tree, even if he is standing in one place.

Some researchers see action as an important outcome of the perceptual process because of its importance for survival. David Milner and Melvyn Goodale (1995) propose that early in the evolution of animals, the major goal of visual processing was not to create a conscious perception or “picture” of the environment but to help the animal control navigation, catch prey, avoid obstacles, and detect predators—all crucial functions for the animal’s survival.

The fact that perception often leads to action—whether it be an animal’s increasing its vigilance when it hears a twig snap in the forest or a person’s deciding to interact with an object or just look more closely at something that looks interesting—means that perception is a continuously changing process. For example, the image of the tree on the back of the eye changes every time the person moves his body or his eyes relative to the tree, and this change creates new representations and a new series of transformations. Thus, although we can describe the perceptual process as a series of steps that “begins” with the distal stimulus and “ends” with perception, recognition, and action, the overall process is dynamic and continually changing.

Knowledge

Our diagram of the perceptual process includes one more factor: **knowledge**. **Knowledge** is any information that the perceiver brings to a situation. Knowledge is placed inside the person’s brain in Figure 1.1 because it can affect a number of the steps in the perceptual process. Knowledge that a person brings to a situation can be information acquired years ago or, as in the following demonstration, information just recently acquired.

DEMONSTRATION | Perceiving a Picture

After looking at the drawing in **Figure 1.7**, close your eyes, turn to page 11, and open and shut your eyes rapidly to briefly expose the picture in **Figure 1.11**. Decide what the picture is; then open your eyes and read the explanation below it. Do this now, before reading further.



Figure 1.7 See “Demonstration: Perceiving a Picture” for instructions. (Adapted from Bugelski & Alampay, 1961)

Did you identify Figure 1.11 as a rat (or a mouse)? If you did, you were influenced by the clearly rat- or mouselike figure you observed initially. But people who first observe Figure 1.14 (page 13) instead of Figure 1.7 usually identify Figure 1.11 as a man. (Try this on someone else.) This demonstration, which is called the **rat-man demonstration**, shows how recently acquired knowledge (“that pattern is a rat”) can influence perception.

An example of how knowledge acquired years ago can influence the perceptual process is your ability to **categorize**—to place objects into categories. This is something you do every time you name an object. “Tree,” “bird,” “branch,” “car,” and everything else you can name are examples of objects being placed into categories that you learned as a young child and that have become part of your knowledge base.

Another way to describe the effect of information that the perceiver brings to the situation is by distinguishing between bottom-up processing and top-down processing. **Bottom-up processing** (also called **data-based processing**) is processing that is based on the stimuli reaching the receptors. These stimuli provide the starting point for perception because, with the exception of unusual situations such as drug-induced perceptions or “seeing stars” from a bump to the head, perception involves activation of the receptors. The woman sees the moth on the tree in **Figure 1.8** because of processes triggered by the moth’s image on her retina. The image is the “incoming data” that is the basis of bottom-up processing.

Top-down processing (also called **knowledge-based processing**) refers to processing that is based on knowledge. When the woman labels what she is seeing as a “moth” or perhaps a particular kind of moth, she is accessing what she has learned about moths. Knowledge such as this isn’t always involved in perception, but as we will see, it often is—sometimes without our even being aware of it.

To experience top-down processing in action, try reading the following sentence:

M*RY H*D * L*TTL* L*MB

Figure 1.8 Perception is determined by an interaction between bottom-up processing, which starts with the image on the receptors, and top-down processing, which brings the observer’s knowledge into play. In this example, (a) the image of the moth on the woman’s retina initiates bottom-up processing; and (b) her prior knowledge of moths contributes to top-down processing.

If you were able to do this, even though all of the vowels have been omitted, you probably used your knowledge of English words, how words are strung together to form sentences, and your familiarity with the nursery rhyme to create the sentence (Denes & Pinson, 1993).

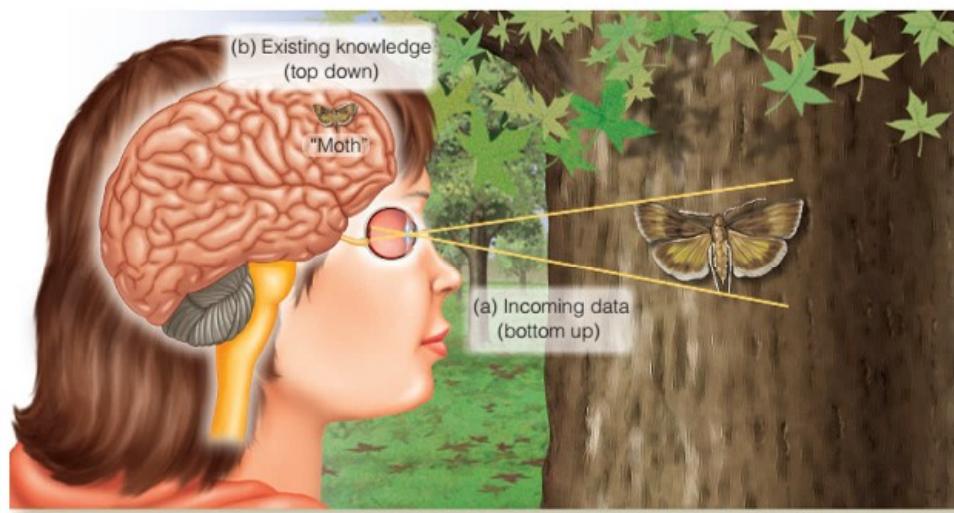
Students often ask whether top-down processing is always involved in perception. The answer to this question is that it is “very often” involved. There are some situations, typically involving very simple stimuli, in which top-down processing may not be involved. For example, perceiving a single flash of easily visible light is probably not affected by a person’s prior experience. However, as stimuli become more complex, the role of top-down processing increases. In fact, a person’s past experience is usually involved in perception of real-world scenes, even though in most cases the person is unaware of this influence. One of the themes of this book is that our knowledge of how things usually appear in the environment can play an important role in determining what we perceive.

Studying the Perceptual Process

The goal of perceptual research is to understand each of the steps in the perceptual process that lead from the stimulus to the behavioral responses of perception, recognition, and action. (For simplicity, we will use the term *perception* to stand for all of these behavioral outcomes in the discussion that follows.) One way the perceptual process has been studied is by determining the following three relationships, shown in **Figure 1.9**:

- Relationship A: The stimulus-perception relationship
- Relationship B: The stimulus-physiological relationship
- Relationship C: The physiology-perception relationship

To illustrate how these relationships have been measured in actual experiments, we consider how researchers have studied a



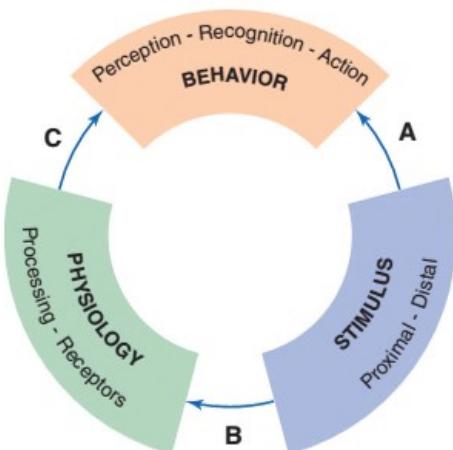


Figure 1.9 Simplified perceptual process showing the three relationships described in the text. The three boxes represent the three major components of the seven-step perceptual process: Stimuli (Steps 1 and 2); Physiology (Steps 3 and 4); and the three Behavioral responses (Steps 5–7). The three relationships that are usually measured to study the perceptual process are (A) the stimulus–perception relationship; (B) the stimulus–physiology relationship; and (C) the physiology–perception relationship.

phenomenon called the oblique effect. The **oblique effect** is that people see vertical or horizontal lines better than lines oriented obliquely (at any orientation other than vertical or horizontal). We will first consider how the oblique effect has been studied, by measuring relationships A and B, which both involve stimuli.

The Two “Stimulus” Relationships (A and B)

The stimulus is involved in two relationships, one behavioral (Arrow A in Figure 1.9, from the stimulus to behavioral responses), the other physiological (Arrow B, from the stimulus to physiological responses). Relationship A, the first stimulus relationship, is the **stimulus–perception relationship**, which relates stimuli (Steps 1 and 2 in Figure 1.1) to behavioral responses (Steps 5–7). This was the main relationship measured during the first 100 years of the scientific study of perception, before physiological methods became widely available.

To illustrate this relationship, let's consider an experiment that measures the oblique effect. The oblique effect has been demonstrated by presenting black and white striped stimuli called gratings, and measuring **grating acuity**, the smallest width of lines that subjects can detect. One way to measure grating acuity is to ask subjects to indicate the grating's orientation and testing with thinner and thinner lines. Eventually, the lines are so thin that they can't be seen, and the area inside the circle looks uniform, so subjects can no longer indicate the grating's orientation. The smallest line-width at which the subject can still indicate the correct orientation is the grating acuity (**Figure 1.10**). When grating acuity is determined for different orientations, the acuity is best for gratings oriented vertically or horizontally (Appelle, 1972). This is a behavioral demonstration of the oblique effect.

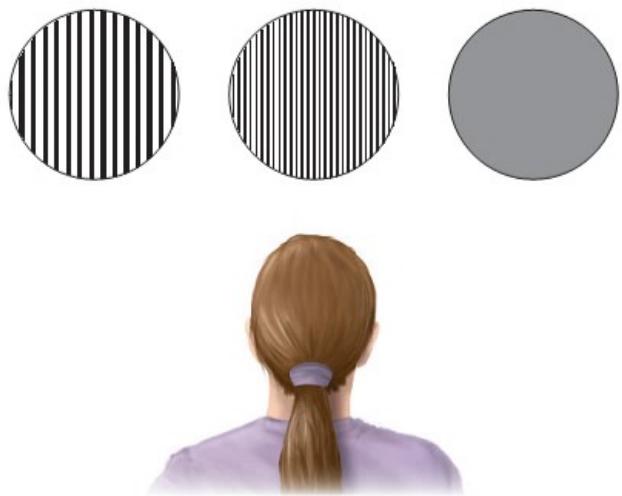


Figure 1.10 Measuring grating acuity. The finest line width at which a subject can perceive the bars in a black-and-white grating stimulus is that subject's grating acuity. Stimuli with different line widths are presented one at a time, and the subject indicates the grating's orientation until the lines are so close together that the subject can no longer indicate the orientation.

The second stimulus relationship (Arrow B in Figure 1.9) is the **stimulus–physiology relationship**, the relationship between stimuli (Steps 1–2) and physiological responses (Steps 3–4). David Coppola and coworkers (1998) measured the oblique effect physiologically by presenting lines with different orientations (**Figure 1.12a**) to ferrets. When they measured the ferret's brain activity using a technique called *optical brain imaging* that measures activity over a large area of the ferret's visual cortex, they found that horizontal or vertical orientations caused larger brain responses than oblique orientations (**Figure 1.12b**).² This is a physiological demonstration of the oblique effect.



Figure 1.11 Did you see a “rat” or a “man”? Looking at the more ratlike picture in Figure 1.7 increased the chances that you would see this one as a rat. But if you had first seen the man version (Figure 1.14), you would have been more likely to perceive this figure as a man. (Adapted from Bugelski & Alampay, 1961)

²Because a great deal of physiological research has been done on animals, students often express concerns about how these animals are treated. All animal research in the United States follows strict guidelines for the care of animals established by organizations such as the American Psychological Association and the Society for Neuroscience. The central tenet of these guidelines is that every effort should be made to ensure that animals are not subjected to pain or distress. Research on animals has provided essential information for developing aids for people with sensory disabilities such as blindness and deafness and for helping develop techniques to ease severe pain.

(a) **Stimuli:** vertical, horizontal, slanted



(b) **Brain response:** Bigger to vertical and horizontal orientations



Miodrag Hlavac/Shutterstock.com

Figure 1.12 Coppola and coworkers (1998) measured the relationship between bar orientation (stimuli) and brain activity (physiology) in ferrets. Verticals and horizontals generated the greatest brain activity.

Note that even though the stimulus-perception experiment was carried out on humans and the stimulus-physiology experiment was carried out on ferrets, the results are similar. Horizontal and vertical orientations result in better acuity (Relationship A) and larger physiological responses (Relationship B) than oblique orientations. When behavioral and physiological responses to stimuli are similar like this, researchers often infer relationship C, between physiological responding and perception, which in this case would be the association between greater physiological responses to horizontals and verticals and better perception of horizontals and verticals. But in some cases, researchers have measured the physiology-perception relationship directly.

The Physiology-Perception Relationship (C)

The physiology-perception relationship relates physiological responses (Steps 3–4 in Figure 1.1) and behavioral responses (Steps 5–7) (Arrow C in Figure 1.9). Christopher Furmanski and Stephen Engel (2000) determined this relationship for different line orientations by measuring the brain response and behavioral sensitivity in the same subjects. The behavioral measurements were made by decreasing the intensity difference between light and dark bars of a grating until the subject could no longer detect the grating's orientation. Subjects were able to detect the horizontal (90°) and vertical (0°) orientations at smaller light-dark differences than for the oblique orientations (45° and 135°). This

means that subjects were more sensitive to the horizontal and vertical orientations (**Figure 1.13a**). The physiological measurements were made using a technique called functional magnetic resonance imaging (fMRI), which we will describe in Chapter 4 (see page 75). These measurements showed larger brain responses to vertical or horizontal gratings than to oblique gratings (**Figure 1.13b**).

The results of this experiment, therefore, are consistent with the results of the other two experiments, which both demonstrated the oblique effect. The beauty of this experiment is that the behavioral and physiological responses were measured in the same subjects. The reason for the visual system's preference for horizontal and vertical orientations, which has to do with the prevalence of verticals and horizontals in the environment, will be discussed in Chapter 5.

Cognitive Influences on Perception

As we study perception measuring the three relationships in Figure 1.9, we will also be concerned with how the knowledge, memories, and expectations that people bring to a situation influence their perceptions. These factors, which we have

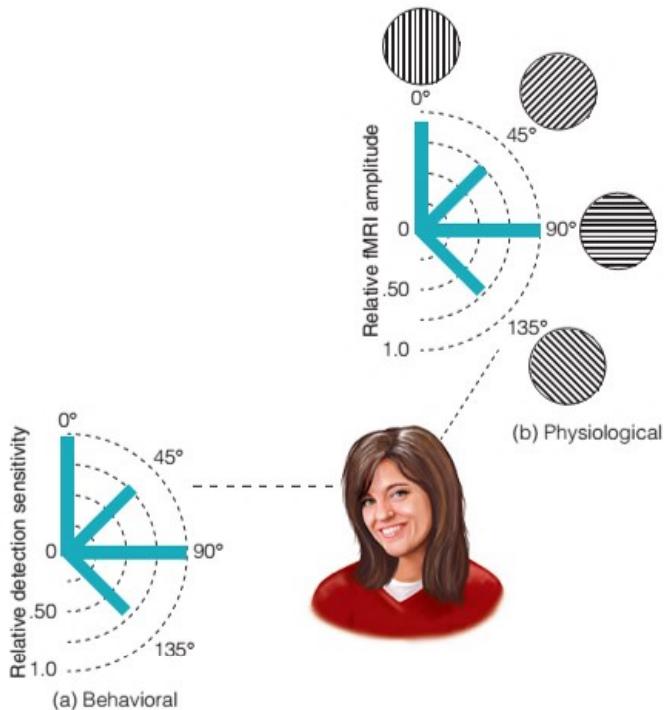


Figure 1.13 Furmanski and Engel (2000) made both behavioral and physiological measurements of subjects' response to oriented gratings. (a) Bars indicate sensitivity to gratings of different orientations. Sensitivity is highest to the vertical (0 degree) and horizontal (90 degree) orientations; (b) Bars indicate fMRI amplitude to different orientations. Amplitudes were greater to the 0- and 90-degree orientations.

described as the starting place for top-down processing, are called **cognitive influences on perception**. These cognitive influences were represented by the word “knowledge” inside the person’s brain in the perceptual cycle in Figure 1.1. Researchers study cognitive influences by measuring how knowledge and other factors, such as memories and expectations, affect all of the relationships in Figure 1.9.

For example, consider the rat-man demonstration. If we were to measure the stimulus–perception relationship by showing just Figure 1.11 to a number of people, we would probably find that some people see a rat and some people see a man. But when we add some “knowledge” by first presenting the more rat-like picture in Figure 1.7, most people see Figure 1.11 as a “rat” or “mouse.” Thus, in this example, knowledge has affected the stimulus–perception relationship. As we will see throughout this book, these cognitive influences affect perception not only for demonstrations like rat–man, in which knowledge is presented just before testing the subject, but also for other perceptual phenomena, in which knowledge has been accumulated over a long period of time.

One of the things that becomes apparent when we step back and look at the three relationships is that each one provides information about different aspects of the perceptual process. An important message of this book is that to truly understand perception, we have to study it by measuring both behavioral (A) and physiological (B and C) relationships. Only by considering both behavior and physiology together can we create a complete picture of the mechanisms responsible for perception.

TEST YOURSELF 1.1

1. What are some reasons for studying perception?
2. Describe the process of perception as a series of seven steps, beginning with the distal stimulus and culminating in the behavioral responses of perceiving, recognizing, and acting.
3. What is the role of higher-level or “cognitive” processes in perception? Be sure you understand the difference between bottom-up and top-down processing.
4. What does it mean to say that perception can be studied by measuring three relationships? Give an example of how the oblique effect was studied by measuring each relationship.

Measuring Perception

So far we’ve pictured the perceptual process as having a number of steps (Figure 1.1), and we’ve demonstrated how we can study the process by studying three different relationships (Figure 1.9). But what, exactly, do we *measure* to determine these relationships? In this section we will describe a number of different ways to measure behavioral responses. We will describe physiological methods in the chapters that follow.

What is measured in an experiment looking at the relationship between stimuli and behavior? The grating acuity experiment described on page 11 (Figure 1.10) measured the threshold for seeing fine lines, where the *threshold* is the smallest line width that can be detected. **Thresholds** measure the limits of sensory systems; they are measures of minimums—the smallest line-width that can be detected, the smallest amount of light energy we can see, the smallest amount of sound energy we can hear, the smallest concentration of a chemical we can taste or smell. Thresholds have an important place in the history of perceptual psychology, and of psychology in general, so let’s consider them in more detail before describing other ways of measuring perception. As we will now see, the importance of being able to accurately measure thresholds was recognized very early in the history of the scientific study of the senses.

Gustav Fechner Introduces Methods to Measure Thresholds

Gustav Fechner (1801–1887), professor of physics at the University of Leipzig, had wide-ranging interests, having published papers on electricity, mathematics, color perception, aesthetics (the judgment of art and beauty), the mind, the soul, and the nature of consciousness. But of all his accomplishments, the most significant one was providing a new way to study the mind.

Fechner’s thinking about the mind must be viewed against the backdrop of how people thought about the mind in the mid-1800s. Prevailing thought at that time was that it was impossible to study the mind. The mind and the body were thought to be totally separate from one another. People saw the body as physical and therefore something that could be seen, measured, and studied, whereas the mind was considered not physical and was therefore invisible and something that couldn’t be measured and studied. Another reason proposed to support the idea that the mind couldn’t be studied was the assertion that it is impossible for the mind to study itself.

Against this backdrop of skepticism regarding the possibility of studying the mind, Fechner, who had been thinking about this problem for many years, had an insight, the story goes, while lying in bed on the morning of October 22, 1850. His insight was that the mind and body should not be thought of as totally separate from one another but as two



Figure 1.14 Man version of the rat–man stimulus. (Adapted from Bugelski & Alampay, 1961)

sides of a single reality (Wozniak, 1999). Most important, Fechner proposed that the mind could be studied by measuring the relationship between changes in physical stimulation (the body part of the relationship) and a person's experience (the mind part). This proposal was based on the observation that as physical stimulation is increased—for example, by increasing the *intensity* of a light—the person's perception of the *brightness* of the light also increases.

Ten years after having his insight about the mind, Fechner (1860/1966) published his masterpiece, *Elements of Psychophysics*, in which he coined the term **psychophysics**—the study of the relation between mental (psycho) and physical (physics)—and proposed a number of methods for measuring this relationship. One of the major contributions of *Elements of Psychophysics* was the proposal of three methods for measuring the threshold. One of these methods, called the **method of limits**, is described in the Methods section below.

Every so often we will introduce a new method by describing it in a "Method" section. Students are sometimes tempted to skip these sections because they think the content is unimportant. However, you should resist this temptation because these methods are essential tools for the study of perception. These "Method" sections are often related to experiments described immediately afterward and also provide the background for understanding experiments that are described later in the book.

METHOD Method of Limits

In the **method of limits**, the experimenter presents stimuli in either ascending order (intensity is increased) or descending order (intensity is decreased), as shown in **Figure 1.15**, which indicates the results of an experiment that measures a person's threshold for hearing a tone.

Intensity	1	2	3	4	5	6	7	8
103	Y		Y		Y		Y	
102	Y		Y		Y		Y	
101	Y		Y		Y		Y	Y
100	Y	Y	Y	Y			Y	Y
99	Y	N	Y	N	Y	Y	Y	Y
98	N	N	Y	N	N	N	N	Y
97	N	N	N		N		N	
96	N		N		N		N	
95	N		N		N		N	

Crossover → 98.5 99.5 97.5 99.5 98.5 98.5 98.5 97.5
values

Threshold = Mean of crossovers = 98.5

Figure 1.15 The results of an experiment to determine the threshold using the method of limits. The dashed lines indicate the crossover point for each sequence of stimuli. The threshold—the average of the crossover values—is 98.5 in this experiment.

On the first series of trials, the experimenter begins by presenting a tone with an intensity we will call 103, and the observer indicates by a "yes" response that he hears the tone. This response is indicated by a Y at an intensity of 103 in the far left column of the table. The experimenter then presents another tone, at a lower intensity, and the observer responds to this tone. This procedure continues, with the observer making a judgment at each intensity until he responds "no," he did not hear the tone. This change from "yes" to "no," indicated by the dashed line, is the *crossover point*, and the threshold for this series is taken as the mean between 99 and 98, or 98.5. The next series of trials begins below the observer's threshold, so that he says "no" on the first trial (intensity 95), and continues until he says "yes" (when the intensity reaches 100). Notice that the crossover point when starting below the threshold is slightly different. Because the crossover points may vary slightly, this procedure is repeated a number of times, starting above the threshold half the time and starting below the threshold half the time. The threshold is then determined by calculating the average of all of the crossover points.

The method of limits takes into account the variability of human perception by averaging the results of a number of trials. Fechner's other two methods, *adjustment* and *constant stimuli*, which are described in Appendix A (page 384), also do this. Taken together, these methods, which are called the **classical psychophysical methods**, opened the way for the founding of scientific psychology by providing methods to measure an aspect of the mind. Because of the impact of Fechner's ideas, October 22, the date Fechner awoke with his insight that led to the founding of psychophysics, is known among psychophysical researchers as "Fechner Day." Add that date to your calendar if you're looking for another holiday to celebrate!

The example used to illustrate the method of limits involves measuring the **absolute threshold**—the smallest stimulus level that can just be detected. Another type of threshold is the **difference threshold**—the smallest *difference* between two stimuli that enables us to tell the difference between them. In *Elements of Psychophysics*, Fechner not only proposed his psychophysical methods but also described the work of Ernst Weber (1795–1878), a physiologist who, a few years before the publication of Fechner's book, measured the difference threshold for different senses. See Appendix B (page 385) for more details about difference thresholds.

Fechner's and Weber's methods not only made it possible to measure the ability to detect stimuli but also made it possible to determine *mechanisms* responsible for experiences. For example, consider what happens when you enter a dark place and then stay there for a while. At first you may not be able to see much (**Figure 1.16a**), but eventually your vision gets better and you are able to see light and objects that were invisible before (**Figure 1.16b**). This improved vision occurs because your threshold for seeing light is becoming smaller and smaller as you stay in the dark.



(a)



(b)

© Bruce Goldstein

Figure 1.16 (a) How a dark scene might be perceived when seen just after being in the light. (b) How the scene would be perceived after spending 10 to 15 minutes adapting to the dark. The improvement in perception after spending some time in the dark reflects a decrease in the threshold for seeing light.

By measuring how a person's threshold changes moment by moment, we can determine a function called the *dark adaptation curve* that shows how the threshold becomes smaller as the person spends more time in the dark. Thus, measuring thresholds takes us beyond simply saying that "we see better when we spend time in the dark" to providing a quantitative description of what is happening from moment to moment as a person's ability to see improves. In Chapter 2, we will show how measuring the dark adaptation curve has enabled researchers to determine the physiological mechanisms that cause our vision to improve in the dark, and later in the book we will describe other experiments in which measuring thresholds has helped uncover other perceptual mechanisms.

As significant as the methods for measuring thresholds are, we know that perception includes far more than just what happens at threshold. To understand the richness of experience, we need to be able to measure other aspects of sensory experience in addition to thresholds. We will describe some of the ways perceptual researchers measure sensory experience above threshold by considering five questions about the perceptual world and the techniques used to answer these questions.

Five Questions About the Perceptual World

We begin with a question about stimuli that are easy to detect because they are above threshold.

Question 1: What Is the Perceptual Magnitude of a Stimulus? Technique: Magnitude Estimation

Things are big and small (an elephant; a bug), loud and soft (rock music; a whisper); intense and just perceptible (sunlight;

a dim star), overpowering and faint (heavy pollution; a faint smell). Fechner was not only interested in measuring thresholds using the classical psychophysical methods; he was also interested in determining the relationship between physical stimuli (like rock music and a whisper) and the perception of their magnitude (like perceiving one to be *loud* and the other *soft*). Fechner created a mathematical formula relating physical stimuli and perception; modern psychologists have modified Fechner's equation based on a method not available in Fechner's time called **magnitude estimation** (Stevens, 1957, 1961).

METHOD | Magnitude Estimation

The procedure for a magnitude estimation experiment is relatively simple: The experimenter first presents a "standard" stimulus to the subject (let's say a light of moderate intensity) and assigns it a value of, say, 10. The subject then sees lights of different intensities, and is asked to assign a number to each of these lights that is proportional to the brightness of the original light. This number for "brightness" is the **perceived magnitude** of the stimulus. If the light appears twice as bright as the standard, it gets a rating of 20; half as bright, a 5; and so on. Thus, the subject assigns a brightness to each light intensity.

The results of experiments using magnitude estimation to measure brightness are discussed further in the "Something to Consider" section at the end of this chapter, and the mathematical formulas relating physical intensity and perceptual magnitude are discussed in Appendix C (p. 386).

Question 2: What Is the Identity of the Stimulus?

Technique: Recognition Testing When you name things, you are categorizing them (see page 10). The process of



Figure 1.17 A stimulus like those used in an experiment in which subjects are asked to recognize a rapidly flashed scene. Subjects can often recognize general properties of a rapidly flashed scene, such as “houses near water and a boat,” but need more time to perceive the details.

categorizing, which is called **recognition**, is measured in many different types of perceptual experiments. One application is testing the ability of people with brain damage. As we saw earlier in this chapter, Dr. P’s brain damage led him to have trouble recognizing common objects, like a glove. The recognition ability of people with brain damage is tested by asking them to name objects or pictures of objects.

Recognition is also used to assess the perceptual abilities of people without brain damage. In Chapter 5 we will describe experiments that show that people can identify rapidly flashed pictures (“It’s a docking area for boats lined with houses”), although seeing all of the details requires more time (**Figure 1.17**).

Recognition is not only visual; it can also include hearing (“that’s a car revving its engine”), touch (identifying an object by scanning it with your fingers), taste (“mmm, chocolate”), and smell (“that’s a rose”). Because recognizing objects is so crucial for our survival, many perception researchers have shifted their emphasis from asking “What do you see?” (perception) to asking “What is that called?” (recognition).

Question 3: How Quickly Can I React to It?

Technique: Reaction Time The speed with which we react to something can be determined by measuring **reaction time**—the time between presentation of a stimulus and the person’s reaction to it. An example of a reaction time experiment is to ask subjects to keep their eyes fixed on the + in the display in **Figure 1.18a** and pay attention to location A on the left rectangle. Because the subject is *looking at* the + but *paying attention to* the top of the left rectangle, this task resembles what happens when you are looking in one direction but are paying attention to something off to the side.

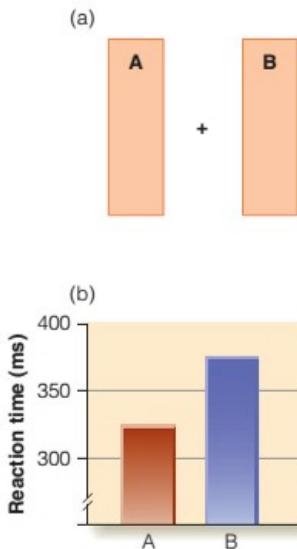


Figure 1.18 (a) A reaction time experiment in which the subject is told to look at the + sign, but pay attention to the location at A, and to push a button as quickly as possible when a dark target flashes anywhere on the display. (b) Reaction times in milliseconds, which indicates that reaction time was faster when the target was flashed at A, where the subject was attending, than when it was flashed at B, where the subject was not attending. (Data from Egly et al., 1994)

While directing attention to the top of the left rectangle, the subject’s task was to push a button as quickly as possible when a dark target flashed anywhere on the display. The results, shown in **Figure 1.18b**, indicate that the subject responded more quickly when the target was flashed at A, where he or she was directing attention, compared to B, off to the side (Egly et al., 1994). These findings are relevant to a topic we will discuss in Chapter 7: How does talking on a cell phone while driving affect the ability to drive?

Question 4: How Can I Describe What Is Out There? Technique: Phenomenological Report

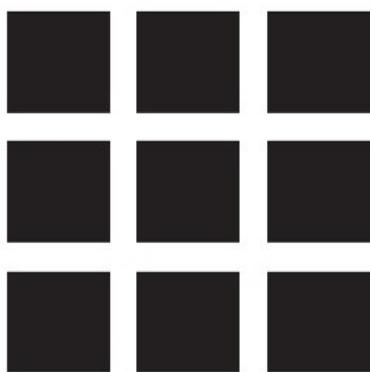
Look around. Describe what you see. You could name the objects you recognize, or you could describe the pattern of lights and darks and colors, or how things are arranged in space, or that two objects appear to be the same or different sizes or colors. Describing what is out there is called **phenomenological report**. For example, do you see a vase or two faces in **Figure 1.19a**? We will see in Chapter 5 that displays like this are used to study how people perceive objects in front of backgrounds.

Another exercise in phenomenal reporting is to describe what you see in **Figure 1.19b**, which is called the **Hermann grid**. People often report that there are dark spots in the white areas at the intersections, but when they look directly at an intersection, the spot vanishes. (Try it!) We will discuss this interesting illusion in Chapter 3.

Phenomenological reports are important because they define the perceptual phenomena we want to explain and once a phenomenon is identified, we can then study it using other methods. For example, once a display like the Hermann grid is



(a)



(b)

Figure 1.19 (a) Vase–face stimulus used to demonstrate how people perceive objects in front of a background. (b) Hermann grid. Notice the dark spots at the intersections of the white “corridors.” These spots occur even though the corridors are the same white all over.

identified, we can then do experiments using other methods to determine why the spots are occurring.

Question 5: How Can I Interact With It? Technique: Physical Tasks and Judgments All of the other questions have focused on different ways of measuring what we perceive. This last question is concerned not with perception but with actions that follow perception. Many perceptual researchers believe that one of the primary functions of perception is to enable us to take action within our environment. Look at it this way: Morg the caveman sees a dangerous tiger in the woods. He could stand there and marvel at the beauty of its fur, or the power of its legs, but if he doesn’t take action by either hiding or getting away and the tiger sees him, his days of perceiving will be over. On a less dramatic level, we need to be able to see a saltshaker and then accurately reach across the table to pick it up, or navigate from one place on campus to another to get to class. Research on perception and action, which we will describe in Chapter 7, has subjects carry out tasks that involve both perception and action, such as reaching for a target, navigating through a maze, or driving a car, under different conditions.

Physical tasks have also been studied by having people make judgments about tasks before they actually carry them out. For example, we will see in Chapter 7 that people judge a box to be heavier if they think they will be lifting it than when they think someone will be helping them.

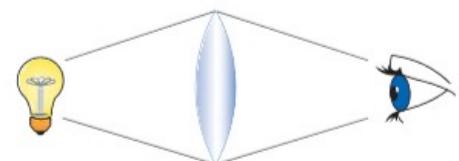
The examples above provide a hint as to the wide range of methods that are used in perception research. This book discusses research using the methods described above, plus others as well. Although we won’t describe the details of the methods used in every experiment we consider, we will highlight the most important methods in “Methods” sections like the ones on the method of limits and on magnitude estimation in this chapter. Additionally, many physiological methods will be described in Methods sections in the chapters that follow. What will emerge as you read this book is a story in which important roles are played by both behavioral and physiological methods, which combine to create a more complete understanding of perception than is possible using either type of method alone.

SOMETHING TO CONSIDER:

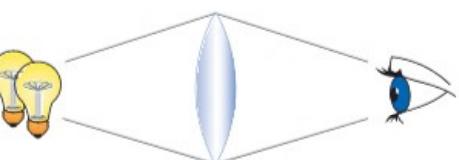
Why Is the Difference Between Physical and Perceptual Important?

One of the most crucial distinctions in the study of perception is the distinction between *physical* and *perceptual*. To illustrate the difference, consider the two situations in **Figure 1.20**. In (a), the light from one light bulb with a physical intensity of 10 is focused into a person’s eye. In (b), the light from two light bulbs, with a total physical intensity of 20, is focused into the person’s eye. All of this so far has been *physical*. If we were to measure the intensities of the lights with a light meter we would find that the person receives twice as much light in (b) as in (a).

But what does the person *perceive*? Perception of the light is measured not by determining the intensity but by



(a) One-bulb; Intensity = 10.



(b) Two-bulbs; Intensity = 20.

Figure 1.20 A subject (indicated by the eye) is viewing lights with different physical intensities. The two lights at (b) have twice the physical intensity as the single light at (a). However, when the subject is asked to judge brightness, which is a perceptual judgment, the light at (b) is judged to be only about 20 or 30 percent brighter than the light at (a).

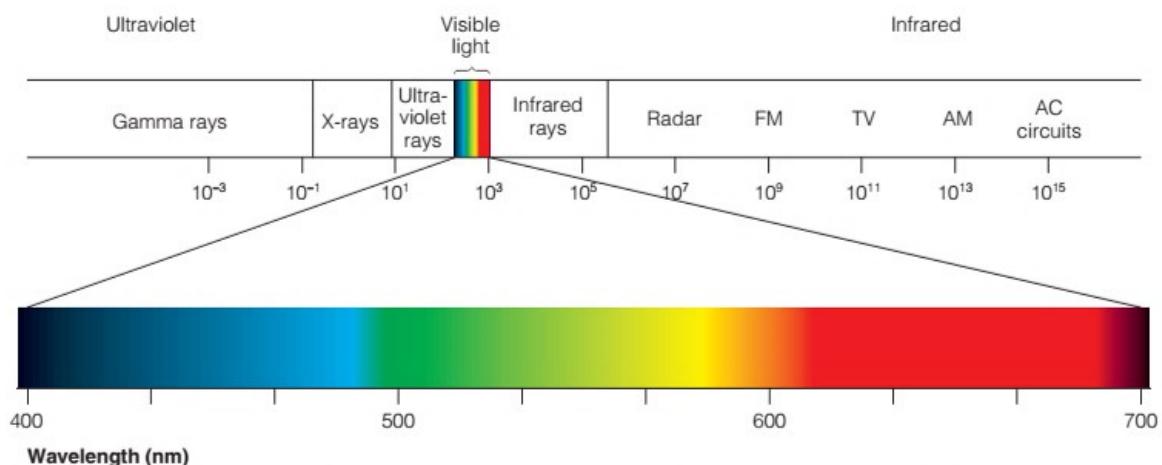


Figure 1.21 The electromagnetic spectrum, shown on top, stretches from gamma rays to AC circuits. The visible spectrum, shown exploded below, accounts for only a small part of the electromagnetic spectrum. We are blind to energy outside of the visible spectrum.

determining *perceived brightness* using a method such as magnitude estimation (see page 15). What happens to brightness when we double the intensity from (a) to (b)? The answer is that (b) will appear brighter than (a), but not twice as bright. If the brightness is judged to be 10 for light (a), the brightness of light (b) will be judged to be about 12 or 13 (Stevens, 1962; also see Appendix C, page 386). Thus, there is not a one-to-one relationship between the physical intensity of the light and our perceptual response to the light.

Another example of the distinction between physical and perceptual is the Hermann grid in Figure 1.19b, because while the white corridors are all exactly the same white, people perceive dark spots at the intersections. Physical and perceptual are clearly not the same in this situation.

The Hermann grid creates an “illusory perception” in which we perceive dark spots that aren’t physically present. But sometimes we fail to perceive stimuli that *are* physically present. Consider, for example the **electromagnetic spectrum** in **Figure 1.21**. The electromagnetic spectrum is a band of energy ranging from gamma rays at the short-wave end of the spectrum to AM radio and AC circuits at the long-wave end. But we see just the small band of energy called visible light, sandwiched between the ultraviolet and infrared energy bands. We are blind to ultraviolet and shorter wavelengths (although hummingbirds can see ultraviolet wavelengths that are invisible to us). We also can’t see at the high end of the spectrum, in the infrared and

above, which is probably a good thing—imagine the visual clutter we would experience if we could see all of those cell phone conversations carrying their messages through the air!

What these examples illustrate is that what physical measuring instruments record and what we perceive are two different things. Ludy Benjamin, in his book *A History of Psychology* (1997), makes this point when he observes that “If changes in physical stimuli always resulted in similar changes in perception of those stimuli . . . there would be no need for psychology; human perception could be wholly explained by the laws of the discipline of physics” (p. 120). But perception is psychology, not physics, and perceptual responses are not necessarily the same as the responses of physical measuring devices. We will, therefore, be careful, throughout this book, to distinguish between physical stimuli and the perceptual responses to these stimuli.

TEST YOURSELF 1.2

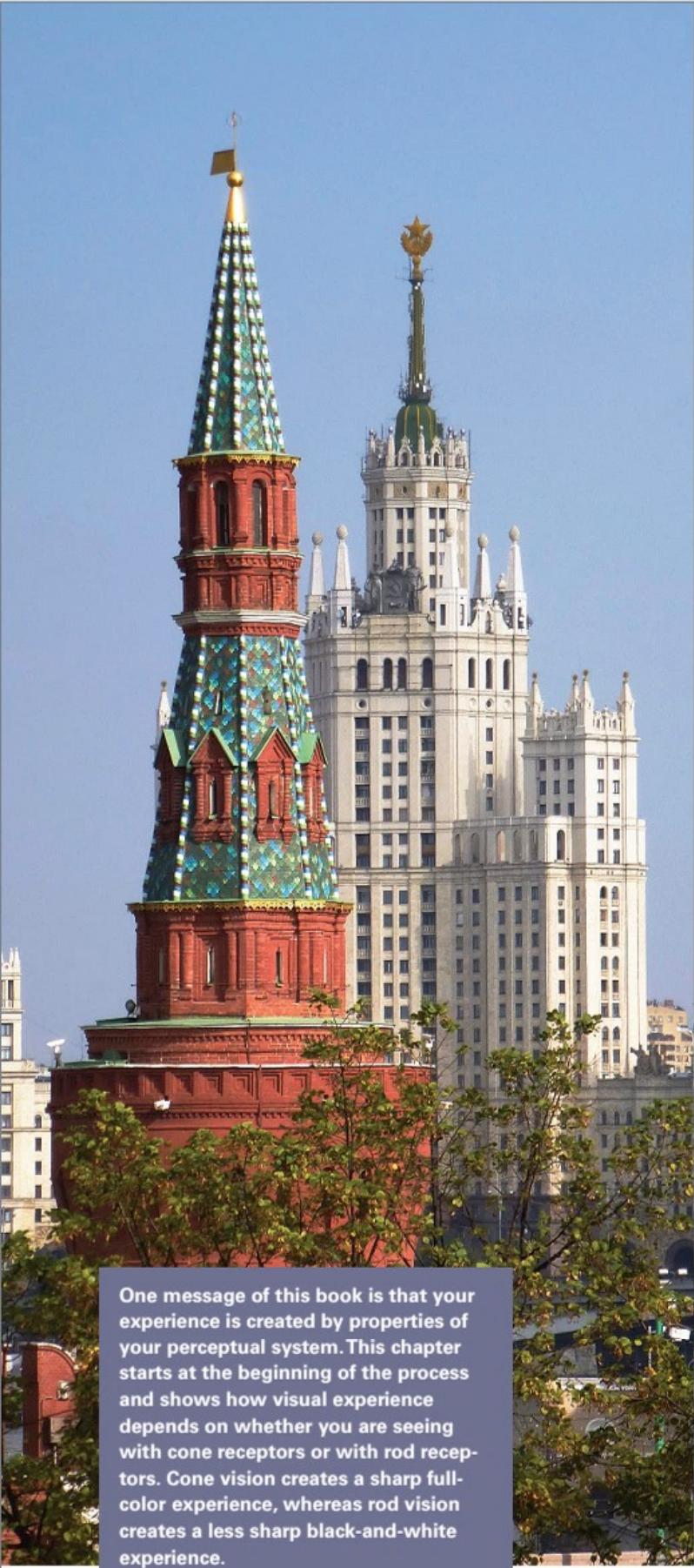
1. What was Fechner’s contribution to psychology?
2. Describe the five questions that can be asked about the world out there and the measurement techniques that are used to answer them.
3. Why is it important to distinguish between physical and perceptual?

THINK ABOUT IT

1. This chapter argues that although perception seems simple, it is actually extremely complex when we consider “behind the scenes” activities that are not obvious as a person is experiencing perception. Cite an example of a similar situation from your own experience, in which an “outcome” that might seem as though it was achieved easily actually involved a complicated process that most people are unaware of.
2. Describe a situation in which you initially thought you saw or heard something but then realized that your initial perception was in error. What was the role of bottom-up and top-down processing in this example of first having an incorrect perception and then realizing what was actually there?

KEY TERMS

Absolute threshold (p. 14)	Method of limits (p. 14)	Psychophysics (p. 14)
Action (p. 9)	Neural processing (p. 8)	Rat-man demonstration (p. 10)
Bottom-up processing (p. 10)	Oblique effect (p. 11)	Reaction time (p. 16)
Categorize (p. 10)	Occipital lobe (p. 8)	Recognition (p. 16)
Cerebral cortex (p. 8)	Parietal lobe (p. 8)	Sensation (p. 5)
Classical psychophysical methods (p. 14)	Perceived magnitude (p. 15)	Sensory receptors (p. 7)
Cognitive influences on perception (p. 13)	Perception (p. 4)	Stimulus-perception relationship (p. 11)
Difference threshold (p. 14)	Perceptual process (p. 5)	Stimulus-physiology relationship (p. 11)
Distal stimulus (p. 6)	Phenomenological report (p. 16)	Temporal lobe (p. 8)
Electromagnetic spectrum (p. 18)	Physiology-perception	Thresholds (p. 13)
Frontal lobe (p. 8)	relationship (p. 12)	Top-down processing (knowledge-based
Grating acuity (p. 11)	Primary receiving area (p. 8)	processing) (p. 10)
Hermann grid (p. 16)	Principle of representation (p. 7)	Transduction (p. 7)
Knowledge (p. 9)	Principle of transformation (p. 7)	Visual form agnosia (p. 8)
Magnitude estimation (p. 15)	Proximal stimulus (p. 7)	Visual pigment (p. 7)



One message of this book is that your experience is created by properties of your perceptual system. This chapter starts at the beginning of the process and shows how visual experience depends on whether you are seeing with cone receptors or with rod receptors. Cone vision creates a sharp full-color experience, whereas rod vision creates a less sharp black-and-white experience.



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The Beginning of the Perceptual Process

CHAPTER CONTENTS

Starting at the Beginning	Adapting to the Dark	Convergence Causes the Rods to Be More Sensitive Than the Cones
Light, the Eye, and the Visual Receptors	Spectral Sensitivity	Lack of Convergence Causes the Cones to Have Better Acuity Than the Rods
Light: The Stimulus for Vision	Electrical Signals in Neurons	SOMETHING TO CONSIDER: Early Events Are Powerful
The Eye	Recording Electrical Signals in Neurons	DEVELOPMENTAL DIMENSION: Infant Visual Acuity
Focusing Light Onto the Receptors	Basic Properties of Action Potentials	THINK ABOUT IT
Receptors and Perception	Chemical Basis of Action Potentials	
Transforming Light Energy Into Electrical Energy	Transmitting Information Across a Gap	
	Neural Convergence and Perception	

Some Questions We Will Consider:

- How does the focusing system at the front of our eye affect our perception? (p. 25)
- How do chemicals in the eye called visual pigments affect our perception? (p. 30)
- How can the way neurons are “wired up” affect perception? (p. 39)

How does a tree become a perception of a tree? One way to answer this question is to refer back to the perceptual process shown in Figure 1.1: Information about the tree (*distal stimulus*) is carried in light reflected from the tree and into the eye. When this light reaches the receptors in the retina, creating the *proximal stimulus*, it becomes transformed into electrical signals that contain information about the tree, which are transmitted to the brain, where eventually these electrical signals become transformed into a *perception* of the tree.

In this chapter we will focus on the beginning of the perceptual process. Although we will use visual examples to describe the initial processes of the perceptual process, many of the principles we will be describing hold for the other senses as well. Just as the person from Chapter 1 sees the tree because light is reflected from it into his eyes, he hears the rustle of its branches because sound energy in the form of pressure changes

in the air enters his ears. In both cases, stimuli trigger a process that ends up with perception occurring as a result of activity in the brain. Similar events occur for feeling the texture of the tree’s bark, smelling its blossoms, and tasting its fruit. By the time you finish this book, you will see that although there are numerous differences between the senses, they all operate according to similar principles.

Starting at the Beginning

The idea that perception starts at the beginning of the perceptual process may sound obvious. But as we will see, there is enough going on right at the beginning of the perceptual process to fill a whole chapter and more, and most of what goes on can affect perception. So, the first step in understanding perception is to take a close look at the processes that begin, in the case of vision, with light reflected from an object into the eye.

Figure 2.1 shows the first four steps of the visual process, which starts on the right and moves to the left to match the perceptual process in Figure 1.1. Following the sequence of the physical events in the process, shown in black along the bottom of the figure, we begin with Step 1, the distal stimulus (the tree); then move to Step 2, in which light is reflected from the tree and enters the eye to create the proximal stimulus on

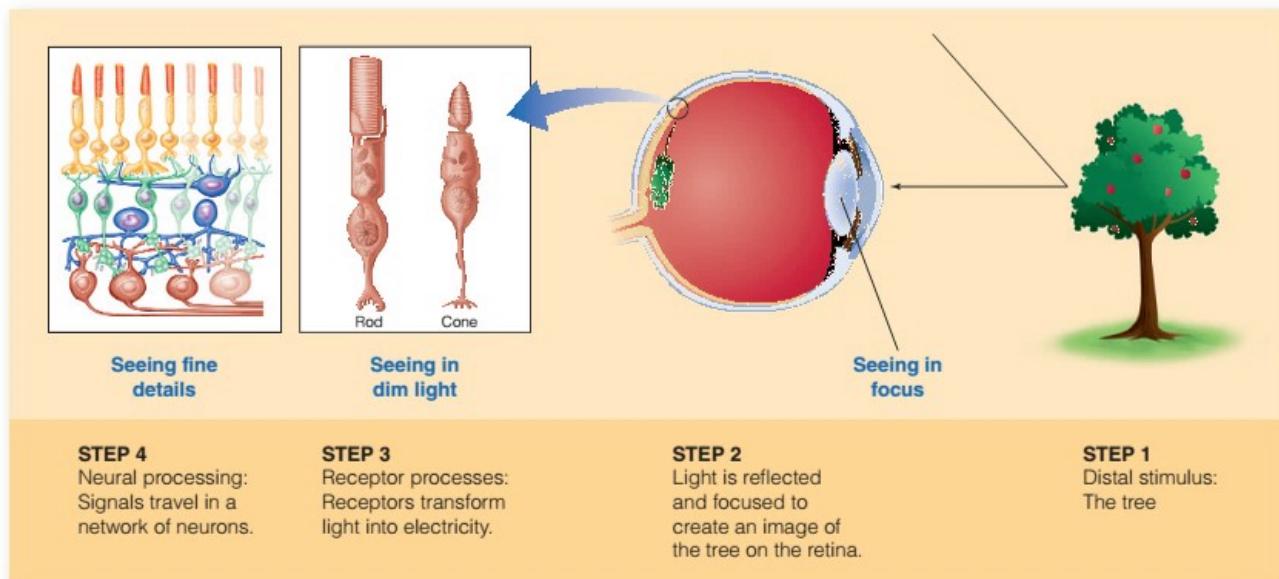


Figure 2.1 Chapter preview. This chapter will describe the first three steps of the perceptual process for vision and will introduce Step 4. Physical processes are indicated in black; the perceptual outcomes of these processes are indicated in blue.

the visual receptors; then to Step 3, in which receptors transform light into electrical signals; and finally to Step 4, in which electrical signals are “processed” as they travel through a network of neurons. Our goal in this chapter is to show how these physical events influence the following aspects of perception, shown in blue in Figure 2.1: (1) seeing in focus, (2) seeing in dim light, and (3) seeing fine details. We begin by describing light, the eye, and the receptors in the retina that line the back of the eye.

Light, the Eye, and the Visual Receptors

The ability to see a tree, or any other object, depends on light being reflected from that object into the eye.

Light: The Stimulus for Vision

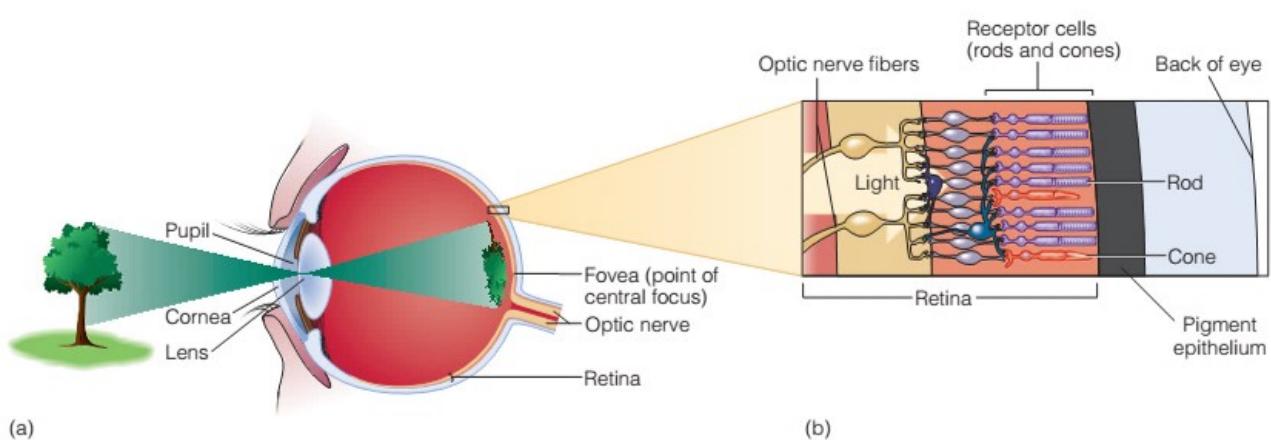
Vision is based on visible light, which is a band of energy within the electromagnetic spectrum. The electromagnetic spectrum is a continuum of electromagnetic energy that is produced by electric charges and is radiated as waves (see Figure 1.21, page 18). The energy in this spectrum can be described by its **wavelength**—the distance between the peaks of the electromagnetic waves. The wavelengths in the electromagnetic spectrum range from extremely short-wavelength gamma rays (wavelength = about 10^{-12} meters, or one ten-billionth of a meter) to long-wavelength radio waves (wavelength = about 10^4 meters, or 10,000 meters).

Visible light, the energy within the electromagnetic spectrum that humans can perceive, has wavelengths ranging from about 400 to 700 nanometers (nm), where 1 nanometer = 10^{-9} meters, which means that the longest visible wavelengths are slightly less than one-thousandth of a millimeter long. For humans and some other animals, the wavelength of visible light is associated with the different colors of the spectrum, with short wavelengths appearing blue, middle wavelengths green, and long wavelengths yellow, orange, and red.

The Eye

The **eyes** contain the receptors for vision. The first eyes, which appeared back in the Cambrian period (570–500 million years ago), were eyespots on primitive animals such as flatworms that could distinguish light from dark but couldn’t detect features of the environment. Detecting an object’s details didn’t become possible until more sophisticated eyes evolved to include optical systems that could produce images and therefore provide information about shapes and details of objects and the arrangement of objects within scenes (Fernald, 2006).

Light reflected from objects in the environment enters the eye through the **pupil** and is focused by the **cornea** and **lens** to form sharp images of the objects on the **retina**, the network of neurons that covers the back of the eye and that contains the receptors for vision (**Figure 2.2a**). There are two types of visual receptors, **rods** and **cones**, so called because of the rod- and cone-shaped **outer segments** (**Figure 2.3**). The outer segments are the part of the receptor that contains light-sensitive



(a)

(b)

Figure 2.2 An image of the tree is focused on the retina, which lines the back of the eye. The close-up of the retina on the right shows the receptors and other neurons that make up the retina.

chemicals called **visual pigments** that react to light and trigger electrical signals. Signals from the receptors flow through the network of neurons that make up the retina (**Figure 2.2b**) and emerge from the back of the eye in the **optic nerve**, which contains a million optic nerve fibers that conduct signals toward the brain.

The rod and cone receptors not only have different shapes, they are also distributed differently across the retina. From **Figure 2.4**, which indicates the rod and cone distributions, we can conclude the following:

1. One small area, the **fovea**, contains only cones. When we look directly at an object, the object's image falls on the fovea.
2. The **peripheral retina**, which includes all of the retina outside of the fovea, contains both rods and cones. It is important to note that although the fovea has *only* cones, there are also many cones in the peripheral retina.

The fovea is so small (about the size of this “o”) that it contains only about 1 percent, or 50,000, of the 6 million cones in the retina (Tyler, 1997a, 1997b).

3. The peripheral retina contains many more rods than cones because there are about 120 million rods and only 6 million cones in the retina.

One way to appreciate the fact that the rods and cones are distributed differently in the retina is by considering what happens when functioning receptors are missing from one area of the retina. A condition called **macular degeneration**, which is most common in older people, destroys the cone-rich fovea and a small area that surrounds it. (*Macula* is a term usually associated with medical practice that includes the fovea plus a small area surrounding the fovea.) This creates a blind region in central vision, so when a person looks directly at something, he or she loses sight of it (**Figure 2.5a**).

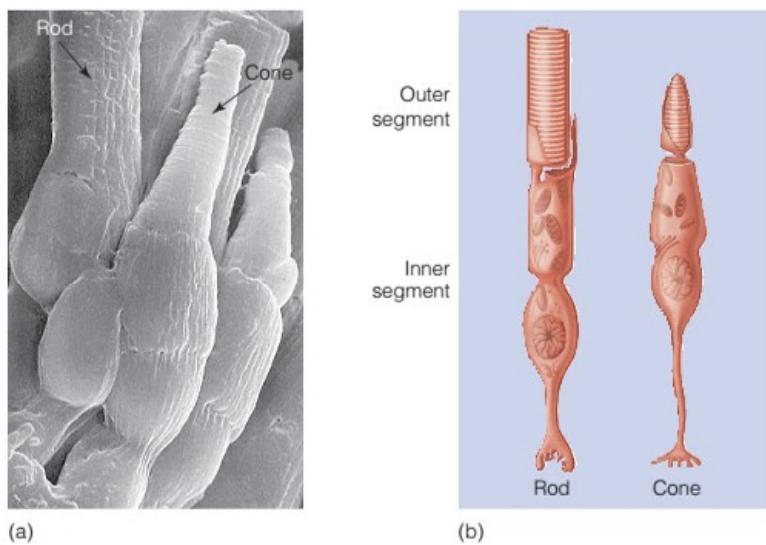


Figure 2.3 (a) Scanning electron micrograph of the rod and cone receptors in the retina, showing the rod-shaped and cone-shaped receptor outer segments. (b) Rod and cone receptors, showing the inner and outer segments. The outer segments contain the light-sensitive visual pigment. (From Lewis et al., 1969)

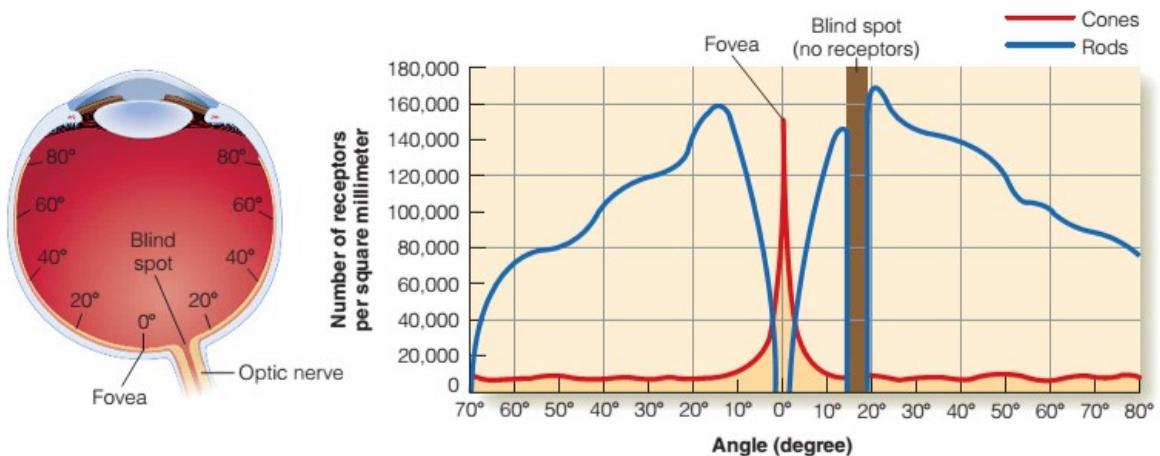


Figure 2.4 The distribution of rods and cones in the retina. The eye on the left indicates locations in degrees relative to the fovea. These locations are repeated along the bottom of the chart on the right. The vertical brown bar near 20 degrees indicates the place on the retina where there are no receptors because this is where the ganglion cells leave the eye to form the optic nerve. (Adapted from Lindsay & Norman, 1977)

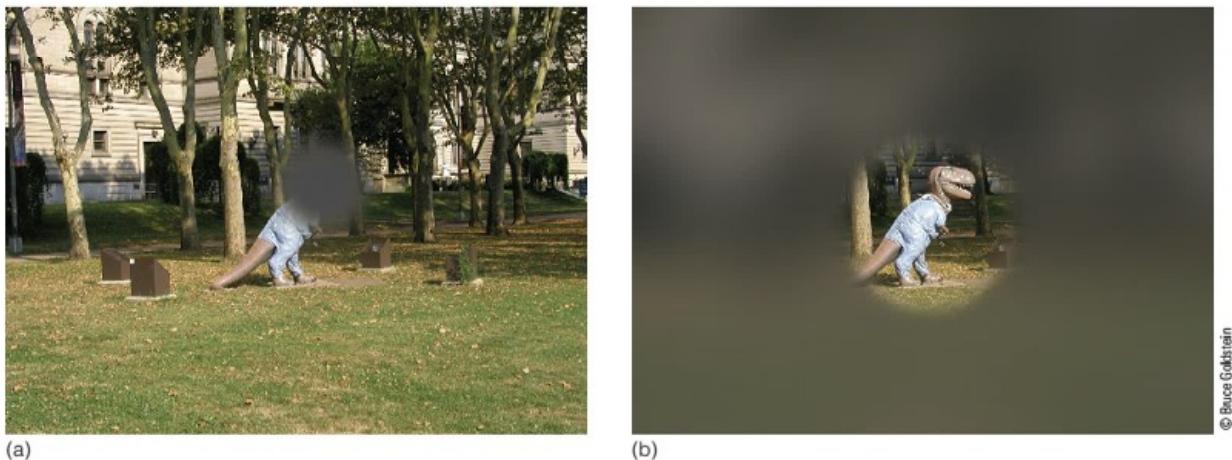


Figure 2.5 (a) In a condition called macular degeneration, the fovea and surrounding area degenerate, so the person cannot see whatever he or she is looking at. (b) In retinitis pigmentosa, the peripheral retina initially degenerates and causes loss of vision in the periphery. The resulting condition is sometimes called "tunnel vision."

Another condition, called **retinitis pigmentosa**, is a degeneration of the retina that is passed from one generation to the next (although not always affecting everyone in a family). This condition first attacks the peripheral rod receptors and results in poor vision in the peripheral visual field (**Figure 2.5b**). Eventually, in severe cases, the foveal cone receptors are also attacked, resulting in complete blindness.

Before leaving the rod-cone distribution shown in Figure 2.4, note that there is one area in the retina, indicated by the vertical brown bar, where there are no receptors. **Figure 2.6** shows a close-up of the place where this occurs, which is where the nerve fibers that make up the optic nerve leave the eye. Because of the absence of receptors, this place is called the **blind spot**. Although you are not normally aware

of the blind spot, you can become aware of it by doing the following demonstration.

DEMONSTRATION | Becoming Aware of the Blind Spot

Place the book (or your electronic device if you are reading the ebook) on your desk. Close your right eye, and position yourself above the book/device so that the cross in **Figure 2.7** is aligned with your left eye. Be sure the book page is flat and, while looking at the cross, slowly move closer. As you move closer, be sure not to move your eye from the cross, but at the same time keep noticing the circle off to the side. At some point, around 3 to 9 inches from the book/device, the circle should disappear. When this happens, the image of the circle is falling on your blind spot.

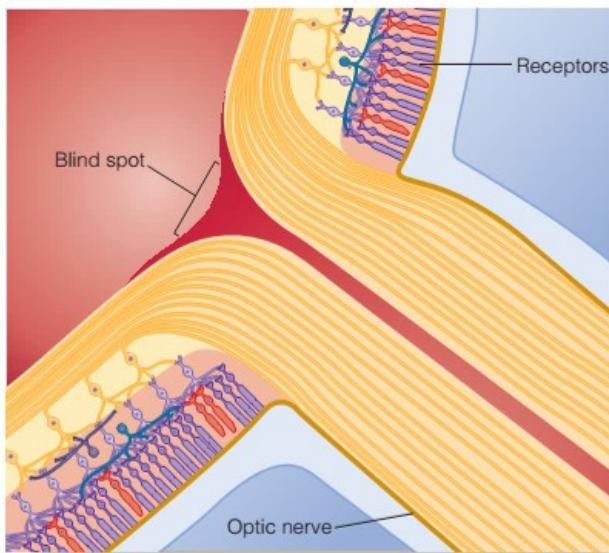


Figure 2.6 There are no receptors at the place where the optic nerve leaves the eye. This enables the receptor's ganglion cell fibers to flow into the optic nerve. The absence of receptors in this area creates the blind spot.



Figure 2.7 Blind spot demonstration.

Why aren't we usually aware of the blind spot? One reason is that the blind spot is located off to the side of our visual field, where objects are not in sharp focus. Because of this and because we don't know exactly where to look for it (as opposed to the demonstration, in which we are focusing our attention on the circle), the blind spot is hard to detect.

But the most important reason that we don't see the blind spot is that some mechanism in the brain "fills in" the place where the image disappears (Churchland & Ramachandran, 1996). The next demonstration illustrates an important property of this filling-in process.

DEMONSTRATION | Filling In the Blind Spot

Close your right eye and, with the cross in **Figure 2.8** lined up with your left eye, move toward the "wheel". When the center of the wheel falls on your blind spot, notice how the spokes of the wheel fill in the hole (Ramachandran, 1992).

These demonstrations show that the brain does not fill in the area served by the blind spot with "nothing"; rather, it creates a perception that matches the surrounding pattern—the white page in the first demonstration, and the spokes of the wheel in the second one. This "filling in" is a preview of one of the themes of the book: how the brain creates a coherent perception of our world. For now, however, we return to the beginning of the perceptual process, as light reflected from objects in the environment is focused onto the receptors.

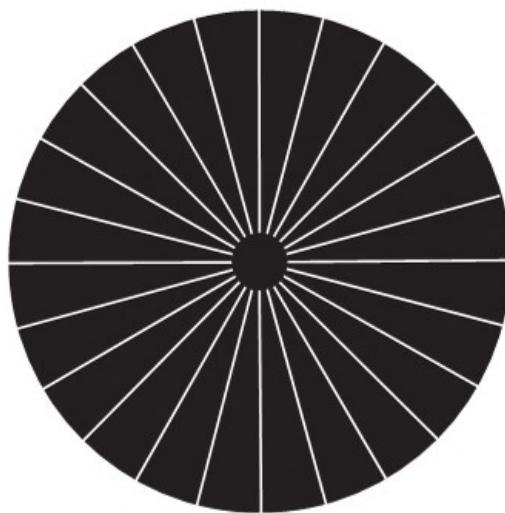


Figure 2.8 View the pattern as described in the text, and observe what happens when the center of the wheel falls on your blind spot. (Adapted from Ramachandran, 1992)

Focusing Light Onto the Receptors

Light reflected from an object into the eye is focused onto the retina by a two-element optical system: the cornea and the lens. The cornea, the transparent covering of the front of the eye, accounts for about 80 percent of the eye's focusing power, but like the lenses in eyeglasses, it is fixed in place so it can't adjust its focus. The lens, which supplies the remaining 20 percent of the eye's focusing power, can change its shape to adjust the eye's focus for objects located at different distances. This change in shape is achieved by the action of *ciliary muscles*, which increase the focusing power of the lens (its ability to bend light) by increasing its curvature (compare **Figure 2.9b** and **Figure 2.9c**).

We can understand why the eye needs to adjust its focus by first considering what happens when the eye is relaxed and a person with normal (20/20) vision views a small object that is far away. If the object is located more than about 20 feet away, the light rays that reach the eye are essentially parallel (**Figure 2.9a**), and the cornea-lens combination brings these parallel rays to a focus on the retina at point A. But if the object moves closer to the eye, the light rays reflected from this object enter the eye at more of an angle, and this pushes the focus point back so if the back of the eye weren't there, light would be focused at point B (**Figure 2.9b**). Because the light is stopped by the back of the eye before it reaches point B, the image on the retina is out of focus. If things remained in this state, the person would see the object as blurred.

The adjustable lens, which controls a process called *accommodation*, comes to the rescue to help prevent blurring. **Accommodation** is the change in the lens's shape that occurs when the ciliary muscles at the front of the eye tighten

and increase the curvature of the lens so that it gets thicker (**Figure 2.9c**). This increased curvature increases the bending of the light rays passing through the lens so the focus point is pulled back to A to create a sharp image on the retina. This means that as you look around at different objects, your eye is constantly adjusting its focus by accommodating, especially for nearby objects. The following demonstration shows that this is necessary because everything is not in focus at once.

DEMONSTRATION | Becoming Aware of What Is in Focus

Accommodation occurs unconsciously, so you are usually unaware that the lens is constantly changing its focusing power to let you see clearly at different distances. This unconscious focusing process works so efficiently that most people assume that everything, near and far, is always in focus. You can demonstrate that this is not so by holding a pen or a pencil, point up, at arm's length, closing one eye, and looking past the pencil at

an object that is at least 20 feet away. As you stay focused on the faraway object, notice the pencil point without actually looking at it (be sure to stay focused on the far object). The point will probably appear slightly blurred.

Then slowly move the pencil toward you while still looking at the far object. Notice that as the pencil moves closer, the point becomes more blurred. When the pencil is about 12 inches away, shift your focus to the pencil point. This shift in focus causes the pencil point to appear sharp, but the far object is now out of focus.

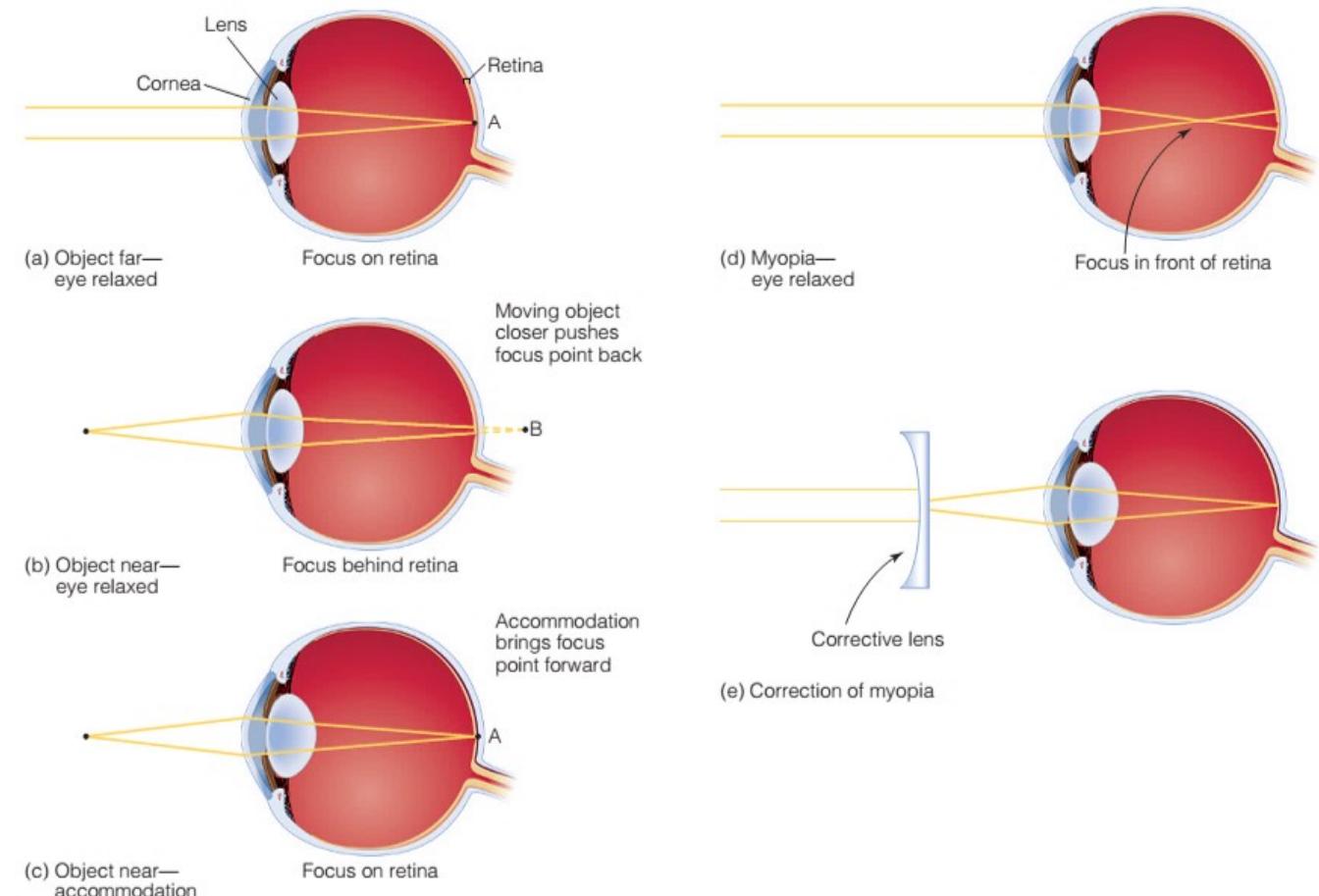


Figure 2.9 Focusing of light rays by the eye. (a) Rays of light coming from a small light source that is more than 20 feet away are approximately parallel. The focus point for parallel light is at A on the retina. (b) Moving an object closer to the relaxed eye pushes the focus point back. Here the focus point is at B, but light is stopped by the back of the eye, so the image on the retina is out of focus. (c) Accommodation of the eye (indicated by the fatter lens) increases the focusing power of the lens and brings the focus point for a near object back to A on the retina, so it is in focus. This accommodation is caused by the action of the ciliary muscles, which are not shown. (d) In the myopic (nearsighted) eye, parallel rays from a distant spot of light are brought to a focus in front of the retina, so distant objects appear blurred. (e) A corrective lens bends light so it is focused on the retina.

so they become unable to accommodate enough to see objects, or read, at close range. This loss of the ability to accommodate, called **presbyopia** (for “old eye”), can be dealt with by wearing reading glasses, which brings near objects into focus by replacing the focusing power that can no longer be provided by the lens.

Another problem that can be solved by a corrective lens is **myopia**, or **nearsightedness**, an inability to see distant objects clearly. The reason for this difficulty, which affects more than 70 million Americans, is illustrated in **Figure 2.9d**. Myopia occurs when the optical system brings parallel rays of light into focus at a point in front of the retina, so the image that reaches the retina is blurred. This problem can be caused by either of two factors: (1) **refractive myopia**, in which the cornea and/or the lens bends the light too much, or (2) **axial myopia**, in which the eyeball is too long. Either way, images of faraway objects are not focused sharply, so objects look blurred. Corrective lenses can solve this problem, as shown in **Figure 2.9e**.

Finally, people with **hyperopia**, or **farsightedness**, can see distant objects clearly but have trouble seeing nearby objects because the focus point for parallel rays of light is located behind the retina, usually because the eyeball is too short. Young people can bring the image forward onto the retina by accommodating. However, older people, who have difficulty accommodating, often use corrective lenses that bring the focus point forward onto the retina.

Focusing an image clearly onto the retina is the initial step in the process of vision, but although a sharp image on the retina is essential for clear vision, we do not see the image on the retina. Vision occurs not in the retina but in the brain. Before the brain can create vision, the light on the retina must activate the visual receptors in the retina.

Receptors and Perception

Light entering visual receptors triggers electrical signals when the light is absorbed by light-sensitive **visual pigment** molecules in the receptors. This step is crucial for vision because it creates

electrical signals that eventually signal the properties of the distal stimulus to the brain. But the importance of these visual pigments extends beyond triggering electrical signals. Visual pigments also shape our perceptions by determining our ability to see dim lights and our ability to see light in different parts of the visual spectrum. In this section, we first describe transduction, and then how the receptors shape perception.

Transforming Light Energy Into Electrical Energy

Transduction is the transformation of one form of energy into another form of energy (see Chapter 1, page 7). Visual transduction occurs in the rod and cone receptors, which transform light into electricity. The starting point for understanding how the rods and cones create electricity are the millions of molecules of a light-sensitive visual pigment that are contained in the outer segments of the receptors (Figure 2.3). Visual pigments have two parts: a long protein called **opsin** and a much smaller light-sensitive component called **retinal**. **Figure 2.10a** shows a model of a retinal molecule attached to opsin (Wald, 1968). Note that only a small part of the opsin is shown here; it is actually hundreds of times longer than the retinal.

Despite its small size compared to the opsin, retinal is the crucial part of the visual pigment molecule, because when the retinal and opsin are combined, the resulting molecule absorbs visible light. When the retinal part of the visual pigment molecule absorbs light, the retinal changes its shape, from being bent, as shown in Figure 2.10a, to straight, as shown in **Figure 2.10b**. This change of shape, called **isomerization**, creates a chemical chain reaction, illustrated in **Figure 2.11**, that activates thousands of charged molecules to create electrical signals in receptors.

What is important about the chain reaction that follows isomerization is that it amplifies the effect of isomerization. Isomerizing one visual pigment molecule triggers a chain of chemical reactions that releases as many as a million charged molecules, which leads to activation of the receptor (Baylor, 1992; Hamer et al., 2005).

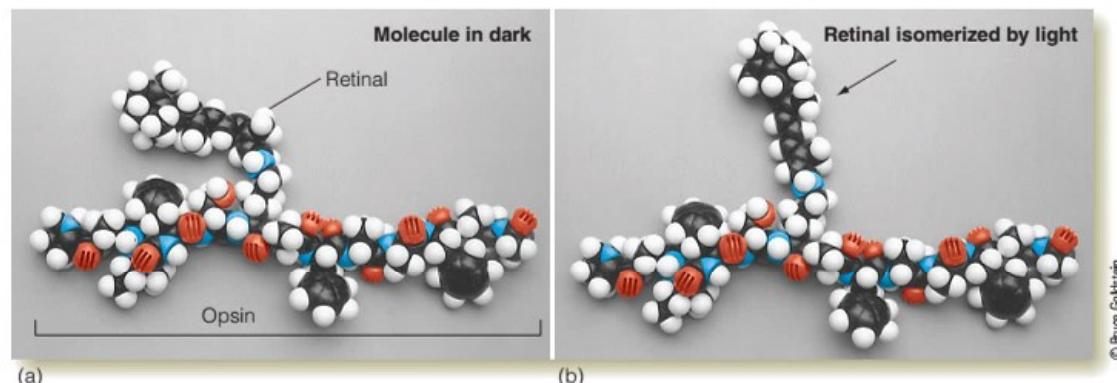


Figure 2.10 Model of a visual pigment molecule. The horizontal part of the model shows a tiny portion of the huge opsin molecule near where the retinal is attached. The smaller molecule on top of the opsin is the light-sensitive retinal. (a) The retinal molecule’s shape before it absorbs light. (b) The retinal molecule’s shape after it absorbs light. This change in shape, which is called isomerization, triggers a sequence of reactions that culminates in generation of an electrical response in the receptor.

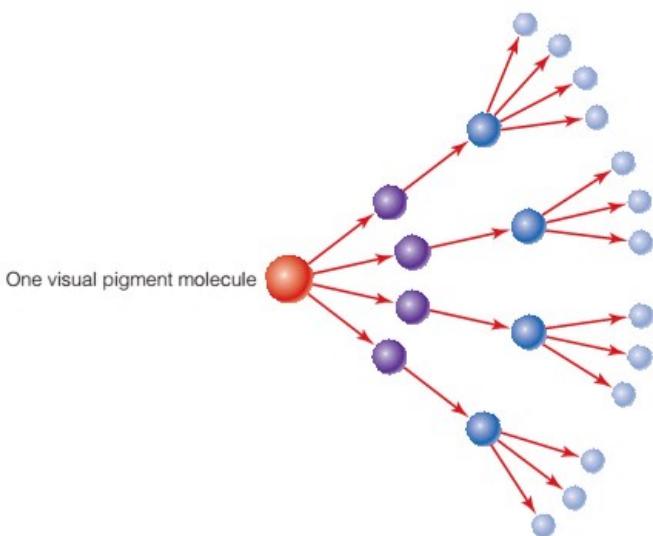


Figure 2.11 This sequence symbolizes the chain reaction that is triggered when a single visual pigment molecule is isomerized by absorption of a single photon of light. In the actual sequence of events, each visual pigment molecule activates hundreds more molecules, which, in turn, each activate about a thousand molecules. Isomerization of just one visual pigment molecule activates about a million other molecules, which activates the receptor.

Visual pigments not only create electrical signals in the receptors, they also shape specific aspects of our perceptions. Next, we will demonstrate how properties of the pigments influence perception. We do this by comparing the perceptions caused by the rod and cone receptors. As we will see, the visual pigments in these two types of receptors influence two aspects of visual perception: (1) how we adjust to darkness, and (2) how well we see light in different parts of the spectrum.

Adapting to the Dark

When we discussed measuring perception in Chapter 1, we noted that when a person goes from a lighted environment to a dark place, it may be difficult to see at first, but that after some time in the dark, the person becomes able to make out lights and objects that were invisible before (Figure 1.16, page 15). This process of increasing sensitivity in the dark, called **dark adaptation**, is measured by determining a **dark adaptation curve**. In this section we will show how the rod and cone receptors control an important aspect of vision: the ability of the visual system to adjust to dim levels of illumination. We will describe how the dark adaptation curve is measured, and how the increase in sensitivity that occurs in the dark has been linked to properties of the rod and cone visual pigments.

Measuring the Dark Adaptation Curve The study of dark adaptation begins with measuring the dark adaptation curve, which is the function relating sensitivity to light to time in the dark, beginning when the lights are extinguished.

METHOD Measuring the Dark Adaptation Curve

The first step in measuring a dark adaption curve is to have the subject look at a small fixation point while paying attention to a flashing test light that is off to the side (**Figure 2.12**). Because the subject is looking directly at the fixation point, its image falls on the fovea, so the image of the test light falls on the peripheral retina, which contains both rods and cones. While still in the light, the subject turns a knob that adjusts the intensity of the flashing light until it can just barely be seen. This threshold for seeing the light, the minimum amount of energy necessary to just barely see the light, is then converted to *sensitivity*. Because $\text{sensitivity} = 1/\text{threshold}$, this means that a *high threshold* corresponds to *low sensitivity*. The sensitivity measured in the light is called the **light-adapted sensitivity**, because it is measured while the eyes are adapted to the light. Because the room (or adapting) lights are on, the intensity of the flashing test light has to be high to be seen. At the beginning of the experiment, then, the threshold is high and the sensitivity is low.

Once the light-adapted sensitivity to the flashing test light is determined, the adapting light is extinguished so the subject is in the dark. The subject continues adjusting the intensity of the flashing light so he or she can just barely see it, tracking the increase in sensitivity that occurs in the dark. As the subject becomes more sensitive to the light, he or she must decrease the light's intensity to keep it just barely visible. The result, shown as the red curve in **Figure 2.13**, is a dark adaptation curve.

The dark adaptation curve shows that as adaptation proceeds, the subject becomes more sensitive to the light. Note that higher sensitivity is at the bottom of this graph, so movement of the dark adaptation curve downward means that the subject's sensitivity is increasing. The red dark adaptation curve indicates that the subject's sensitivity increases in two phases. It increases rapidly for the first 3 to 4 minutes after the light is extinguished and then levels off. At about 7 to 10 minutes, it begins increasing again and continues to do so until the subject has been in the dark for about 20 or 30 minutes (Figure 2.13). The sensitivity at the end of dark adaptation, labeled **dark-adapted sensitivity**, is about 100,000 times greater than the light-adapted sensitivity measured before dark adaptation began.

Dark adaptation was involved in a 2007 episode of the *Mythbusters* program on the Discovery Channel, which was devoted

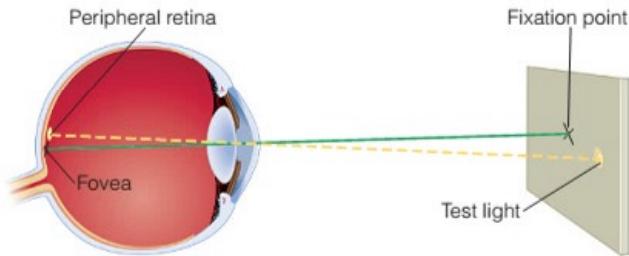


Figure 2.12 Viewing conditions for a dark adaptation experiment. In this example, the image of the fixation point falls on the fovea, and the image of the test light falls on the peripheral retina.

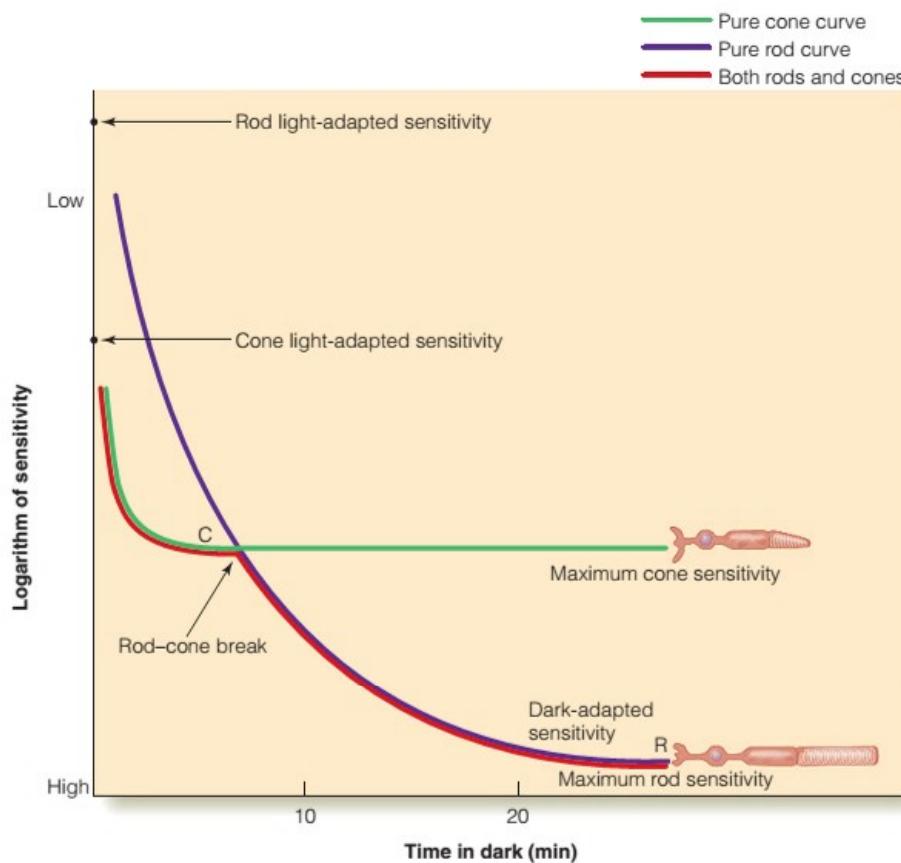


Figure 2.13 Three dark adaptation curves. The red line is the two-stage dark adaptation curve, with an initial cone branch and a later rod branch, which occurs when the test light is in the peripheral retina, as shown in Figure 2.12. The green line is the cone adaptation curve, which occurs when the test light falls on the fovea. The purple curve is the rod adaptation curve measured in a rod monochromat. Note that the downward movement of these curves represents an *increase* in sensitivity. The curves actually begin at the points indicating “light-adapted sensitivity,” but there is a slight delay between the time the lights are turned off and when measurement of the curves begins.

to investigating myths about pirates. One of the myths was that pirates wore eye patches to preserve night vision in one eye so that when they went from the bright light outside to the darkness below decks, removing the patch would enable them to see. To determine whether this would work, the Mythbusters carried out some tasks in a dark room just after both of their eyes had been in the light and did some different tasks with an eye that had previously been covered with a patch for 30 minutes. It isn't surprising that they completed the tasks much more rapidly when using the eye that had been patched. Anyone who has taken a course on sensation and perception could have told the Mythbusters that the eye patch would work because keeping an eye in the dark triggers the process of dark adaptation, which causes the eye to increase its sensitivity in the dark.

Whether pirates actually used patches to help them see below decks remains an unproven hypothesis. One argument against the idea that pirates wore eye patches to keep their sensitivity high is that patching one eye causes a decrease in depth perception, which might be a serious disadvantage when the pirate is working on deck. We will discuss why two eyes are important for depth perception in Chapter 10.

Although the Mythbusters showed that dark adapting one eye made it easier to see with that eye in the dark, we have a more specific goal. We are interested in showing that the first part of the dark adaptation curve is caused by the cones and the second part is caused by the rods. We will do this by running two

additional dark adaptation experiments, one measuring adaptation of the cones and another measuring adaptation of the rods.

Measuring Cone Adaptation The reason the red curve in Figure 2.13 has two phases is that the flashing test light fell on the peripheral retina, which contains both rods and cones. To measure dark adaptation of the cones alone, we have to ensure that the image of the test light falls only on cones. We achieve this by having the subject look directly at the test light so its image falls on the all-cone fovea, and by making the test light small enough so that its entire image falls within the fovea. The dark adaptation curve determined by this procedure is indicated by the green line in Figure 2.13. This curve, which measures only the activity of the cones, matches the initial phase of our original dark adaptation curve but does not include the second phase. Does this mean that the second part of the curve is due to the rods? We can show that the answer to this question is “yes” by doing another experiment.

Measuring Rod Adaptation We know that the green curve in Figure 2.13 is due only to cone adaptation because our test light was focused on the all-cone fovea. Because the cones are more sensitive to light at the beginning of dark adaptation, they control our vision during the early stages of adaptation, so we can't see what the rods are doing. In order to reveal how the sensitivity of the rods is changing at the very beginning of

dark adaptation, we need to measure dark adaptation in a person who has no cones. Such people, who have no cones because of a rare genetic defect, are called **rod monochromats**. Their all-rod retinas provide a way for us to study rod dark adaptation without interference from the cones. (Students sometimes wonder why we can't simply present the test flash to the peripheral retina, which contains mostly rods. The answer is that there are enough cones in the periphery to influence the beginning of the dark adaptation curve.)

Because the rod monochromat has no cones, the light-adapted sensitivity we measure just before we turn off the lights is determined by the rods. The sensitivity we determine, which is labeled "rod light-adapted sensitivity" in Figure 2.13, indicates that the rods are much less sensitive than the cone light-adapted sensitivity we measured in our original experiment. We can also see that once dark adaptation begins, the rods increase their sensitivity, as indicated by the purple curve, and reach their final dark-adapted level in about 25 minutes (Rushton, 1961). The end of this rod adaptation measured in our monochromat matches the second part of the two-stage dark adaptation curve.

Based on the results of our dark adaptation experiments, we can summarize the process of dark adaptation. As soon as the light is extinguished, the sensitivity of *both* the cones *and* the rods begins increasing. However, because the cones are much more sensitive than the rods at the beginning of dark adaptation, we see with our cones right after the lights are turned out. One way to think about this is that the cones have "center stage" at the beginning of dark adaptation, while the rods are working "behind the scenes." However, after about 3 to 5 minutes in the dark, the cones have reached their maximum sensitivity, as indicated by the leveling off of the dark adaptation curve. Meanwhile, the rods are still adapting, behind the scenes, and by about 7 minutes in the dark, the rods' sensitivity

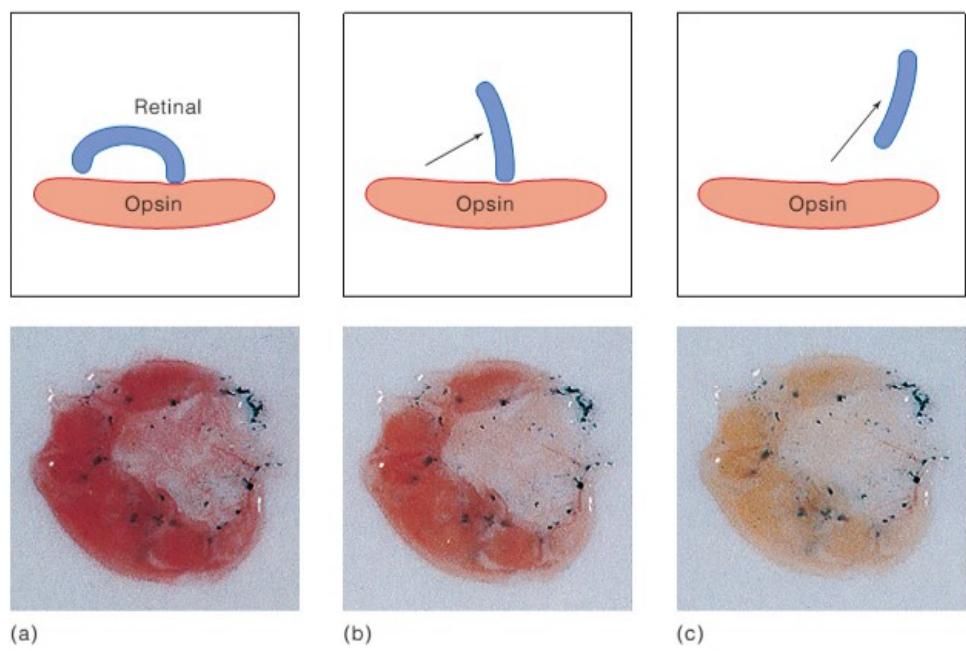
finally catches up to the cones'. The rods then become more sensitive than the cones, and rod adaptation, indicated by the second branch of the dark adaptation curve, becomes visible. The place where the rods begin to determine the dark adaptation curve is called the **rod-cone break**.

Why do the rods take about 20 to 30 minutes to reach their maximum sensitivity (point R on the curve) compared to only 3 to 4 minutes for the cones (point C)? The answer to this question involves a process called *visual pigment regeneration*, which occurs more rapidly in the cones than in the rods.

Visual Pigment Regeneration From our description of transduction earlier in the chapter, we know that light causes the retinal part of the visual pigment molecule, which is initially bent as shown in Figure 2.10a, to change its shape as in Figure 2.10b. This change from bent to straight is shown in the upper panels of **Figure 2.14**, which also shows how the retinal eventually separates from the *opsin* part of the molecule. This change in shape and separation from the opsin causes the molecule to become lighter in color, a process called **visual pigment bleaching**. This bleaching is shown in the lower panels of Figure 2.14. **Figure 2.14a** is a picture of a frog retina that was taken moments after it was illuminated with light. The red color is the visual pigment. As the light remains on, more and more of the pigment's retinal is isomerized and breaks away from the opsin, so the retina's color changes as shown in **Figures 2.14b** and **2.14c**.

When the pigments are in their lighter bleached state, they are no longer useful for vision. In order to do their job of changing light energy into electrical energy, the retinal needs to return to its bent shape and become reattached to the opsin. This process of reforming the visual pigment molecule is called **visual pigment regeneration**.

Figure 2.14 A frog retina was dissected from the eye in the dark and then exposed to light. The top row shows how the relationship between retinal and opsin changes after the retinal absorbs light. Only a small part of the opsin molecule is shown. The photographs in the bottom row show how the color of the retina changes after it is exposed to light. (a) This picture of the retina was taken just after the light was turned on. The dark red color is caused by the high concentration of visual pigment in the receptors that are still in the unbleached state. (b, c) After the retinal isomerizes, the retinal and opsin break apart, and the retina becomes bleached, as indicated by the lighter color.



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When you are in the light, as you are now as you read this book, some of your visual pigment molecules are isomerizing and bleaching, as shown in Figure 2.14, while at the same time, others are regenerating. This means that in most normal light levels, your eye always contains some bleached visual pigment and some intact visual pigment. When you turn out the lights, the bleached visual pigment continues to regenerate, but there is no more isomerization, so eventually the concentration of regenerated pigment builds up so your retina contains only intact visual pigment molecules.

This increase in visual pigment concentration that occurs as the pigment regenerates in the dark is responsible for the increase in sensitivity we measure during dark adaptation. This relationship between pigment concentration and sensitivity was demonstrated by William Rushton (1961), who devised a procedure to measure the regeneration of visual pigment in humans by measuring the darkening of the retina that occurs during dark adaptation. (Think of this as Figure 2.14 proceeding from right to left.)

Rushton's measurements showed that cone pigment takes 6 minutes to regenerate completely, whereas rod pigment takes more than 30 minutes. When he compared the course of pigment regeneration to the dark adaptation curve, he found that the rate of cone dark adaptation matched the rate of cone pigment regeneration and the rate of rod dark adaptation matched the rate of rod pigment regeneration. These results demonstrated two important connections between perception and physiology:

1. Our sensitivity to light depends on the concentration of a chemical—the visual pigment.
2. The speed at which our sensitivity increases in the dark depends on a chemical reaction—the regeneration of the visual pigment.

What happens to vision if something prevents visual pigments from regenerating? This is what occurs when a person's retina becomes detached from the *pigment epithelium* (see Figure 2.2b), a layer that contains enzymes necessary for pigment regeneration. This condition, called **detached retina**, can occur as a result of traumatic injuries of the eye or head, as when a baseball player is hit in the eye by a line drive. When this occurs, the bleached pigment's separated retinal and opsin can no longer be recombined, and the person becomes blind in the area of the visual field served by the separated area of the retina. This condition is permanent unless the detached area of retina is reattached, which can be accomplished by laser surgery.

Spectral Sensitivity

Our discussion of rods and cones has emphasized how they control our vision as we adapt to darkness. Rods and cones also differ in the way they respond to light in different parts of the *visible spectrum* (Figure 1.21, page 18). The differences in the rod and cone responses to the spectrum have been studied by measuring the **spectral sensitivity** of rod vision and cone vision, where spectral sensitivity is the eye's sensitivity to light as a function of the light's wavelength. Spectral sensitivity is

measured by determining the **spectral sensitivity curve**—the relationship between wavelength and sensitivity.

Spectral Sensitivity Curves The following is the psychophysical method used to measure a spectral sensitivity curve.

METHOD | Measuring a Spectral Sensitivity Curve

To measure sensitivity to light at each wavelength across the spectrum, we present one wavelength at a time and measure the subject's sensitivity to each wavelength. Light of a single wavelength, called **monochromatic light**, can be created by using special filters or a device called a *spectrometer*. To determine a person's spectral sensitivity, we determine the person's threshold for seeing monochromatic lights across the spectrum using one of the psychophysical methods for measuring threshold described in Chapter 1 (p. 14) and Appendix A (p. 384). The threshold is usually not measured at *every* wavelength, but at regular intervals. Thus, we might measure the threshold first at 400 nm, then at 410 nm, and so on. The result is the curve in **Figure 2.15a**, which shows that the threshold is higher at short

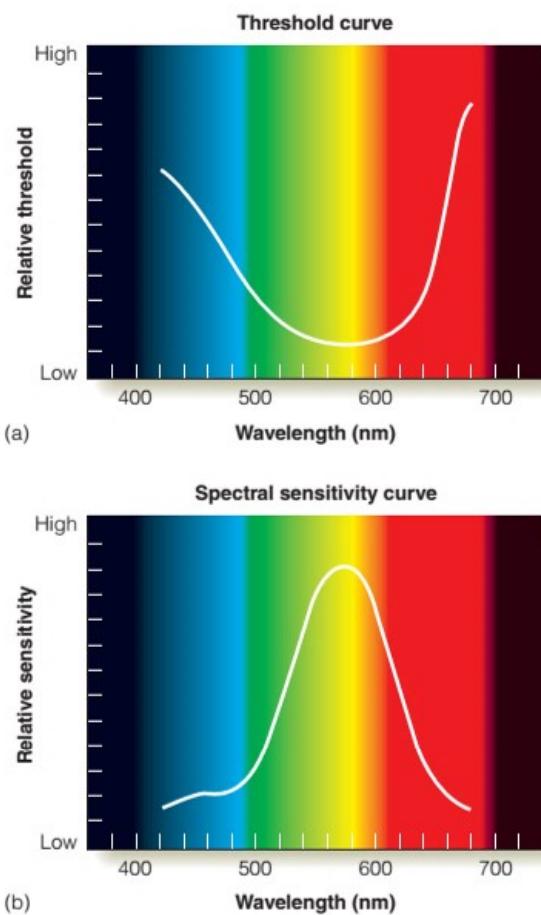


Figure 2.15 (a) The threshold for seeing a light as a function of wavelength. (b) Relative sensitivity as a function of wavelength—the **spectral sensitivity curve**. (Adapted from Wald, 1964)

and long wavelengths and lower in the middle of the spectrum; that is, less light is needed to see wavelengths in the middle of the spectrum than to see wavelengths at either the short- or long-wavelength end of the spectrum.

The ability to see wavelengths across the spectrum is often plotted not in terms of *threshold* versus wavelength, as in Figure 2.15a, but in terms of *sensitivity* versus wavelength. Using the equation, sensitivity = 1/threshold, we can convert the threshold curve in Figure 2.15a into the curve in **Figure 2.15b**, which is called the *spectral sensitivity curve*.

We measure the **cone spectral sensitivity** curve by having a subject look directly at a test light so that it stimulates only the cones in the fovea. We measure the **rod spectral sensitivity curve** by measuring sensitivity after the eye is dark adapted (so the rods control vision because they are the most sensitive receptors) and presenting test flashes in the peripheral retina, off to the side of the fixation point.

The cone and rod spectral sensitivity curves in **Figure 2.16** show that the rods are more sensitive to short-wavelength light than are the cones, with the rods being most sensitive to light of 500 nm and the cones being most sensitive to light of 560 nm. This difference in the sensitivity of cones and rods to different wavelengths means that as vision shifts from the cones in the light-adapted eye to the rods after the eye has become dark adapted, our vision shifts to become relatively more sensitive to short-wavelength light—that is, light nearer the blue and green end of the spectrum.

You may have noticed an effect of this shift to short-wavelength sensitivity if you have observed how green foliage seems to stand out more near dusk. This enhanced perception of short wavelengths during dark adaptation is called the **Purkinje (Pur-kin'-jee) shift** after Johann Purkinje, who described this effect in 1825. You can experience this shift in color sensitivity during dark adaptation by closing one eye for

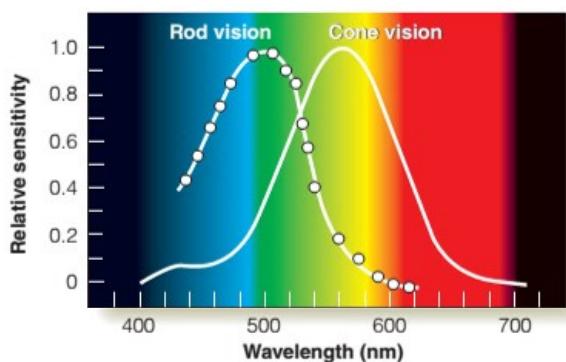


Figure 2.16 Spectral sensitivity curves for rod vision (left) and cone vision (right). The maximum sensitivities of these two curves have been set equal to 1.0. However, the relative sensitivities of the rods and the cones depend on the conditions of adaptation: The cones are more sensitive in the light, and the rods are more sensitive in the dark. The circles plotted on top of the rod curve are the absorption spectrum of the rod visual pigment. [From Wald & Brown, 1958]

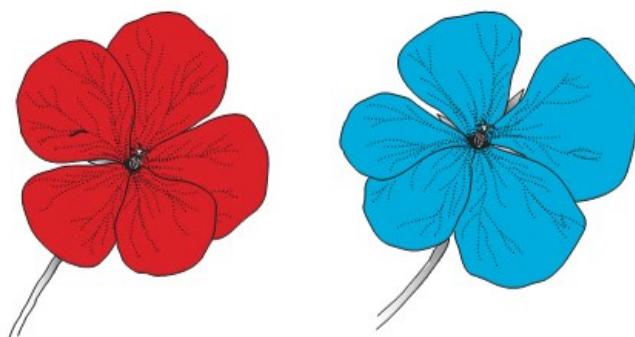


Figure 2.17 Flowers for demonstrating the Purkinje shift. See text for explanation.

5 to 10 minutes so it dark adapts, then switching back and forth between your eyes and noticing how the blue flower in **Figure 2.17** is brighter compared to the red flower in your dark-adapted eye.

Rod- and Cone-Pigment Absorption Spectra Just as we can trace the difference in the rate of rod and cone dark adaptation to a property of the visual pigments (the cone pigment regenerates faster than the rod pigment), we can trace the difference in the rod and cone spectral sensitivity curves to the rod and cone pigment *absorption spectra*. A pigment's *absorption spectrum* is a plot of the amount of light absorbed versus the wavelength of the light. The absorption spectra of the rod and cone pigments are shown in **Figure 2.18**. The rod pigment absorbs best at 500 nm, the blue-green area of the spectrum.

There are three absorption spectra for the cones because there are three different cone pigments, each contained in its own receptor. The short-wavelength pigment (S) absorbs light best at about 419 nm; the medium-wavelength pigment (M) absorbs light best at about 531 nm; and the long-wavelength pigment (L) absorbs light best at about 558 nm. We will have more to say about the three cone pigments in Chapter 9, because they are the basis of our ability to see colors.

The absorption of the rod visual pigment closely matches the rod spectral sensitivity curve (Figure 2.18), and the short-, medium-, and long-wavelength cone pigments add together to result in a psychophysical spectral sensitivity curve that peaks at 560 nm. Because there are fewer short-wavelength receptors and therefore much less of the short-wavelength pigment, the cone spectral sensitivity curve is determined mainly by the medium- and long-wavelength pigments (Bowmaker & Dartnall, 1980; Stiles, 1953).

It is clear from the evidence we have presented that the increase in sensitivity that occurs in the dark (dark adaptation) and the sensitivity to different wavelengths across the spectrum (spectral sensitivity) are determined by the properties of the rod and cone visual pigments. Thus, even though perception—the conscious experience that results from stimulation of the senses—does not occur in the eye, our experience is definitely affected by what happens there.

We have now traveled through the first three steps in the perceptual process. The tree (Step 1) reflects light, which is

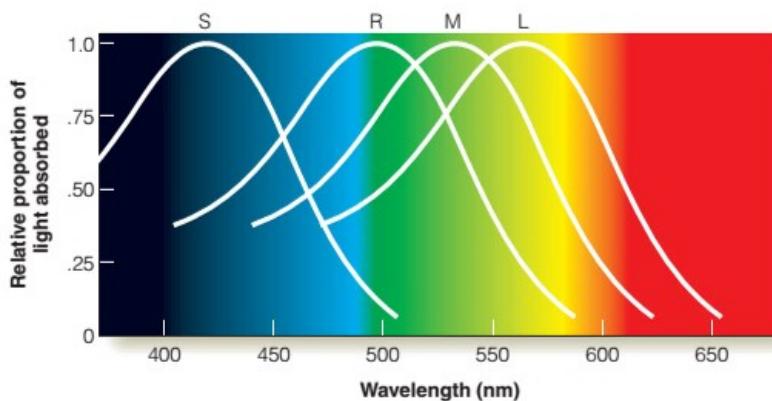


Figure 2.18 Absorption spectra of the rod pigment (R), and the short- (S), medium- (M), and long-wavelength (L) cone pigments. (Based on Dartnall, Bowmaker, & Mollon, 1983)

focused onto the retina by the eye's optical system (Step 2). The visual receptors shape perception as they transform light energy into electrical energy (Step 3). We are now ready to move to Step 4, the transmission and processing of electrical signals. But before we can begin describing electrical signals and what happens to them on their journey from receptors to the brain, we need to spend a few pages describing these electrical signals.

TEST YOURSELF 2.1

1. Describe light, the structure of the eye, and the rod and cone receptors. How are the rods and cones distributed across the retina?
2. How does moving an object closer to the eye affect how light reflected from the object is focused on the retina?
3. How does the eye adjust the focusing of light by accommodation? Describe the following conditions that can cause problems in focusing: presbyopia, myopia, hyperopia. How are these problems solved through either accommodation or corrective lenses?
4. Where on the retina does a researcher need to present a stimulus to test dark adaptation of the cones? How is this related to the distribution of the rods and cones on the retina? How can the adaptation of cones be measured without

any interference from the rods? How can adaptation of the rods be measured without any interference from the cones?

5. Describe how rod and cone sensitivity changes starting when the lights are turned off and how this change in sensitivity continues for 20 to 30 minutes in the dark. When do the rods begin adapting? When do the rods become more sensitive than the cones?
6. What happens to visual pigment molecules when they (a) absorb light and (b) regenerate? What is the connection between visual pigment regeneration and dark adaptation?
7. What is spectral sensitivity? How is a cone spectral sensitivity curve determined? A rod spectral sensitivity curve?
8. What is a pigment absorption spectrum? How do rod and cone pigment absorption spectra compare, and what is their relationship to rod and cone spectral sensitivity?

Electrical Signals in Neurons

Electrical signals occur in structures called **neurons**, like the ones shown in **Figure 2.19**. The key components of neurons, shown in the neuron on the right in Figure 2.19, are the **cell body**, which contains mechanisms to keep the cell alive; **dendrites**, which branch out from the cell body to receive electrical signals from other neurons; and the **axon**, or **nerve fiber**,

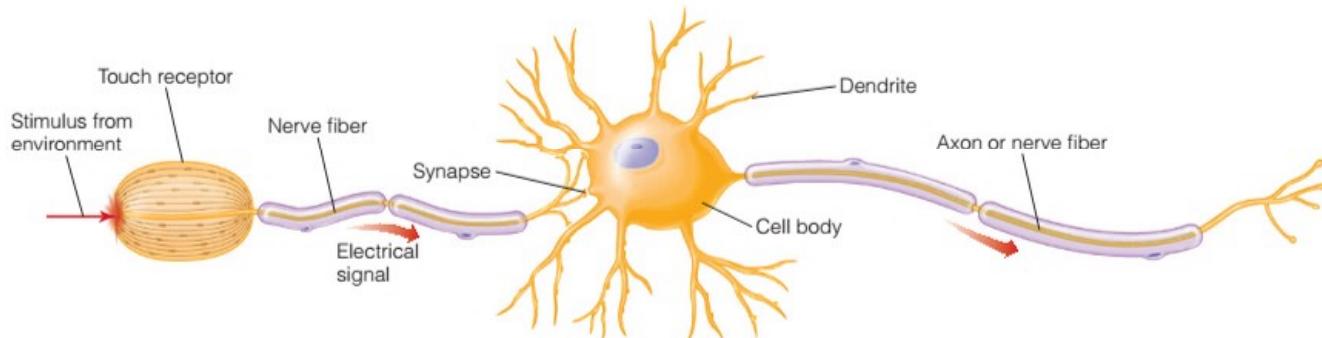
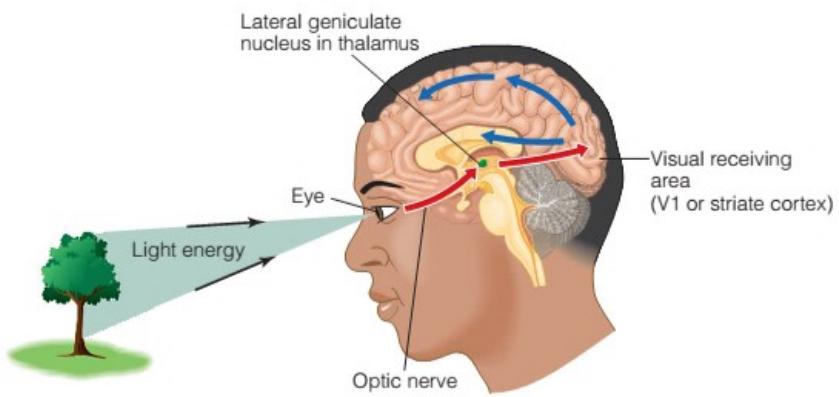


Figure 2.19 The neuron on the right consists of a cell body, dendrites, and an axon, or nerve fiber. The neuron on the left that receives stimuli from the environment has a receptor in place of the cell body.

Figure 2.20 Side view of the visual system showing the three major sites along the primary visual pathway: the eye, the lateral geniculate nucleus, and the visual receiving area, which is also called the striate cortex or Area V1.



which is filled with fluid that conducts electrical signals. There are variations on this basic neuron structure: Some neurons have long axons; others have short axons or none at all. Especially important for perception are *sensory receptors*, which are neurons specialized to respond to environmental stimuli. In Figure 2.19, the receptor on the left responds to touch stimuli.

Individual neurons do not, of course, exist in isolation. There are hundreds of millions of neurons in the nervous system and, as we will see, each neuron is connected to many other neurons. In the case of vision, each eye contains more than 100 million receptors, each of which transmits signals to neurons within the retina. These signals are transmitted out of the back of the eye in the optic nerve to a group of neurons called the *lateral geniculate nucleus* and then to the *visual receiving area* in the cortex (Figure 2.20). All along this pathway from eye to cortex, and then within the cortex, individual neurons are transmitting messages about the tree.

One of the most important ways of studying how the tree is represented by electrical signals is to record signals from single neurons. We can appreciate the importance of being able to record from single neurons by considering the following analogy: You walk into a large room in which hundreds of people are talking about a political speech they have just heard. There is a great deal of noise and commotion in the room as people react to the speech. Based on hearing this “crowd noise,” all you can say about what is going on is that the speech seems to have generated a great deal of excitement. To get more specific information about the speech, you need to listen to what individual people are saying.

Just as listening to individual people provides valuable information about what is happening in a large crowd, recording from single neurons provides valuable information about what is happening in the nervous system. Recording from single neurons is like listening to individual voices. It is important to record from as many neurons as possible, of course, because just as individual people may have different opinions about the speech, different neurons may respond differently to a particular stimulus or situation.

The ability to record electrical signals from individual neurons ushered in the modern era of brain research, and in the 1950s and 1960s, development of sophisticated electronics and the availability of computers made possible more detailed analysis of how neurons function.

Recording Electrical Signals in Neurons

Electrical signals are recorded from the axons (or nerve fibers) of neurons using small electrodes to pick up the signals.

METHOD | The Setup for Recording From a Single Neuron

Figure 2.21a shows a typical setup used for recording from a single neuron. There are two electrodes: a *recording electrode*, shown with its recording tip inside the neuron,¹ and a *reference electrode*, located some distance away so it is not affected by the electrical signals. These two electrodes are connected to a meter that records the difference in charge between the tips of the two electrodes. This difference is displayed on a computer screen, like the one shown in Figure 2.22, which shows electrical signals being recorded from a neuron in a laboratory setting.

When the axon, or nerve fiber, is at rest, the difference in the electrical potential between the tips of the two electrodes is -70 millivolts (mV, where a millivolt is $1/1,000$ of a volt), as shown on the right in Figure 2.21a. This means that the inside of the axon is 70 mV more negative than the outside. This value, which stays the same as long as there are no signals in the neuron, is called the *resting potential*.

Figure 2.21b shows what happens when the neuron's receptor is stimulated so that a signal is transmitted down the axon. As the signal passes the recording electrode, the charge inside the axon rises to $+40$ millivolts compared to the outside. As the signal continues past the electrode, the charge inside the fiber reverses course and starts becoming negative again (Figure 2.21c), until it returns to the resting level (Figure 2.21d). This signal, which is called the *action potential*, lasts about 1 millisecond ($1/1,000$ second).

Basic Properties of Action Potentials

An important property of the action potential is that it is a *propagated response*—once the response is triggered, it

¹In practice, most recordings are achieved with the tip of the electrode positioned just outside the neuron because it is technically difficult to insert electrodes into the neuron, especially if it is small. However, if the electrode tip is close enough to the neuron, the electrode can pick up the signals generated by the neuron.

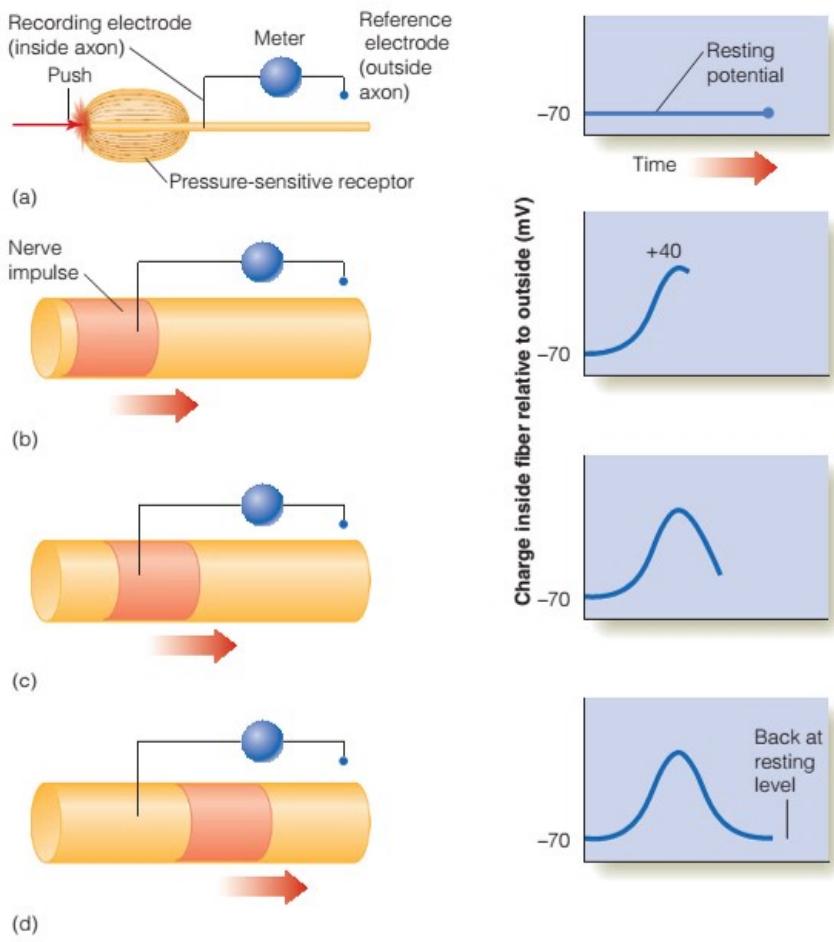


Figure 2.21 (a) When a nerve fiber is at rest, there is a difference in charge of -70 mV between the inside and the outside of the fiber. This difference, which is measured by the meter indicated by the blue circle, is displayed on the right. (b) As the nerve impulse, indicated by the red band, passes the electrode, the inside of the fiber near the electrode becomes more positive. This positivity is the rising phase of the action potential. (c) As the nerve impulse moves past the electrode, the charge inside the fiber becomes more negative. This is the falling phase of the action potential. (d) Eventually the neuron returns to its resting state.

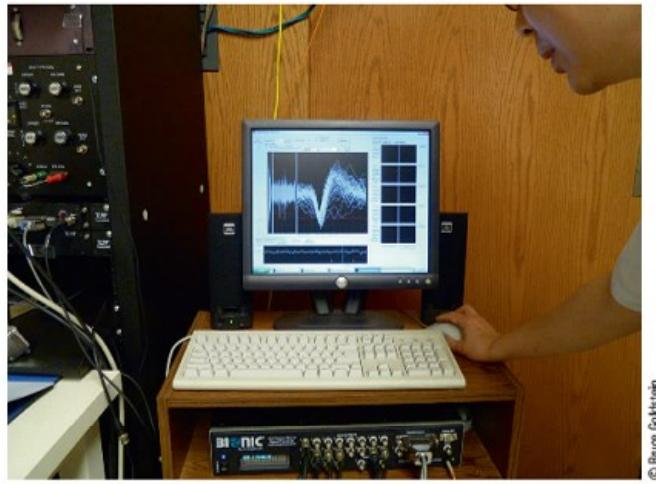


Figure 2.22 Electrical signals being displayed on a computer screen, in an experiment in which responses are being recorded from a single neuron. The signal on the screen shows the difference in voltage between two electrodes as a function of time. In this example, many signals are superimposed on one another, creating a thick white tracing. (Photographed in Tai Sing Lee's laboratory at Carnegie Mellon University)

travels all the way down the axon without decreasing in size. This means that if we were to move our recording electrode in Figure 2.21 to a position nearer the end of the axon, the electrical response would take longer to reach the electrode, but it would still be the same size (increasing from -70 to $+40\text{ mV}$) when it got there. This is an extremely important property of the action potential because it enables neurons to transmit signals over long distances.

Another property is that the action potential remains the same size no matter how intense the stimulus is. We can demonstrate this by determining how the neuron fires to different stimulus intensities. **Figure 2.23** shows what happens when we do this. Each action potential appears as a sharp spike in these records because we have compressed the time scale to display a number of action potentials.

The three records in Figure 2.23 represent the axon's response to three intensities of pushing on the skin. **Figure 2.23a** shows how the axon responds to gentle stimulation applied to the skin, and **Figures 2.23b** and **2.23c** show how the response changes as the pressure is increased. Comparing these three records leads to an important conclusion: Changing the stimulus intensity does not affect the *size* of the action potentials but does affect the *rate* of firing.

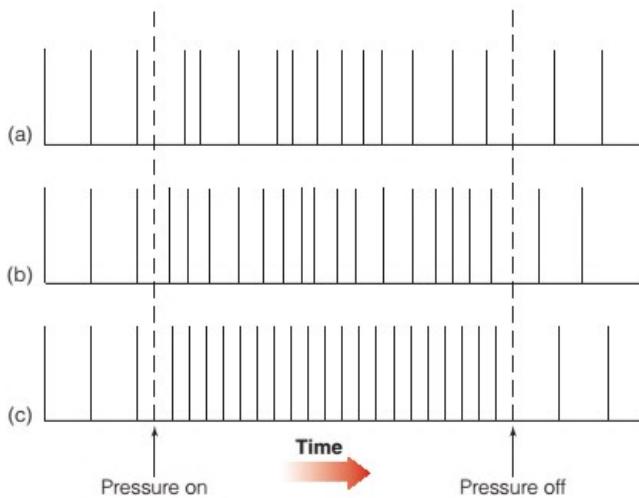


Figure 2.23 Response of a nerve fiber to (a) soft, (b) medium, and (c) strong stimulation. Increasing the stimulus strength increases both the *rate* and the *regularity* of nerve firing in this fiber, but has no effect on the *size* of the action potentials.

Although increasing the stimulus intensity can increase the rate of firing, there is an upper limit to the number of nerve impulses per second that can be conducted down an axon. This limit occurs because of a property of the axon called the **refractory period**—the interval between the time one nerve impulse occurs and the next one can be generated in the axon. Because the refractory period for most neurons is about 1 ms, the upper limit of a neuron's firing rate is about 500 to 800 impulses per second.

Another important property of action potentials is illustrated by the beginning of each of the records in Figure 2.23. Notice that a few action potentials are occurring even before the pressure stimulus is applied. Action potentials that occur in the absence of stimuli from the environment are called **spontaneous activity**. This spontaneous activity establishes a baseline level of firing for the neuron. The presence of stimulation usually causes an increase in activity above this spontaneous level, but under some conditions, which we will describe shortly, it can cause firing to decrease below the spontaneous level.

Chemical Basis of Action Potentials

What causes these rapid changes in charge that travel down the axon? Because this is a traveling electrical charge, we might be tempted to equate it to the electrical signals that are conducted along electrical power lines or the wires used for household appliances. But action potentials create electricity not in the dry environment of metal wires, but in the wet environment of the body.

The key to understanding the “wet” electrical signals transmitted by neurons is understanding the components of the neuron’s liquid environment. Neurons are bathed in a liquid solution rich in **ions**, molecules that carry an electrical charge (**Figure 2.24**). Ions are created when molecules gain or

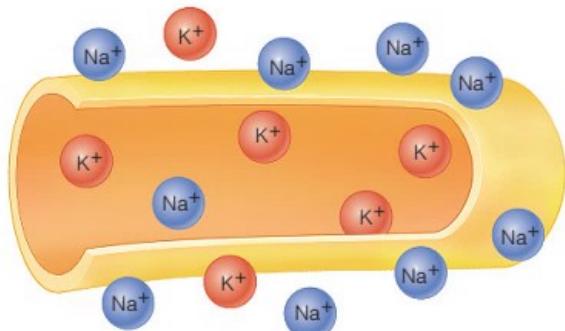


Figure 2.24 A nerve fiber, showing the high concentration of sodium outside the fiber and potassium inside the fiber. Other ions, such as negatively charged chlorine, are not shown.

lose electrons, as happens when compounds are dissolved in water. For example, adding table salt (sodium chloride, NaCl) to water creates positively charged sodium ions (Na^+) and negatively charged chlorine ions (Cl^-). The solution outside the axon of a neuron is rich in positively charged sodium (Na^+) ions, whereas the solution inside the axon is rich in positively charged potassium (K^+) ions.

You can understand how these ions result in the action potential by imagining yourself just outside an axon next to a recording electrode (**Figure 2.25a**). (You will have to shrink yourself down to a very small size to do this!) Everything is quiet until an action potential begins traveling down the axon. As it approaches, you see positively charged sodium ions (Na^+) rushing into the axon (**Figure 2.25b**). This occurs because channels in the membrane have opened to allow Na^+ to flow across the membrane. This opening of sodium channels represents an increase in the membrane’s **permeability** to sodium, where permeability refers to the ease with which a molecule can pass through the membrane. In this case, permeability is selective, which means that the fiber is highly permeable to one specific type of molecule (Na^+ in this case), but not to others. The inflow of positively charged sodium causes an increase in the positive charge inside the axon from the resting potential of -70 mV until it reaches the peak of the action potential of $+40\text{ mV}$. This increase in potential from -70 mV to $+40\text{ mV}$ is the **rising phase of the action potential** (**Figure 2.25b**).

Continuing your vigil, you notice that once the charge inside the neuron reaches $+40\text{ mV}$, the sodium channels close (the membrane becomes impermeable to sodium), and potassium channels open (the membrane becomes selectively permeable to potassium). Positively charged potassium rushes out of the axon, causing the charge inside the axon to become more negative. This increase in negativity from $+40\text{ mV}$ back to -70 mV is the **falling phase of the action potential** (**Figure 2.25c**). Once the potential has returned to the -70 mV resting level, the K^+ flow stops (**Figure 2.25d**).

After reading this description of ion flow, students often ask why the sodium-in, potassium-out flow that occurs during the action potential doesn’t cause sodium to build up inside the axon, and potassium to build up outside. The answer is

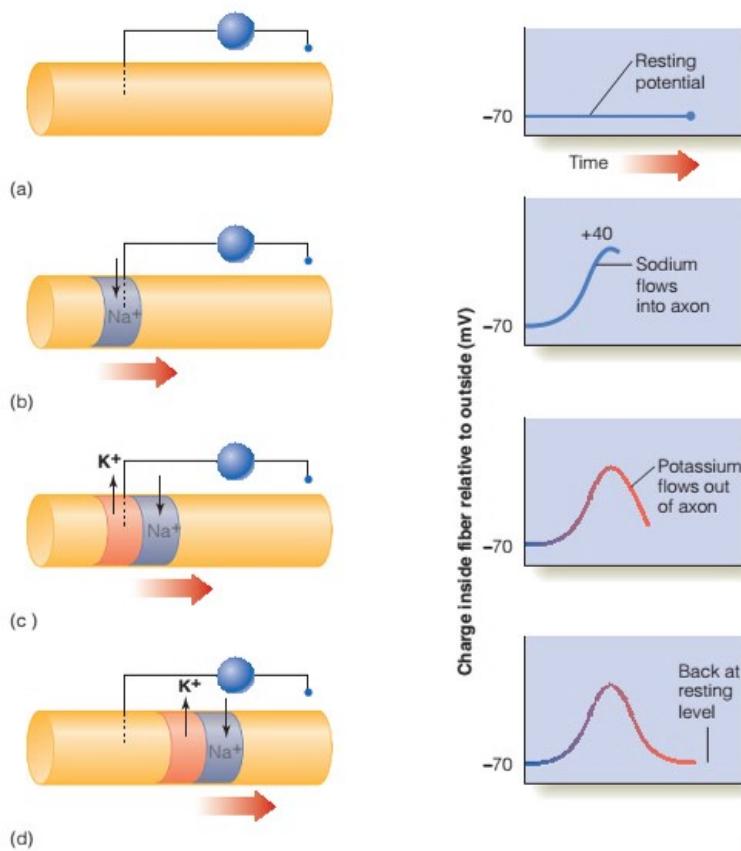


Figure 2.25 How the flow of sodium and potassium creates the action potential. (a) When the fiber is at rest, there is no flow of ions, and the record indicates the -70 mV resting potential. (b) Ion flow occurs when an action potential travels down the fiber. Initially, positively charged sodium (Na^+) flows into the axon, causing the inside of the neuron to become more positive (rising phase of the action potential). (c) Later, positively charged potassium (K^+) flows out of the axon, causing the inside of the axon to become more negative (falling phase of the action potential). (d) When the action potential has passed the electrode, the charge returns to the resting level.

that a mechanism called the *sodium-potassium pump* keeps this buildup from happening by continuously pumping sodium out and potassium into the fiber.

Transmitting Information Across a Gap

We have seen that action potentials caused by sodium and potassium flow down the axon without decreasing in size. But what happens when the action potential reaches the end of the axon? How is the action potential's message transmitted to other neurons? The problem is that there is a very small space between neurons, known as a **synapse** (Figure 2.26). The discovery of the synapse raised the question of how the electrical signals generated by one neuron are transmitted across the space separating the neurons. As we will see, the answer lies in a remarkable chemical process that involves molecules called **neurotransmitters**.

Early in the 1900s, it was discovered that when action potentials reach the end of a neuron, they trigger the release of chemicals called **neurotransmitters** that are stored in structures called *synaptic vesicles* in the sending neuron (Figure 2.26b). The neurotransmitter molecules flow into the synapse to small areas on the receiving neuron called

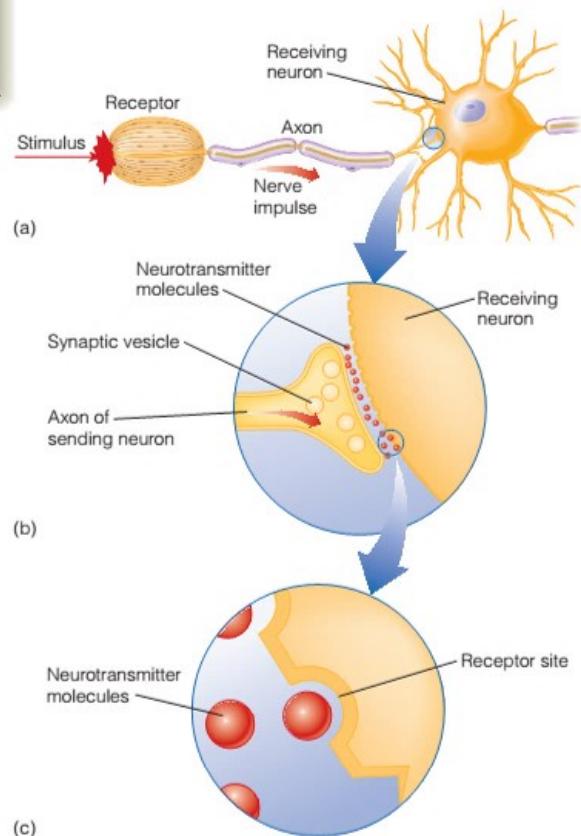


Figure 2.26 Synaptic transmission from one neuron to another. (a) A signal traveling down the axon of a neuron reaches the synapse at the end of the axon. (b) The nerve impulse causes the release of neurotransmitter molecules from the synaptic vesicles of the sending neuron. (c) The neurotransmitters fit into receptor sites that are shaped like the transmitter and cause a voltage change in the receiving neuron.

receptor sites that are sensitive to specific neurotransmitters (**Figure 2.26c**). These receptor sites exist in a variety of shapes that match the shapes of particular neurotransmitter molecules. When a neurotransmitter makes contact with a receptor site matching its shape, it activates the receptor site and triggers a voltage change in the receiving neuron. A neurotransmitter is like a key that fits a specific lock. It has an effect on the receiving neuron only when its shape matches that of the receptor site.

Thus, when an electrical signal reaches the synapse, it triggers a chemical process that causes a new electrical signal in the receiving neuron. The nature of this signal depends on both the type of transmitter that is released and the nature of the receptor sites in the receiving neuron. Two types of responses can occur at these receptor sites, *excitatory* and *inhibitory*. An **excitatory response** occurs when the inside of the neuron becomes more positive, a process called **depolarization**. **Figure 2.27a** shows this effect. Notice, however, that this response is much smaller than the positive action potential. To generate an action potential, enough excitation must occur to increase depolarization to the level indicated by the dashed line. Once depolarization reaches that level, an action potential is triggered (**Figure 2.27b**). Depolarization is an excitatory response because it causes the charge to change in the direction that triggers an action potential.

An **inhibitory response** occurs when the inside of the neuron becomes more negative, a process called **hyperpolarization**.

Figure 2.27c shows this effect. Hyperpolarization is an inhibitory response because it causes the charge inside the axon to move away from the level of depolarization, indicated by the dashed line, needed to generate an action potential.

We can summarize this description of the effects of excitation and inhibition as follows: Excitation increases the chances that a neuron will generate action potentials and is associated with increasing rates of nerve firing. Inhibition decreases the chances that a neuron will generate action potentials and is associated with lowering rates of nerve firing. Since a typical neuron receives both excitation and inhibition, the response of the neuron is determined by the interplay of excitation and inhibition, as illustrated in **Figure 2.28**. In **Figure 2.28a**, excitation (E) is much stronger than inhibition (I), so the neuron's firing rate is high. However, as inhibition becomes stronger and excitation becomes weaker, the neuron's firing decreases, until in **Figure 2.28e**, inhibition has eliminated the neuron's spontaneous activity and has decreased firing to zero.

Why does inhibition exist? If one of the functions of a neuron is to transmit its information to other neurons, what would be the point of decreasing or eliminating firing in the next neuron? The answer to this question is that the function of neurons is not only to transmit information but also to *process* it, and, as we will see in Chapter 3, both excitation and inhibition are involved in this processing.

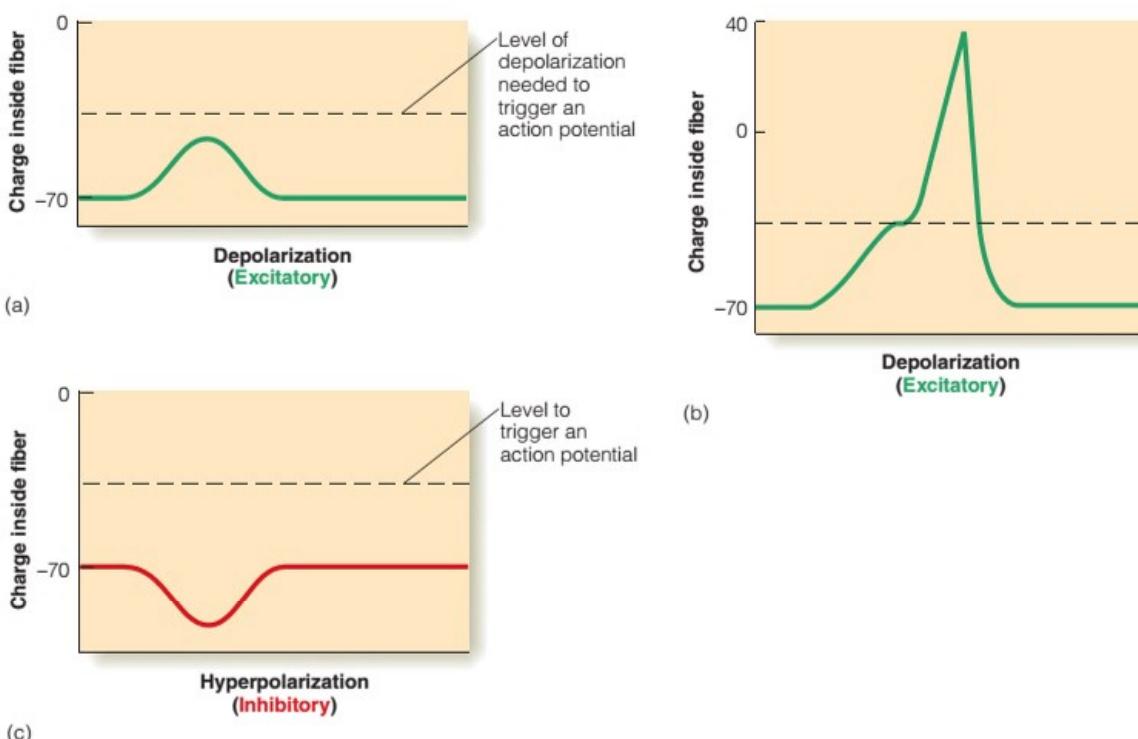


Figure 2.27 (a) Excitatory transmitters cause depolarization, an increased positive charge inside the neuron. (b) When the level of depolarization reaches threshold, indicated by the dashed line, an action potential is triggered. (c) Inhibitory transmitters cause hyperpolarization, an increased negative charge inside the axon.

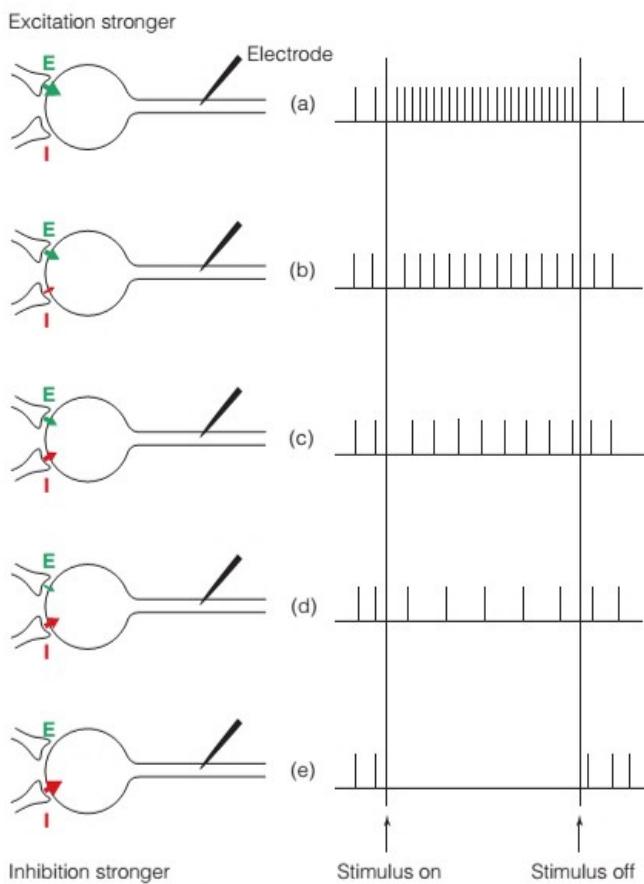


Figure 2.28 Effect of excitatory (E) and inhibitory (I) input on the firing rate of a neuron. The amount of excitatory and inhibitory input to the neuron is indicated by the size of the arrows at the synapse. The responses recorded by the electrode are indicated by the records on the right. The firing that occurs before the stimulus is presented is spontaneous activity. In (a), the neuron receives only excitatory transmitter, which causes the neuron to fire. In (b) to (e), the amount of excitatory transmitter decreases while the amount of inhibitory transmitter increases. As inhibition becomes stronger relative to excitation, firing rate decreases, until eventually the firing rate becomes zero.

Neural Convergence and Perception

Now, with some background about neurons and the electrical signals in neurons, we are ready to look for more connections between physiology and perception. Step 4 in the perceptual process, the transmission and processing of electrical signals, is the topic of Chapters 3 and 4. But we introduce neural processing in this chapter by returning to the rods and cones and showing how perception is related to the way they are “wired up” in the retina.

Figure 2.29a is a cross section of a monkey retina that has been stained to reveal the retina’s layered structure.

Figure 2.29b shows the five types of neurons that make up

these layers and that create **neural circuits**—interconnected groups of neurons—within the retina. Signals generated in the receptors (R) travel to the **bipolar cells** (B) and then to the **ganglion cells** (G). The receptors and bipolar cells do not have long axons, but the ganglion cells have axons like the neurons in Figure 2.19. These axons transmit signals out of the retina in the optic nerve (see Figure 2.6).

In addition to the receptors, bipolar cells, and ganglion cells, there are two other types of neurons that connect neurons across the retina: **horizontal cells** and **amacrine cells**. Signals can travel between receptors through the horizontal cells, and between bipolar cells and between ganglion cells through the amacrine cells. We will return to the horizontal and amacrine cells in Chapter 3. For now we will focus on the direct pathway from the receptors to the ganglion cells. We focus specifically on the property of **neural convergence** (or just **convergence** for short).

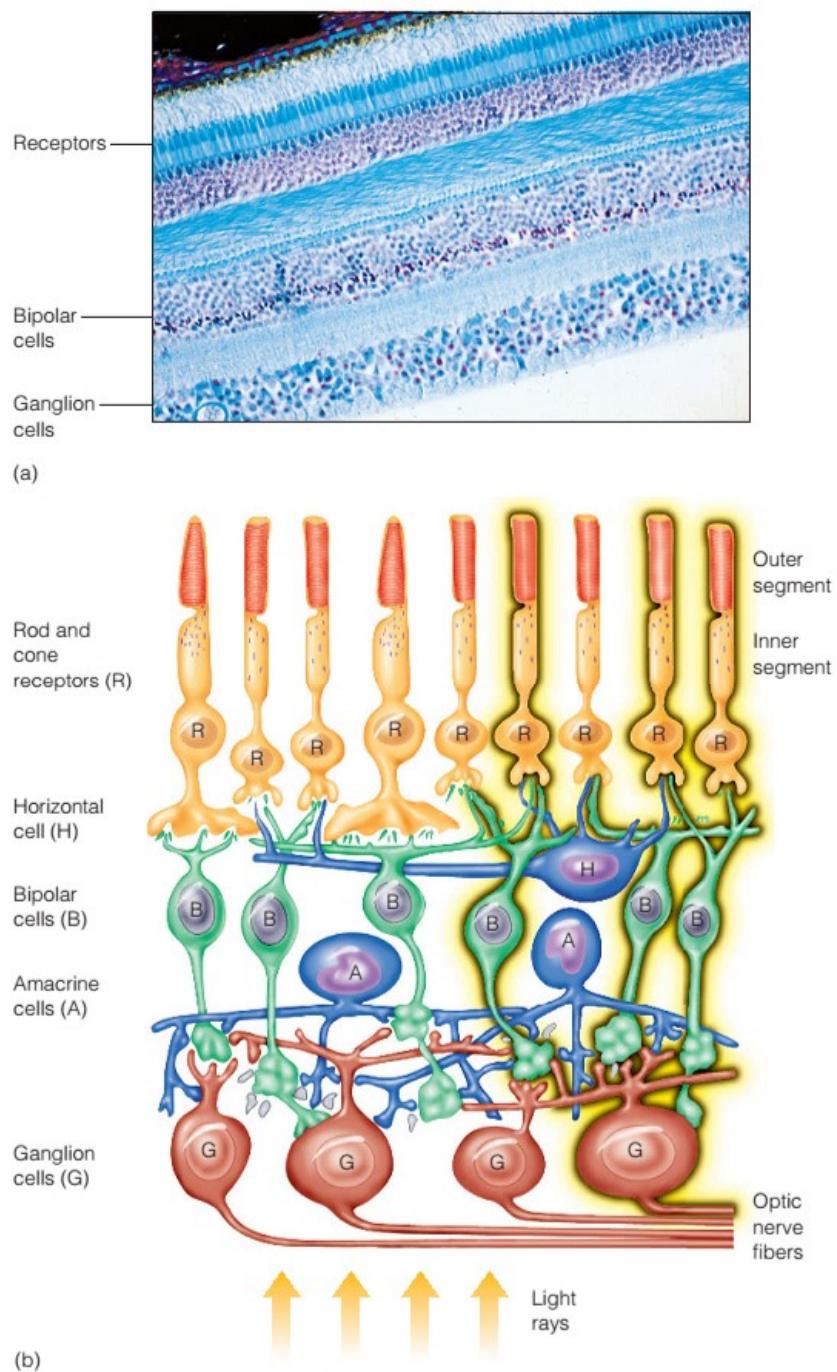
Convergence occurs when a number of neurons synapse onto a single neuron. A great deal of convergence occurs in the retina because each eye has 126 million receptors but only 1 million ganglion cells. Thus, on the average, each ganglion cell receives signals from 126 receptors. We can show how convergence can affect perception by returning to the rods and cones. An important difference between rods and cones is that the signals from the rods converge more than do the signals from the cones. We can appreciate this difference by noting that there are 120 million rods in the retina, but only 6 million cones. Thus, on the average, about 120 rods send their signals to one ganglion cell, but only about 6 cones send signals to a single ganglion cell.

This difference between rod and cone convergence becomes even greater when we consider the cones in the fovea. (Remember that the fovea is the small area that contains only cones.) Many of these foveal cones have “private lines” to ganglion cells, so that each ganglion cell receives signals from only one cone, with no convergence. The greater convergence of the rods compared to the cones translates into two differences in perception: (1) the rods result in better sensitivity than the cones, and (2) the cones result in better detail vision than the rods.

Convergence Causes the Rods to Be More Sensitive Than the Cones

In the dark-adapted eye, rod vision is more sensitive than cone vision (see “dark-adapted sensitivity” in the dark adaptation curve of Figure 2.13). This is why in dim light conditions we use our rods to detect faint stimuli. A demonstration of this effect, which has long been known to astronomers and amateur stargazers, is that some very dim stars are difficult to detect when looked at directly (because the star’s image falls on the cones in the fovea), but these same stars can often be seen when they are located off to the side of where the person is looking (because then the star’s image falls on the rod-rich peripheral retina). One reason for this greater sensitivity of rods, compared to cones, is that it takes less light to generate a response from an individual rod receptor than from an individual cone receptor (Barlow & Mollon, 1982; Baylor, 1992). But there is another reason as well: The rods have greater convergence than the cones.

Figure 2.29 (a) Cross section of a monkey retina, which has been stained to show the various layers. Light is coming from the bottom. The purple circles are cell bodies of the receptors, bipolar cells, and ganglion cells. (b) Cross section of the primate retina showing the five major cell types and their interconnections: receptors (R), bipolar cells (B), ganglion cells (G), horizontal cells (H), and amacrine cells (A). Signals from the three highlighted rods on the right reach the highlighted ganglion cell. This is an example of convergence. (Based on Dowling & Boycott, 1966)



Keeping this basic principle in mind, we can see how the difference in rod and cone convergence translates into differences in the maximum sensitivities of the rods and the cones. In the two circuits in **Figure 2.30**, five rod receptors converge onto one ganglion cell and five cone receptors each send signals onto their own ganglion cells. We have left out the bipolar, horizontal, and amacrine cells in these circuits for simplicity, but our conclusions will not be affected by these omissions.

For the purposes of our discussion, we will assume that we can present small spots of light to individual rods

and cones. We will also make the following additional assumptions:

1. One unit of light intensity causes the release of one unit of excitatory transmitter, which causes one unit of excitation in the ganglion cell.
2. The ganglion cell fires when it receives 10 units of excitation.
3. When the ganglion cell fires, the light is perceived.

When we present spots of light with an intensity of 1 to each receptor, the rod ganglion cell receives 5 units of excitation,

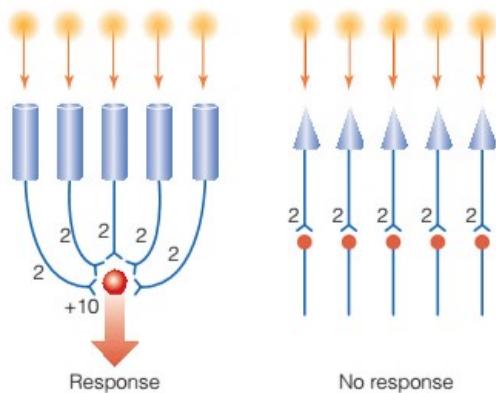


Figure 2.30 The wiring of the rods (left) and the cones (right). The yellow dot and arrow above each receptor represents a “spot” of light that stimulates the receptor. The numbers represent the number of response units generated by the rods and the cones in response to a spot intensity of 2.

1 from each of the 5 rod receptors. In contrast, each cone ganglion cell receives 1 unit of excitation, 1 from each cone receptor. Thus, when intensity = 1, the rod ganglion cell receives more excitation than the cone ganglion cells because of convergence, but not enough to cause it to fire. If, however, we increase the intensity to 2, as shown in the figure, the rod ganglion cell receives 2 units of excitation from each of its 5 receptors, for a total of 10 units of excitation. This causes the ganglion cell to fire, and the light is perceived. Meanwhile, at the same intensity, the cones’ ganglion cells are each receiving only 2 units of excitation. For the cones’ ganglion cells to fire, we must increase the intensity to 10.

The operation of these circuits demonstrates how the rods’ high sensitivity compared to the cones’ is caused by the rods’ greater convergence. Many rods sum their responses by feeding into the same ganglion cell, but only one or a few cones send their responses to any one ganglion cell. The fact that rod and cone sensitivity is determined not by individual receptors but by groups of receptors converging onto other neurons means that when we describe “rod vision” and “cone vision” we are actually referring to the way *groups* of rods and cones participate in determining our perceptions.

Lack of Convergence Causes the Cones to Have Better Acuity Than the Rods

While rod vision is more sensitive than cone vision because the rods have *more* convergence, the cones have *better visual acuity* because they have *less* convergence. Acuity refers to the ability to see details; thus, being able to see very small letters on an eye chart in the optometrist’s or ophthalmologist’s office translates into high acuity. (Also, remember grating acuity from Chapter 1, page 11).

One way to appreciate the high acuity of the cones is to think about the last time you were looking for one thing that was hidden among many other things. This could be searching for your cell phone on the clutter of your desk or locating a friend’s face in a crowd. To find what you are looking for, you usually need to move your eyes from one place to another. When you move your eyes to look at different things in this way, what you are doing

is scanning with your cone-rich fovea (remember that when you look directly at something, its image falls on the fovea). This is necessary because your visual acuity is highest in the fovea; objects that are imaged on the peripheral retina are not seen as clearly.

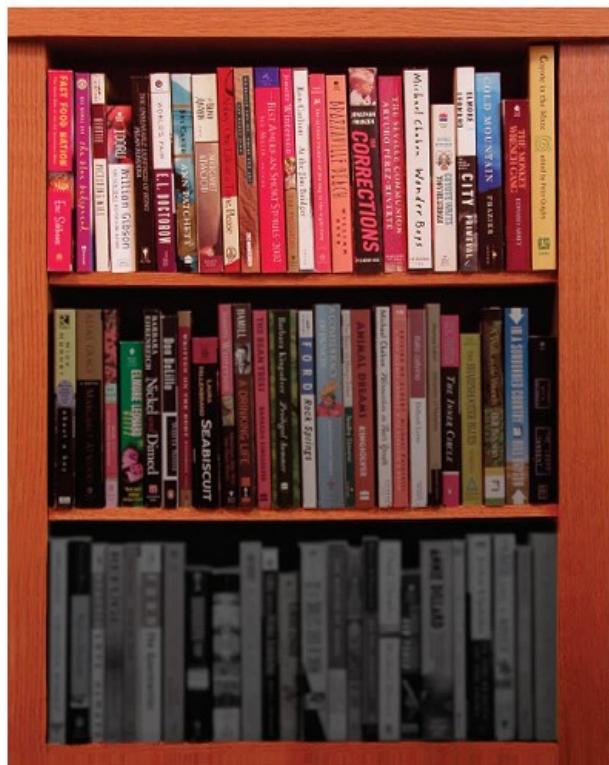
DEMONSTRATION | Foveal Versus Peripheral Acuity

D I H C N R L A Z I F W N S M Q P Z K D X

You can demonstrate that foveal vision is superior to peripheral vision for seeing details by looking at the X on the right and, without moving your eyes, seeing how many letters you can identify to the left. If you do this without cheating (resist the urge to look to the left!), you will find that although you can read the letters right next to the X, which are imaged on or near the fovea, it is difficult to read letters that are further off to the side, which are imaged on the peripheral retina.

This demonstration shows that acuity is better in the fovea than in the periphery. Because you were light adapted, the comparison in this demonstration was between the foveal cones, which are tightly packed, and the peripheral cones, which are more widely spaced. Comparing the foveal cones to the rods results in even greater differences in acuity. We can make this comparison by noting how acuity changes during dark adaptation.

The picture of the bookcase in **Figure 2.31** simulates the change in acuity that occurs during dark adaptation. The



© Bruce Goldstein

Figure 2.31 Simulation of the change from colorful sharp perception to colorless fuzzy perception that occurs during the shift from cone vision to rod vision during dark adaptation. The top shelf simulates cone vision; the bottom shelf, rod vision.

books on the top shelf represent the details we see when viewing the books in the light, when our cones are controlling vision. The books on the middle shelf represent how we might perceive the details midway through the process of dark adaptation, when the rods are beginning to determine our vision, and the books on the bottom shelf represent the poor detail vision of the rods. The poor detail vision of the rods is why it is difficult to read in dim illumination. (Also note that color has disappeared. We will describe why this occurs in Chapter 9.)

We can understand how differences in rod and cone wiring explain the cones' greater acuity by returning to our rod and cone neural circuits. First consider the rod circuit in **Figure 2.32a**. When we present two spots of light next to each other, as on the left, the rod's signals cause the ganglion cell to fire. When we separate the two spots, as on the right, the two separated rods feed into the same ganglion cell and cause it to fire. In both cases, the ganglion cell fires. Thus, firing of the ganglion cell provides no information about whether there are two spots close together or two separated spots.

We now consider the cones in **Figure 2.32b**, each of which synapses on its own ganglion cell. When we present a light that

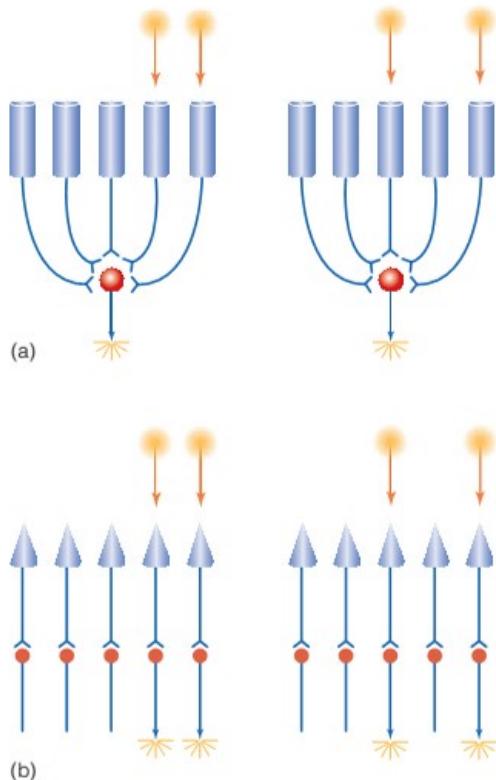


Figure 2.32 How the wiring of the rods and cones determines detail vision. (a) Rod neural circuits. On the left, stimulating two neighboring rods causes the ganglion cell to fire. On the right, stimulating two separated rods causes the same effect. (b) Cone neural circuits. On the left, stimulating two neighboring cones causes two neighboring ganglion cells to fire. On the right, stimulating two separated cones causes two separated ganglion cells to fire. This firing of two neurons, with a space between them, indicates that two spots of light have been presented to the cones.

stimulates two neighboring cones, as on the left, two adjacent ganglion cells fire. But when we separate the spots, as on the right, two separate ganglion cells fire. This separation between two firing cells provides information that there are two separate spots of light. Thus, the cones' lack of convergence causes cone vision to have higher acuity than rod vision.

Convergence is therefore a double-edged sword. High convergence results in high sensitivity but poor acuity (the rods). Low convergence results in low sensitivity but high acuity (cones). The way the rods and cones are wired up in the retina, therefore, influences what we perceive. In Chapter 3 we will provide more examples of how neural wiring can influence perception, and we will show how the addition of inhibition adds another dimension to neural processing.

SOMETHING TO CONSIDER:

Early Events Are Powerful

In 1990, a rocket blasted off from Cape Canaveral to place the Hubble space telescope into earth orbit. The telescope's mission was to provide high-resolution images from its vantage point above the interference of the earth's atmosphere. But it took only a few days of data collection to realize that something was wrong. Images of stars and galaxies that should have been extremely sharp were blurred (**Figure 2.33a**). The cause of the problem, it turned out, was that the telescope's lens was ground to the wrong curvature. Although a few of the planned observations were possible, the telescope's mission was severely compromised. Three years later, the problem was solved when a corrective lens was fitted over the original one. The new Hubble, with its "eyeglasses," could now see stars as sharp points (**Figure 2.33b**).

This diversion to outer space emphasizes that what happens early in a system can have a large, often crucial, effect on the outcome. No matter how sophisticated Hubble's electronic computer and processing programs were, the distorted image caused by the faulty lens had fatal effects on the quality of the telescope's image. Similarly, if problems in the eye's focusing system deliver degraded images to the retina, no amount of processing by the brain can create sharp perception.

What we see is also determined by the energy that can enter the eye and can activate the receptors. Although there is a huge range of electromagnetic energy in the environment, the visual pigments in the receptors limit our sensitivity by absorbing only a narrow range of wavelengths. One way to think about the effect of pigments is that they act like filters, only making available for vision the wavelengths they absorb. Thus, at night, when we are perceiving with our rods, we see only wavelengths between about 420 and 580 nm, with the best sensitivity at 500 nm. However, in daylight, when we are perceiving with our cones, we become more sensitive to longer wavelengths, as the best sensitivity shifts to 560 nm.

This idea of visual pigments as limiting our range of seeing is dramatically illustrated by the honeybee, which, as we



Wide field planetary camera 1
(a) Before



Wide field planetary camera 2
(b) After correction

Figure 2.33 (a) Image of a galaxy taken by the Hubble telescope before the lens was corrected. (b) The same galaxy after the lens was corrected.

will see in the chapter on color vision, has a visual pigment that absorbs light all the way down to 300 nm (see Figure 9.43, page 221). This very-short-wavelength pigment enables the honeybee to perceive ultraviolet wavelengths that are invisible to us, so the honeybee can see markings on flowers that reflect



(a)



(b)

Brian Rundlett

Figure 2.34 (a) A black-and-white photograph of a flower as seen by a human. (b) The same flower, showing markings that become visible to sensors that can detect ultraviolet light. Although we don't know exactly what honeybees see, their short-wavelength cone pigment makes it possible for them to sense these markings.

ultraviolet light (**Figure 2.34**). Thus, as we noted earlier in this chapter, although perception does not *occur* in the eye, what we see is affected by what happens there. Similar effects occur in the other senses as well. Damage to the receptors in the ear is the main cause of hearing loss (Chapter 11, page 281); differences in the number of “bitter” receptors on people’s tongues can cause two people to have different taste experiences to the same substance (Chapter 15, page 368).

DEVELOPMENTAL DIMENSION Infant Visual Acuity

Some chapters in this book will include “Developmental Dimensions,” such as this one, which describe perceptual capacities of infants and young children that are related to material in the chapter.

One of the challenges of determining infant capacities is that infants can’t respond by saying “yes, I perceive it”

or “no, I don’t perceive it” in reaction to a stimulus. But this difficulty has not stopped developmental psychologists from devising clever ways to determine what infants or young children are perceiving. One method that has been used to measure infant visual acuity is the **preferential looking (PL) technique**.

METHOD Preferential Looking

The key to measuring infant perception is to pose the correct question. To understand what we mean by this, let's consider how we might determine infants' *visual acuity*, their ability to see details. To test adults, we can ask them to read the letters or symbols on an eye chart. But to test infant acuity, we have to ask another question and use another procedure. A question that works for infants is "Can you tell the difference between the stimulus on the left and the one on the right?" The way infants answer this question is by looking more at one of the stimuli.

In the preferential looking (PL) technique, two stimuli like the ones the infant is observing in **Figure 2.35** are presented, and the experimenter watches the infant's eyes to determine where the infant is looking. In order to guard against bias, the experimenter does not know which stimulus is being presented on the left or right. If the infant looks at one stimulus more than the other, the experimenter concludes that he or she can tell the difference between them.

The reason preferential looking works is that infants have *spontaneous looking preferences*; that is, they prefer to look at certain types of stimuli. For example, infants choose to look at objects with contours over ones that are homogeneous (Fantz et al., 1962). Thus, when we present a grating stimulus (alternating white and black bars like the one shown in Figure 2.35) with large bars on one side, and a gray field that reflects the same total amount of light that the grating would reflect on the other side (again, like the one shown in Figure 2.35), the infant can easily see the bars and therefore looks at the side with the bars more than the side with the gray field. If the infant looks preferentially at the side with the bars when the bars are switched randomly from side to



Figure 2.35 An infant being tested using the preferential looking technique. The mother holds the infant in front of the display, which consists of a grating on the right and a homogeneous gray field on the left. The grating and the gray field have the same average light intensity. An experimenter, who does not know which side the grating is on in any given trial, looks through the peephole between the grating and the gray field and judges whether the infant is looking to the left or to the right.

side on different trials, he or she is telling the experimenter "I see the grating."

But decreasing the size of the bars makes it more difficult for the infant to tell the difference between the grating and gray stimulus. Eventually, the infant begins to look equally at each display, which tells the experimenter that very fine lines and the gray field are indiscriminable. Therefore, we can measure the infant's acuity by determining the narrowest stripe width that results in looking more at the grating stimulus.

How well can infants see details? The red curve in **Figure 2.36** shows acuity over the first year of life measured with the preferential looking technique, in which infants are tested with gratings, as in Figure 2.35. The blue curve indicates acuity determined by measuring an electrical signal called the *visual evoked potential* (VEP), which is recorded by disc electrodes placed on the infant's head over the visual cortex. For this technique, researchers alternate a gray field with a grating or checkerboard pattern. If the stripes or checks are large enough to be detected by the visual system, the visual cortex generates an electrical response called the *visual evoked potential*.

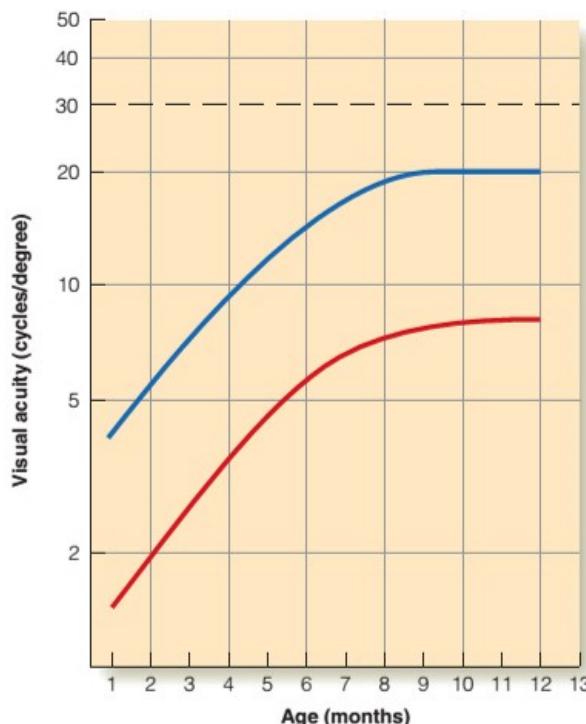


Figure 2.36 Acuity over the first year of life, measured by the visual evoked potential technique (top curve) and the preferential looking technique (bottom curve). The vertical axis indicates the fineness, in cycles per degree, of a grating stimulus that the infant can detect. One cycle per degree corresponds to one pair of black and white lines on a circle the size of a penny viewed from a distance of about a meter. Higher numbers indicate the ability to detect finer lines on the penny-sized circle. The dashed line is adult acuity (20/20 vision). (VEP curve adapted from Norcia & Tyler, 1985; PL curve adapted from Gwiazda et al., 1980, and Mayer et al., 1995)

If, however, the stripes are too fine to be detected by the visual system, no response is generated. Thus, the VEP provides an objective measure of the visual system's ability to detect details.

The VEP usually indicates better acuity than does preferential looking, but both techniques indicate that visual acuity is poorly developed at birth (about 20/400 to 20/600 at 1 month). (The expression 20/400 means that the infant must view a stimulus from 20 feet to see the same thing that an adult with normal vision can see from 400 feet.) Acuity increases rapidly over the first 6 to 9 months (Banks & Salapatek, 1978; Dobson & Teller, 1978; Harris et al., 1976; Salapatek et al., 1976). This rapid improvement of acuity is followed by a leveling-off period, and full adult acuity is not reached until sometime after 1 year of age.

From our discussion of how adult rod and cone visual acuity depends on the wiring of the rods and cones, it would make sense to consider the possibility that infants' low acuity might be traced to the development of their receptors. If we look at the newborn's retina, we find that this is the case. Although the rod-dominated peripheral retina appears adultlike in the newborn, the all-cone fovea contains widely spaced and very poorly developed cone receptors (Abramov et al., 1982).

Figure 2.37a compares the shapes of newborn and adult foveal cones. Remember from our discussion of transduction that the visual pigments are contained in the receptor's outer segments. These outer segments sit on top of the other part of the receptor, the inner segment. The newborn's cones have fat inner segments and very small outer segments, whereas the adult's inner and outer segments are larger and are about the same diameter (Banks & Bennett, 1988; Yuodelis & Hendrickson, 1986). These differences in shape and size have a number of consequences. The small size of the outer segment means that the newborn's cones contain less visual pigment and therefore do not absorb light as effectively as adult cones. In addition,

the fat inner segment creates the coarse receptor lattice shown in **Figure 2.37b**, with large spaces between the outer segments. In contrast, when the adult cones have become thin, they can become packed closely together to create a fine lattice that is well suited to detecting small details. Martin Banks and Patrick Bennett (1988) calculated that the cone receptors' outer segments effectively cover 68 percent of the adult fovea but only 2 percent of the newborn fovea. This means that most of the light entering the newborn's fovea is lost in the spaces between the cones and is therefore not useful for vision.

Thus, adults have good acuity because the cones have low convergence compared to the rods and the receptors in the fovea are packed closely together. In contrast, the infant's poor acuity can be traced to the fact that the infant's cones are spaced far apart. Another reason for the infant's poor acuity is that the visual area of the brain is poorly developed at birth, with fewer neurons and synapses than in the adult cortex. The rapid increase in acuity that occurs over the first 6 to 9 months of life can thus be traced to the fact that during that time, more neurons and synapses are being added to the cortex, and the infant's cones are becoming more densely packed.

TEST YOURSELF 2.2

1. Describe the basic structure of a neuron.
2. Describe how to record electrical signals from a neuron.
3. What are some of the basic properties of action potentials?
4. Describe what happens when an action potential travels along an axon. In your description, indicate how the charge inside the fiber changes, and how that is related to the flow of chemicals across the cell membrane.

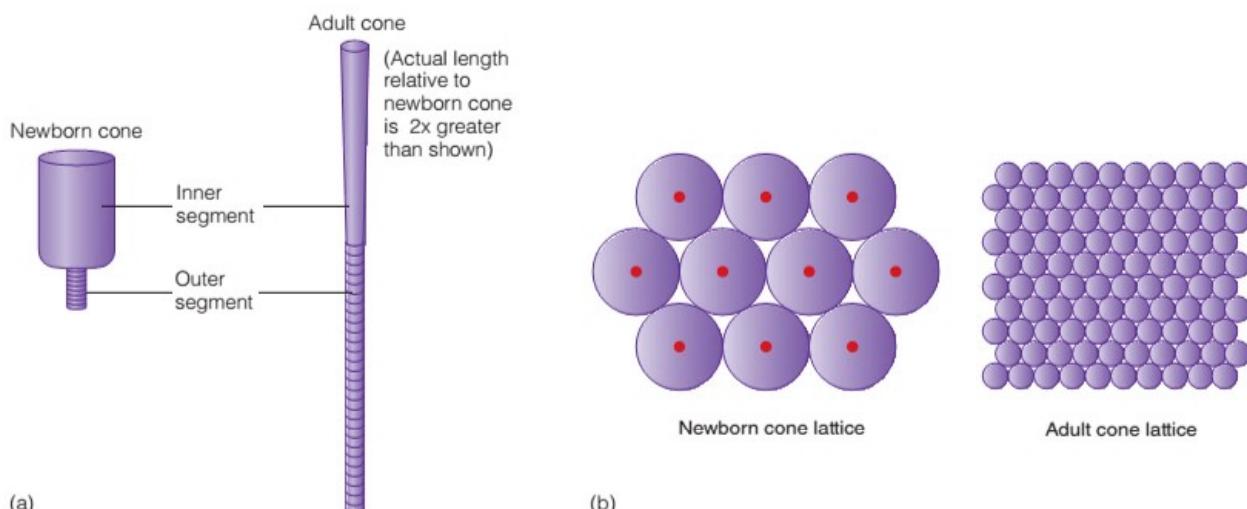


Figure 2.37 (a) Idealized shapes of newborn and adult foveal cones. (Real cones are not so perfectly straight and cylindrical.) Foveal cones are much narrower and longer than the cones elsewhere in the retina, so these look different from the one shown in Figure 2.3. (b) Receptor lattices for newborn and adult foveal cones. The newborn cone outer segments, indicated by the red circles, are widely spaced because of the fat inner segments. In contrast, the adult cones, with their slender inner segments, are packed closely together.
(Adapted from Banks & Bennett, 1988)

- How are electrical signals transmitted from one neuron to another? Be sure you understand the difference between excitatory and inhibitory responses.
- What is convergence, and how can the differences in the convergence of rods and cones explain (a) the rods' greater sensitivity in the dark and (b) the cones' better detail vision?
- What does it mean to say that early events are powerful shapers of perception? Give examples.
- What is the young infant's visual acuity, and how does it change over the first year of life? What is the reason for (a) low acuity at birth and (b) the increase in acuity over the first 6 to 9 months?

THINK ABOUT IT

- Ellen is looking at a tree. She sees the tree because light is reflected from the tree into her eyes, as shown in **Figure 2.38**. One way to describe this is to say that information about the tree is contained in the light. Meanwhile, Roger is off to the side, looking straight ahead. He doesn't see the tree because he is looking away from it. He is however, looking right at the space through which the light that is carrying information from the tree to Ellen is passing. But Roger doesn't see any of this information. Why does this occur? (Hint #1: Consider the idea that "objects make light visible." Hint #2: Outer space contains a great deal of light, but it looks dark, except where there are objects.)
- In the demonstration "Becoming Aware of What Is in Focus" on page 26, you saw that we see things clearly only when we are looking directly at them so that their image falls on the cone-rich fovea. But consider the common observation that the things we aren't looking at do not appear "fuzzy," that the entire scene appears "sharp" or "in focus." How can this be, in light of the results of the demonstration?
- Here's an exercise you can do to get more in touch with the process of dark adaptation: Find a dark place where you can make some observations as you adapt to the dark.

Figure 2.38 Ellen sees the tree because light is reflected from the tree into her eyes. Roger doesn't see the tree because he is not looking at it, but he is looking directly across the space where light from the tree is reflected into Ellen's eyes. Why isn't he aware of the information contained in this light?

A closet is a good place to do this because you can regulate the intensity of light inside the closet by opening or closing the door. The idea is to create an environment in which there is dim light (no light at all, as in a darkroom with the safelight out, is too dark). Take this book into the closet, opened to this page. Close the closet door all the way so it is very dark, and then open the door slowly until you can just barely make out the white circle on the far left in **Figure 2.39** but can't see the others or can see them only as being very dim. As you sit in the dark, become aware that your sensitivity is increasing by noting how the circles to the right in the figure slowly become visible over a period of about 20 minutes. Also note that once a circle becomes visible, it gets easier to see as time passes. If you stare directly at the circles, they may fade, so move your eyes around every so often. Also, the circles will be easier to see if you look slightly above them.

- Because the long axons of neurons look like electrical wires, and both neurons and electrical wires conduct electricity, it is tempting to equate the two. Compare the functioning of axons and electrical wires in terms of their structure and the nature of the electrical signals they conduct.

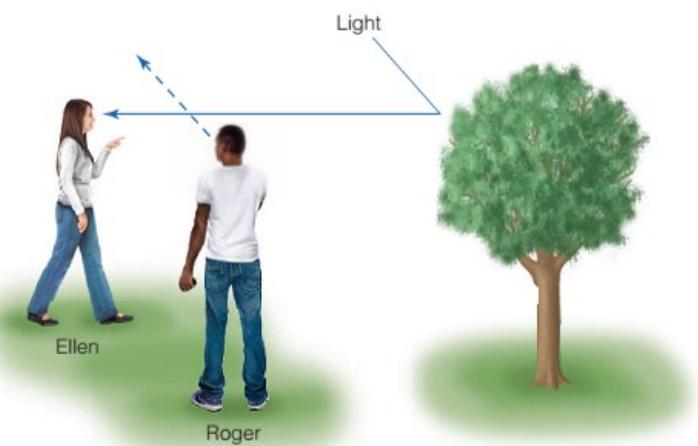


Figure 2.39 Dark adaptation test circles.

KEY TERMS

- | | | |
|--|--|--|
| Absorption spectrum (p. 32) | Ganglion cells (p. 39) | Pupil (p. 22) |
| Accommodation (p. 25) | Horizontal cells (p. 39) | Purkinje shift (p. 32) |
| Action potential (p. 34) | Hyperopia (p. 27) | Receptor sites (p. 38) |
| Amacrine cells (p. 39) | Hyperpolarization (p. 38) | Refractive myopia (p. 27) |
| Axial myopia (p. 27) | Inhibitory response (p. 38) | Refractory period (p. 36) |
| Axon (p. 33) | Ions (p. 36) | Resting potential (p. 34) |
| Bipolar cells (p. 39) | Isomerization (p. 27) | Retina (p. 22) |
| Blind spot (p. 24) | Lens (p. 22) | Retinitis pigmentosa (p. 24) |
| Cell body (p. 33) | Light-adapted sensitivity (p. 28) | Rising phase of the action potential (p. 36) |
| Cones (p. 22) | Macular degeneration (p. 23) | Rod monochromats (p. 30) |
| Cone spectral sensitivity (p. 32) | Monochromatic light (p. 31) | Rods (p. 22) |
| Convergence (p. 39) | Myopia (p. 27) | Rod spectral sensitivity curve (p. 32) |
| Cornea (p. 22) | Nearsightedness (p. 27) | Rod-cone break (p. 30) |
| Dark-adapted sensitivity (p. 28) | Nerve fiber (p. 33) | Spectral sensitivity curve (p. 31) |
| Dark adaptation curve (p. 28) | Neural circuits (p. 39) | Spectral sensitivity (p. 31) |
| Dark adaptation (p. 28) | Neural convergence (p. 39) | Spontaneous activity (p. 36) |
| Dendrites (p. 33) | Neurons (p. 33) | Synapse (p. 37) |
| Depolarization (p. 38) | Neurotransmitters (p. 37) | Transduction (p. 27) |
| Detached retina (p. 31) | Optic nerve (p. 23) | Visible light (p. 22) |
| Excitatory response (p. 38) | Outer segments (p. 22) | Visual acuity (p. 41) |
| Eyes (p. 22) | Peripheral retina (p. 23) | Visual evoked potential (p. 44) |
| Falling phase of the action
potential (p. 36) | Permeability (p. 36) | Visual pigment bleaching (p. 30) |
| Farsightedness (p. 27) | Preferential looking technique (p. 43) | Visual pigment regeneration (p. 30) |
| Fovea (p. 23) | Presbyopia (p. 27) | Visual pigments (p. 23) |
| | Propagated response (p. 34) | Wavelength (p. 22) |