

disease. But supertasters also tend to eat fewer vegetables with cancer-fighting flavonoids (which taste too acrid to them), so they may be more vulnerable to certain cancers. How can our tiny taste buds so powerfully shape our behavior and potentially our health? The first step in tackling this question is to ask how our tongues—or, more broadly, our sense organs—funnel the outside world into our bodies and minds. These questions are central to the psychology of sensation.

Katie's case also reminds us that our senses shape our daily existence. Of course, someone who's blind can have a full, rich life—but nonetheless, walking down a hallway or crossing a street are much more challenging than for someone sighted, and some activities (like driving) are out of the question. Likewise, deaf people live perfectly normal lives in most respects; but they can't respond to the smoke alarm's shriek or the wail of a police siren, and they can converse with only a limited number of people. (Roughly 2 million people are proficient in American Sign Language worldwide; but compare that to, say, the world's 400 million English speakers.) Things are more extreme for individuals lacking other senses—including people who can't sense pain. As we'll see, these people are at risk for many injuries, including biting their tongues while chewing or leaning on a hot stove without realizing it.

Our dependence on the senses raises a question: How reliable are they? You've likely had the experience of spotting a friend in a crowd—only to discover that the person is someone else altogether. You've probably heard someone calling you, but then realized you imagined it. And surely at some point you've failed to hear someone speaking to you. Is it possible that our sensory experiences are often inaccurate or incomplete—so that the world we sense differs from the world as it is?

The world certainly poses a challenge for our sensory apparatus: This page is now in front of your eyes—but you also see your hands, others in the room, the table surface, and more. Your eyes take in a wealth of information from each of these objects—and your eyes and brain constantly collect, encode, interpret, and act upon what you see, even as you simultaneously make sense of an influx of other sensory information.

In this chapter, we'll examine how our senses function, beginning with the questions that launched scientific inquiry in this domain: How accurate and complete are our sensory experiences? And how objective is our perception of the world? We'll then turn to psychologists' methods for addressing these questions. With that base, we'll survey the senses, starting with properties they all have in common and then considering each sense separately.

You may not be a supertaster or have especially acute hearing; you may not be nearsighted or color-blind. But this chapter will help you appreciate the complexity of what may seem to be the simplest of functions—seeing, smelling, hearing, tasting, and feeling the world around us.

THE ORIGINS OF KNOWLEDGE

Where does human knowledge come from? One possibility is that our knowledge comes directly from the world around us, and that our eyes, ears, and other senses are simply collecting the information the world provides. According to this view, our senses faithfully receive and record information much as a camera receives light or a microphone receives sound, and this implies that our perception of the world is a rela-

tively passive affair. After all, a camera doesn't choose which light beams to receive, nor does it interpret any of the light it detects. Instead, it simply records the light available to it. Likewise, a microphone doesn't interpret the speech or appreciate the music; again, in a passive way, it simply receives the sounds and passes them along to an amplifier or recording device. Could this be the way our vision and hearing work?

The Passive Perceiver

Advocates for the philosophical view known as *empiricism* argued that our senses are passive in the way just described. One of the earliest proponents of this position was the 17th-century English philosopher John Locke. He argued that at birth, the human mind is much like a blank tablet—a *tabula rasa*, on which experience leaves its mark (Figure 4.1).

Let us suppose the mind to be, as we say, a white paper void of all characters, without any ideas:—How comes it to be furnished? Whence comes it by that vast store which the busy and boundless fancy of man has painted on it with an almost endless variety? Whence has it all the materials of reason and knowledge? To this I answer, in one word, from experience. In that all our knowledge is founded; and from that it ultimately derives itself. (Locke, 1690)

To evaluate Locke's claim, however, we need to be clear about exactly what information the senses receive. What happens, for example, when we look at another person? We're presumably interested in what the person looks like, who he is, and what he's doing. These are all facts about the **distal stimulus**—the real object (in this case, the person) in the outside world. (The distal stimulus is typically at some distance from the perceiver, hence the term *distal*.)

But it turns out that our information about the distal stimulus is indirect, because we know the distal stimulus only through the energies that actually reach us—the pattern of light reflected off the person's outer surface, collected by our eyes, and cast as an image on the retina, the light-sensitive tissue at the rear of each eyeball. This input—that is, the energies that actually reach us—is called the **proximal (or "nearby") stimulus**.

The distinction between distal and proximal stimuli is crucial for hearing as well as vision. We hear someone speaking and want to know who it is, what she's saying, and whether she sounds friendly or hostile. These are all questions about the speaker herself, so they're questions about the distal stimulus. However, our perception of these points must begin with the stimulus that actually reaches us—the sound-pressure waves arriving at our eardrums. These waves are the proximal stimulus for hearing.

The distinction between distal and proximal stimuli is a problem for empiricists. To see why, let's look at the concerns raised by another empiricist philosopher, George Berkeley. As Berkeley pointed out, a large object that's far away from us can cast the same-size image on our retina as can a small object much closer to us (Figure 4.2). Retinal-image size, therefore, doesn't tell us the size of the distal object. How, then, do we tell the large objects in our world from the small? Berkeley also knew that the retina is a two-dimensional surface, and that all images—from near objects and far—are cast onto the same plane. He argued, therefore, that the retinal image cannot directly inform us about the three-dimensional world. Yet, of course, we have little difficulty moving around the world, avoiding obstacles, grasping the things we want to grasp. How can we explain these abilities in light of the limitations of proximal stimuli?



4.1 John Locke (1632–1704) English philosopher and one of the first advocates for empiricism.

distal stimulus An object or event in the outside world.

proximal stimulus The energies from the outside world that directly reach our sense organs.



4.2 Distal and proximal stimuli When this person looks out on the world, the retinal image cast by his hand will be roughly the same size as the image of the car. But one of these images obviously represents a much larger object! Clearly, then, retinal-image size (the proximal stimulus) alone cannot tell us the size of the distant object (the distal stimulus).



4.3 Distance cues in Renaissance painting This painting by Paris Bordone (1500–1571) shows how distance cues can create a vivid sense of depth on a flat canvas.



4.4 Immanuel Kant (1724–1804) German philosopher who advocated for innate categories of experience.

The empiricists' answer to these questions boils down to a single word: *learning*. We can perceive and move around in the three-dimensional world, they argued, because our *experience* has taught us how to interpret the two-dimensional proximal stimulus. To see how this interpretation unfolds, consider the role of *depth cues* contained within the retinal image. These cues include what's called *visual perspective*—a cue used to convey depth in many paintings (Figure 4.3). The empiricists argued that, in many circumstances, we see the pattern of visual perspective and a moment later reach for or walk toward the objects we're viewing. This experience creates an association in the mind between the visual cue and the appropriate movement; and because this experience has been repeated over and over, the visual cue alone now produces the memory of the movement and thus the sense of depth. (For more on distance cues, see Chapter 5.) In this way, our perception is guided by the proximal stimulus *and* the association.

The Active Perceiver

Other philosophers soon offered a response to the empiricist position, arguing that the perceiver plays a much larger role than the empiricists realized. In this view, the perceiver does far more than supplement the sensory input with associations. In addition—and more important—the perceiver must categorize and interpret the incoming sensory information.

Many scholars have endorsed this general position, but it's often attributed to the German philosopher Immanuel Kant (1724–1804; Figure 4.4). Kant argued that perception is possible only because the mind organizes the sensory information into certain preexisting categories. Specifically, Kant claimed that each of us has an innate grasp of certain spatial relationships, so that we understand what it means for one thing to be *next to* or *far from* another thing, and so on. We also have an innate grasp of temporal relationships (what it means for one event to occur *before* another, or *after*) as well as what it means for one event to cause another. This basic understanding of space, time, and causality brings order to our perception; without this framework, Kant argued, our sensory experience would be chaotic and meaningless. We might detect the individual bits of red or green or heavy or sour; but without the framework supplied by each perceiver, we'd be unable to assemble a coherent sense of the world.

Notice that, in Kant's view, these categories (Kant called them “forms of apperception”) are what make perception possible; without the categories, there can be no perception. The categories must be in place, therefore, before any perceptual experience can occur, so they obviously can't be *derived from* perceptual experience. Instead, they must be built into the very structure of the mind, as part of our biological heritage.

PSYCHOPHYSICS

The debate just described was a debate among philosophers, and it made few appeals to any sort of scientific evidence. Ultimately, though, the questions at stake could be understood as questions about whether our perceptions of the world reflect reality as it truly is, or instead reflect reality as it has been interpreted and categorized by us. These seem like questions that should be open to scientific scrutiny, and so it's not too

surprising that this dispute prodded investigators to explore in a more systematic way just how the senses function.

At the most basic level, this scrutiny must begin with the relationship between the physical inputs we receive—the stimuli—and the psychological experiences these stimuli give rise to. How closely do our experiences correspond to the inputs? Which inputs give rise to which experiences? The area of research that charts these relationships, linking psychological experiences to physical stimuli, is called **psychophysics**—an enterprise that asks questions like these: What will change in our perception of a sound as the frequency of the sound waves changes? What change in the physical attributes of light corresponds to the change from perceiving red to perceiving green? They might seem technical, but such questions are crucial if we are to understand the relationship between the objective, physically defined stimuli we encounter and the subjective, psychological world of our conscious experience. In other words, we're trying to understand the relationship between the world as it actually is and the world as we perceive it to be.

psychophysics An approach to perception that relates the characteristics of physical stimuli to the sensory experiences they produce.

Sensory Thresholds

We can apply the methods of psychophysics to several different questions as well as a wide range of stimuli. Picture this: You're in a restaurant, eating a particularly tasty fish. Knowing you'd like to re-create the dish in your own kitchen, you might ask, "What's the source of that distinctive flavor?" Here you're asking a psychophysical question—what was it in the physical stimulus that led to a particular sensation, a particular taste? You might realize that the flavor came from adding a tiny bit of saffron to the fish, and so you decide to use saffron in your own cooking. But saffron is the world's most expensive spice, so you'd like to add as little as possible. How much saffron do you need—so that people tasting the fish will just pick up the hint of saffron? This is a psychophysical question about people's ability to detect an input. And perhaps you try the dish once, and decide that next time the saffron flavor could be a tiny bit stronger. How much saffron should you add to produce that stronger flavor? This, too, is a psychophysical question—about the ability to detect differences.

Let's start our examination of psychophysics, therefore, with the issue of *detection*: To continue the example, when we try to determine the smallest amount of saffron you can use (so that you get the effect of the spice without straining your budget), we're asking a question about an **absolute threshold**—the smallest quantity of an input that can be detected. The absolute threshold is assessed in precise physical terms—the number of strands of saffron needed; or the amount of light, measured in quanta, needed for someone to see the light; or the loudness, measured in sound pressure levels, needed for someone to hear a sound. However, we can translate these thresholds into common-sense terms—and when we do, it's clear that our thresholds for many stimuli are very low indeed (Table 4.1).

Our cooking example also highlighted a different type of detection—namely, the detection of differences. If we add two more strands of saffron, can we detect this alteration in the stimulus? How about five more grains, or ten? These are questions about someone's **difference threshold**—the smallest *change* in an input that can be detected. When a stimulus is changed by this minimal amount, psychophysicists call it a **just-noticeable difference**, or **jnd**.

We can measure thresholds for many different sensory dimensions—flavors, brightness, loudness, smells, heaviness, pressure, and more. Across all of these dimensions, difference thresholds show a consistent property: They depend on *proportional*

absolute threshold The smallest quantity of a stimulus that an individual can detect.

difference threshold The smallest amount that a given stimulus must be increased or decreased so that an individual can detect the difference.

just-noticeable difference (jnd) The smallest difference that an organism can reliably detect between two stimuli.

TABLE		Absolute Thresholds
4.1	Modality	Example of minimal stimulus that can be detected
	Vision	A candle flame 30 miles away on a dark, clear night
	Hearing	A ticking watch 20 feet away with no other noises
	Taste	A teaspoon of sugar in 2 gallons of water
	Smell	A drop of perfume in 3 rooms
	Touch	The wing of a fly falling on your cheek from a height of 3 inches
Source: Galanter, 1962.		

differences, and not *absolute* differences. To illustrate, let's say that you can tell the difference between a backpack filled with 25 pounds of camping gear and one that contains a half-pound more—and so 25.5 pounds. This does not mean that, in general, you're sensitive to half-pound differences. What matters instead is the proportional change—in this case, a difference of 2%. Thus, you probably would not be able to distinguish between a backpack filled with 50 pounds of gear and one that contains 50.5 pounds. This is still a half-pound difference, but only a 1% change. But you would be able to distinguish 50 pounds from 51, or 75 pounds from 76.5—in each case a 2% difference.

This important role for proportions, first documented by the 19th-century physiologist E. H. Weber, is known as **Weber's law**. Put algebraically, this law is written as

$$\frac{\Delta I}{I} = c$$

In the equation, I is the intensity of the standard stimulus, the one to which comparisons are being made; ΔI is the amount that must be added to this intensity to produce a just-noticeable increase; c is a constant (in our example, it was .02, or 2%). The fraction $\Delta I / I$ is referred to as the *Weber fraction*.

Weber's law is important for several reasons, including the fact that it allows us to compare the sensitivities of different sensory modalities. Suppose we want to know whether the eye is more sensitive than the ear. We cannot compare jnds for brightness and loudness directly; the first is measured in millilamberts, the second in decibels, and there's no way to translate the one into the other. But we can compare the Weber fractions for the two modalities. If the fraction for a specific sense modality is small, then we know that the modality is able to make fine discriminations; that is, it will detect even small percentage changes. And, of course, the smaller the Weber fraction, the more sensitive the sense modality. Using these comparisons, we can show that we are much keener at discriminating brightness (we're sensitive to differences of merely 1.6%) than weight (2%), and more sensitive to differences in weight than we are to differences in loudness (10%). The Weber fractions needed for this comparison, and fractions for other sense modalities, are presented in Table 4.2.

Weber's law also helps us solve a further puzzle: The measurement of difference thresholds tells us whether the perceiver can detect a *change* or not. Often, though, we want to know more than this. We want to know about the perceiver's experience—how bright does the light seem to the perceiver, or how loud does the sound seem? Then we

Weber's law The observation that the size of the difference threshold is proportional to the intensity of the standard stimulus.

TABLE Representative (Middle-Range) Values for the Weber Fraction for the Different Senses			
4.2	Sensory modality	Weber fraction ($\Delta I/I$)	Weber fraction as a percentage
	Vision (brightness, white light)	1/60	1.6%
	Kinesthesia (lifted weights)	1/50	2.0%
	Pain (thermally aroused on skin)	1/30	3.3%
	Hearing (tone of middle pitch and moderate loudness)	1/10	10.0%
	Touch (cutaneous pressure “spot”)	1/7	14.2%
	Smell (odor of India rubber)	1/4	25.0%
	Taste (table salt)	1/3	33.3%

want to link these measurements to the stimulus, so that we can specify the correspondence between the intensity of the stimulus and the intensity of the experience.

More than a hundred years ago, Gustav Fechner was able to address this issue mathematically, building on Weber’s law. His result, often referred to as **Fechner’s law**, describes the relationship between the physical intensity of a stimulus and the psychological intensity of the experience produced by that experience. The law states that the strength of a sensation increases logarithmically with the intensity of the stimulus. Formally, the law is written:

$$S = k \log I$$

In the equation, S stands for psychological (i.e., subjective) magnitude; I is the physical intensity of the stimulus; and k is a constant whose value depends on the value of the Weber fraction.

In the years since Fechner we’ve learned that, in truth, this law does not hold up perfectly in all circumstances. (For example, the perception of *pain* does not show the pattern predicted by Fechner’s law; for pain, a very small increase in the stimulus causes a large increase in the sensation—a pattern that’s useful in compelling us to deal with pain when it arises.) For our purposes, though, the law does hold in a wide range of settings and with a diversity of stimuli. It offers a reasonably accurate characterization of the relationship between stimulus intensity and subjective impression.

Detection and Decision

Sensory thresholds are defined in terms of stimulus intensities—how much intensity do we need before we can detect the stimulus? How much of a change in intensity do we need to detect that two stimuli are different? It turns out, however, that these intensities are not the only factors determining how someone responds in a psychophysical experiment. Indeed, even this early in our description of the sensory processes, we need to realize that we’re not trying to understand how light meters or audiometers work. Instead, we’re discussing the capacities and behaviors of living organisms—and that introduces some complications.

Fechner’s law The observation that the strength of a sensation is proportional to the logarithm of physical stimulus intensity.

it; this sounds like a doctor one should seek out. But it might also mean the doctor has a lax criterion and offers this horrible diagnosis based on relatively thin evidence; now this sounds like a doctor to be avoided! It would obviously be useful to know which of these descriptions is correct, and of course this is precisely the information provided by signal-detection analysis. (For details on how signal detection has been applied to other domains, including medical diagnosis, see, for example, McFall & Treat, 1999; Swets, Dawes, & Monahan, 2000.)

Signal-detection analyses highlight another crucial point: We often make decisions with imperfect information, so it's inevitable that we'll make some errors. What can we do about this? If we are especially concerned about *false alarms* (a cancer test that says someone has the disease even though she doesn't, or a jury that votes "guilty" even though the defendant is innocent), we can take steps to raise the response criterion. This adjustment will decrease the number of false alarms, but it's likely to increase the number of misses (failing to detect an actual tumor, or acquitting someone who is actually guilty). On the other hand, we could shift in the opposite direction—to a lower criterion—but this would lead to the opposite pattern of benefit and risk: Lowering the criterion will decrease the number of misses but increase the number of false alarms.

How should we think about these issues? That depends on the specific case—and, in particular, the potential consequences of a miss or false alarm. Overall, though, when we make decisions (or develop a cancer test, or instruct a jury), it's important to remember that this trade-off between misses and false alarms is in place. If we want to evaluate anything from a cancer test or a jury instruction to the memory effects of hypnosis or the police department's decision about whether to take a bomb threat seriously, signal-detection analyses can provide separate measurements of sensitivity and criterion—information that allows us to ensure that these decision processes are well tuned to our goals.

A SURVEY OF THE SENSES

Psychophysics allows us to specify the correspondence between physical stimuli and psychological experiences, but this is just the first step of our inquiry. We also want to understand *why this correspondence is as it is*. Let's say, for example, that we've learned from psychophysics that placing a particular molecule on the tongue leads someone to say, "Yeah, I can detect a taste—and it's sweet. It's chocolate!" What are the steps that bring us from the molecule to this recognition? As our first question, we might ask how the molecule manages to trigger a response in the nervous system at all. We'd also want to ask why the molecule leads to a sensation of sweet, while some other molecule might lead to a sensation of salty. And once the molecule has triggered a response in the nervous system, how does this response lead to the conscious experience of tasting a delicious bit of chocolate?

To answer questions like these, notice that we need to begin with the physics of the stimulus. From there we'll move to electrochemistry, to examine how physical inputs trigger events in our bodies. Next we need to ask how the nervous system analyzes and then recognizes these incoming signals. Then, finally, we can zero in on our ultimate target—an explanation of the conscious experience of the "chocolate" sensation; or, with a different stimulus, the conscious experience of seeing a beautiful shade of blue.

Let's pause to appreciate the extraordinary ambition of this project. We're seeking to build a bridge from events that are microscopic and objective to events that are large scale and entirely subjective. We're trying to specify the connections that will let us

move seamlessly from a discussion of physics at one end of the process to comments about conscious experience at the other end. Seems ambitious, doesn't it? Maybe so, but we've made enormous progress on this project. In the rest of this chapter, we will survey some of what we've learned. We begin with some considerations that apply to all of the sense modalities. Next we turn to our vestibular sensation (roughly, our sense of up and down and of whether we are moving or still) and then to the sensations of touch, pain, taste, and smell. Near the end of the chapter, we explore the two sense modalities that are unquestionably the most important sources of information for us—namely, hearing and vision.

Sensory Coding

Each of the sense modalities has its own properties and follows its own rules. For some modalities (vision, hearing, taste, and smell), we have specialized organs that collect, concentrate, and amplify the incoming stimulus information. In other cases (the various skin senses), we simply accept the input, unamplified, as it arrives. For some senses, the crucial input consists of some form of energy—a mechanical push against the eardrum in the case of hearing; a photon striking the back of the eyeball for vision. For other senses, the key input is chemical—a molecule on the tongue or in the nose. Some senses (vision, hearing, smell) can respond to stimuli that are far away from us; others (touch, taste) respond only to nearby inputs.

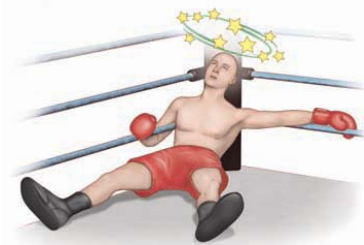
Even with these differences, the various senses have some crucial features in common. In all cases, the physical stimulus must be converted into a neural signal; this is the step of **transduction**. Then, once the stimulus is transduced, the nervous system needs somehow to represent the various qualities of the input. At the coarsest level, the nervous system must register the fact that we saw the pizza but did not taste it, or that we heard the approaching car but did not see it. What's more, the nervous system must somehow represent differences within each sensory system—that the pizza was salty, not sweet; or that the car was remarkably loud. These are all issues of **sensory coding**—how the qualities of the input are translated into specific representations within the nervous system.

One aspect of sensory coding involves *psychological intensity*—the difference between a bright light and a dim one, or a subtle scent of cinnamon in contrast to a dense cloud of the smell. In most cases, the nervous system codes stimulus intensity via the rate of firing by the neurons in a sensory system: the more intense the stimulus, the greater the rate of firing. Stimulus intensity is also encoded via the sheer number of neurons that are triggered by the stimulus: the more intense the stimulus, the more neurons it activates, and the greater the psychological magnitude.

The second aspect of coding is *sensory quality*—how the nervous system represents the difference between, say, vision and hearing; or within a modality, how it represents the difference between, for example, a high-pitched note and a low one, or the difference between a sweet taste and a bitter one. The first of these sensory quality issues—the difference *between* modalities—is straightforward. Almost 200 years ago, Johannes Müller argued that the key lies simply in which nerves are being stimulated. Stimulation of the optic nerve (whether from light or some other source) causes the sense of seeing; this is why strong pressure on the eyeballs leads us to see rings or stars (to the dismay of boxers and the delight of cartoonists; Figure 4.7). Similarly, stimulation of the auditory nerve—whether it's from a sound or something else—causes the sense of hearing. This is why people sometimes experience “ringing in their ears” in the absence of any environmental sound—some illness or injury is causing stimulation of the auditory nerve.

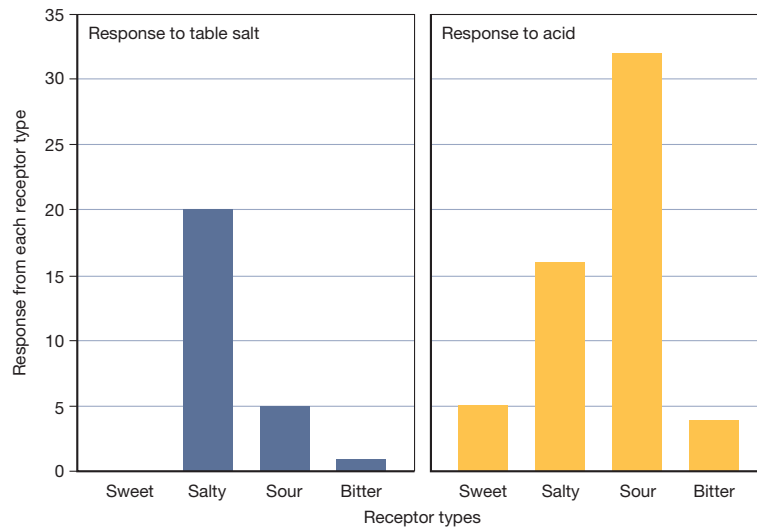
transduction The process through which a physical stimulus is converted into a signal within the nervous system.

sensory coding The process through which the nervous system represents the qualities of the incoming stimulus—whether auditory or visual, for example, or whether a red light or a green one, a sour taste or a sweet taste.



4.7 Seeing stars Whether it comes from light or some other source, stimulation of the optic nerve causes the sense of seeing. This is why boxers sometimes “see stars.” The punches they receive cause the head to move abruptly, making the eyeballs press briefly against their eye sockets. This pressure mechanically stimulates the optic nerves and makes the stars appear.

4.8 Pattern coding Researchers recorded the response from receptors in a monkey's tongue when the monkey was given a taste of sodium chloride (NaCl, or table salt), which humans regard as salty-tasting, or a taste of highly dilute acid, which humans regard as sour-tasting. All four taste receptors responded to the acid, and three responded to the salt. Notice in addition that the response from the salt-preferring receptors was very similar for the two tasks. Results like these make it plain that tastes are not encoded simply by which receptors are responding—because generally all of them are—nor by the strength of response from a single receptor type. Instead, individual tastes are represented within the nervous system only in the pattern of responding across the receptor types.



What about differences *within* a sense modality? For example, blue, green, and red are all visual sensations, so they all involve activity in the optic nerve. But of course each color is qualitatively different from the others. Likewise, sweetness and saltiness are both tastes; but they're plainly distinct for the perceiver. How are differences like these encoded? One hypothesis stays close to Müller's insight and is often referred to as **specificity theory**. This proposal suggests that different sensory qualities (sweet versus sour, red versus green) are signaled by different neurons, just as the different sense modalities (vision versus pressure) are signaled by different nerves. In this conception, the nervous system acts as if these quality-specific neurons were somehow "labeled" with their quality, so that the nervous system registers the presence of "red" whenever there's an incoming signal in the "red neurons," registers the presence of "hot" whenever there's a signal coming from the "hot neurons," and so on.

This proposal turns out to be correct in some cases—for example, specific neurons do seem to convey the sensation of pain. More commonly, though, the data demand a different explanation—usually called **pattern theory** (Figure 4.8). According to this view, what matters for sensory quality is not which neurons are firing. Instead, what allows us to identify the input is the overall *pattern* of activation—which neurons are firing more, and which less, at any given moment.

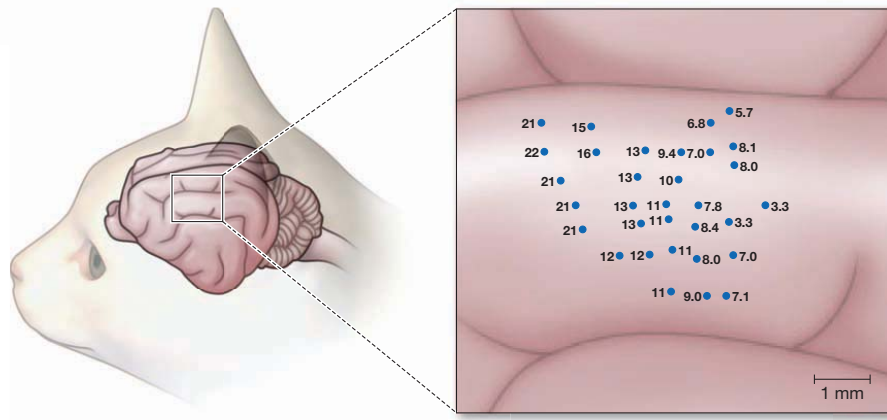
We'll have much more to say about pattern theory in our discussion of the specific modalities. For now, let's just note that there's no single answer to the question of how sensory coding is achieved. The difference among senses (e.g., taste versus sight, hearing versus smell) is certainly signaled by "labeled lines," so activity in the optic nerve causes the sensation of seeing, activity in the auditory nerve causes the sensation of hearing, and so on. Some specific sensations (e.g., pain) may also be signaled by labeled lines; but more commonly, the nervous system uses a pattern code to distinguish the qualities within each sensory modality.

Sensory Adaptation

One further consideration is also relevant to all the sensory systems. Of course, our sensory responses are influenced by the physical magnitude of the stimulus—and so

specificity theory The proposal that different sensory qualities are signaled by different quality-specific neurons. This theory is correct in only a few cases (e.g., pain).

pattern theory The proposal that different sensory qualities are encoded by specific *patterns* of firing among the relevant neurons.



4.22 Tonotopic map Cells close to each other on the auditory cortex respond to similar auditory frequencies. In this figure, the numbers represent the preferred frequency (in kHz) for cells at each position. Cells shown on the right respond to lower frequencies; as we move to the left, we find cells that respond to higher and higher frequencies.

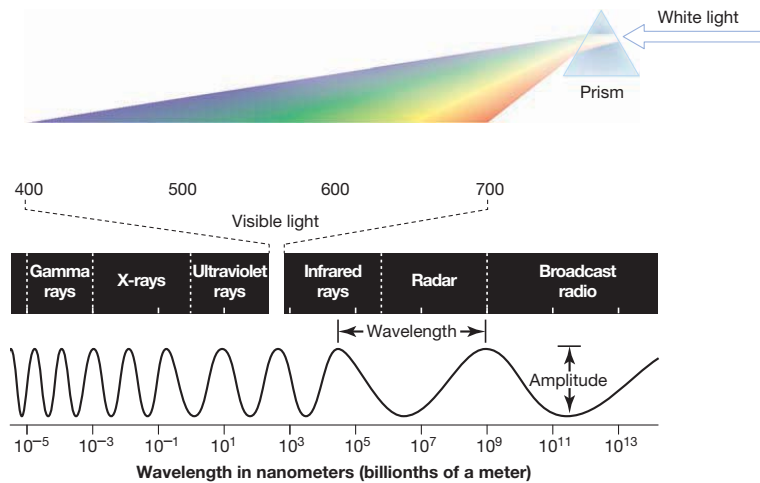
VISION

Vision provides us with an enormous amount of information. It tells us about shapes and colors, about spatial arrangements, and about objects both near and far away. We also tend to put great trust in our vision—it’s why we say things like “seeing is believing.” And it’s easy to document this trust in vision. We can, for example, arrange things so that you *see* a person speaking off to the left but *hear* their voice from your right. In this setting, you’re likely to believe what you see and thus (mis)perceive the voice to be coming from the left. Common experience confirms this point: In large lecture halls, the speaker’s voice sounds like it’s coming from the front of the room—where the plainly visible lecturer is standing. But in many cases, the sound waves are actually reaching you from loudspeakers positioned around the room; you can check this by closing your eyes and paying careful attention to where the sounds are coming from. The moment you open your eyes, though, the sounds again seem to be coming from the front of the lecture hall—the visual information is overruling the evidence you receive from your ears.

How does vision function? In tackling this broad question, we’ll focus on three issues. First, what are the structures for gathering the stimulus, and how do they work? Second, what is the nature of the transduction process that converts the physical energy of the stimulus into a neural signal? Third, what are the coding processes that allow us to discriminate—and then recognize—the millions of shapes, colors, and patterns of movement that make up our visual world?

The Stimulus: Light

Many objects in our surroundings—the sun, candles, lamps, and so on—produce light that’s then reflected off most other objects. It’s usually reflected light—from this book page, for example, or from a friend’s face—that launches the processes of vision.



4.23 The visible spectrum The light that we can see is just a tiny portion of the broader electromagnetic spectrum.

Whether it's emitted or reflected, the stimulus energy we call "light" can be understood as traveling in waves. Like sound waves, these light waves can be described in terms of two measurements. First, light waves can vary in amplitude, which is the major determinant of perceived brightness. A light wave's amplitude is measured as the "height" of the waves, starting from the wave's baseline. Second, light waves vary in frequency—how many times per second the wave reaches its maximum amplitude. As it turns out, these frequencies are extremely high because light travels so swiftly. It's more convenient, therefore, to describe light waves using the inverse of frequency—wavelength, the distance between the crests of two successive waves. Wavelengths are measured in nanometers (billionths of a meter) and are the major determinant of perceived color.

The wavelengths our visual system can sense are only a tiny part of the broader electromagnetic spectrum (Figure 4.23). Light with a wavelength longer than 750 nanometers is invisible to us, although we do feel these longer infrared waves as heat. Ultraviolet light, which has a wavelength shorter than 360 nanometers, is also invisible to us. That leaves the narrow band of wavelengths between 750 and 360 nanometers—the so-called *visible spectrum*. Within this spectrum, we usually see wavelengths close to 400 nanometers as violet, those close to 700 nanometers as red, and those in between as the rest of the colors in the rainbow.

Be aware, though, that the boundaries of the visible spectrum are not physical boundaries indicating some kind of break in the electromagnetic spectrum. Instead, these boundaries simply identify the part of the spectrum that human eyes can detect. Other species, with different types of eyes, perceive different subsets of the broader spectrum. Bees can perceive ultraviolet wavelengths that are invisible to us; other mammals, including some types of monkeys, can tell apart wavelengths that look identical to us.

Gathering the Stimulus: The Eye

Eyes come in many forms. Some invertebrates have simple eyespots that merely sense light or dark; others have complex, multicellular organs with crystalline lenses. In vertebrates, the actual detection of light is done by cells called **photoreceptors**. These cells are located

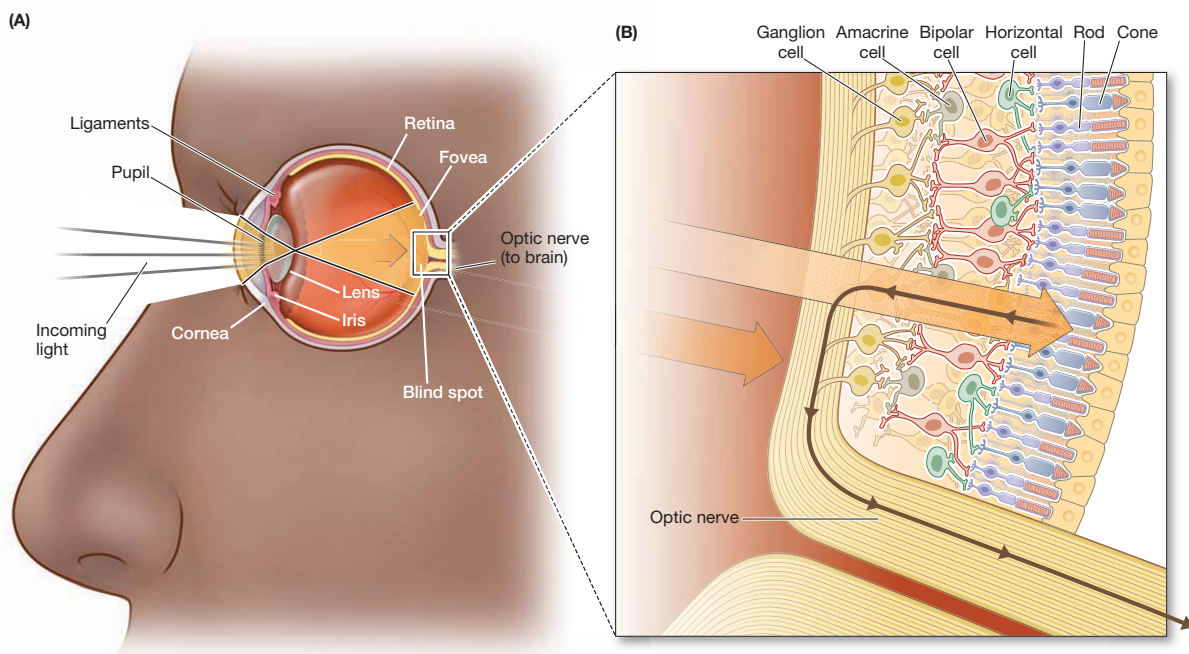
photoreceptor A light-sensitive cell located on the retina that converts light energy into neural impulses.

retinal image The image of an object that is projected on the retina. Its size increases with the size of that object and decreases with the object's distance from the eye.

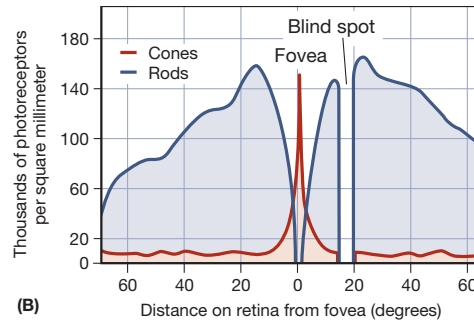
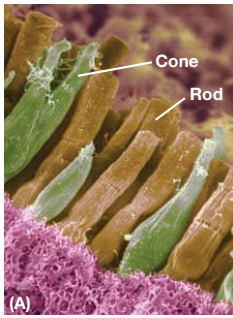
on the retina, a layer of tissue lining the back of the eyeball. Before the light reaches the retina, however, several mechanisms are needed to control the amount of light reaching the photoreceptors and to ensure a clear and sharply focused **retinal image**.

The *iris* is a smooth, circular muscle surrounding the pupillary opening—the opening through which light enters the eye. Adjustments in the iris are under reflex control and cause the pupil to dilate (grow larger) or contract, thus allowing considerable control over how much light reaches the retina.

In the mammalian eye, the *cornea* and the *lens* focus the incoming light just like a camera lens does (Figure 4.24). The cornea has a fixed shape, but it begins the process of bending the light rays so they'll end up properly focused. The fine-tuning is then done by adjustments of the lens, just behind the cornea. The lens is surrounded by a ring of ligaments that exert an outward “pull,” causing the lens to flatten somewhat; this allows the proper focus for objects farther away. To focus on a nearby object, contraction of a muscle in the eye reduces the tension on the ligaments and allows the lens to take on a more spherical shape.



4.24 The human eye (A) Light enters the eye through the cornea, and the cornea and lens refract the light rays to produce a sharply focused image on the retina. The iris can open or close to control the amount of light that reaches the retina. (B) The retina is made up of three main layers: the rods and cones, which are the photoreceptors; the bipolar cells; and the ganglion cells, whose axons make up the optic nerve. Two other kinds of cells, horizontal cells and amacrine cells, allow for lateral (sideways) interaction. You may have noticed that the retina contains an anatomical oddity: the photoreceptors are at the very back, the bipolar cells are in between, and the ganglion cells are at the top. As a result, light has to pass through the other layers (they're not opaque, so this is possible) to reach the rods and cones, whose stimulation starts the visual process.

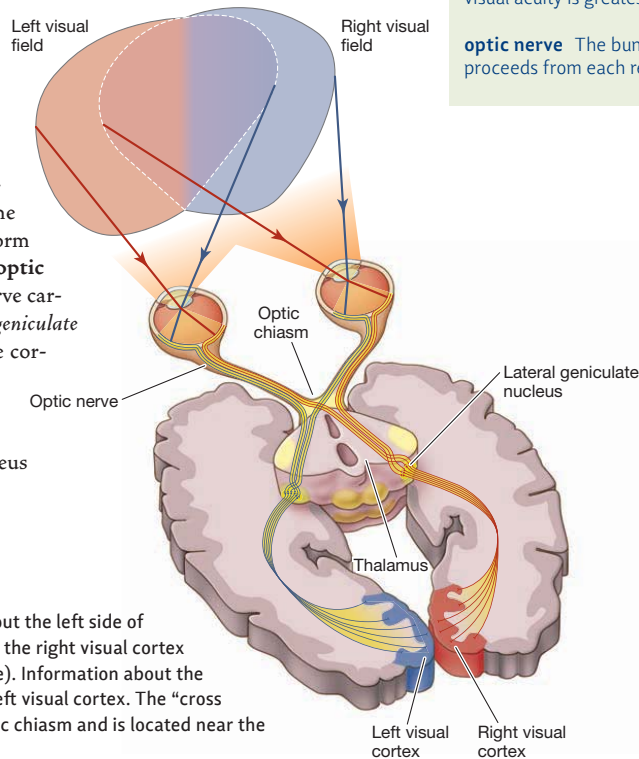


4.25 Rods and cones (A) Rods and cones are receptor cells at the back of the retina that transmit the neural impulses of vision. In this (colorized) photo, cones appear green; rods appear brown. (B) Distribution of photoreceptors. Cones are most frequent at the fovea, and the number of cones drops off sharply if we consider locations away from the fovea. In contrast, there are no rods at all on the fovea. There are neither rods nor cones at the retina's blind spot.

The Visual Receptors

Once light reaches the retina, we leave the domain of optics and enter that of neurophysiology, because it is at the retina that the physical stimulus energy is transduced into a neural impulse. The retina contains two kinds of receptor cells, the **rods** and the **cones**; the names of these cells reflect their different shapes (Figure 4.25). The cones are plentiful in the **fovea**, a small, roughly circular region at the center of the retina; but they become less and less prevalent at the outer edges of the retina. The opposite is true of the rods; they're completely absent from the fovea but more numerous at the retina's edges. In all, there are some 120 million rods and about 6 million cones in the normal human eye.

The rods and cones do not report to the brain directly. Instead, their message is relayed by several other layers of cells within the retina (see Figure 4.24). The receptors stimulate the *bipolar cells*, and these in turn excite the *ganglion cells*. The ganglion cells collect information from all over the retina, and the axons of these cells then converge to form a bundle of fibers that we call the **optic nerve**. Leaving the eyeball, the optic nerve carries information first to the *lateral geniculate nucleus* in the thalamus and then to the cortex (Figure 4.26). (Notice that this pathway resembles the one for auditory signals, which go from the ear to a different section of the geniculate nucleus and then to the cortex.)



4.26 The visual pathway Information about the left side of the visual world is sent, via the thalamus, to the right visual cortex (at the rear of the head, in the occipital lobe). Information about the right side of the visual world is sent to the left visual cortex. The “cross point” for the neural fibers is called the optic chiasm and is located near the thalamus.

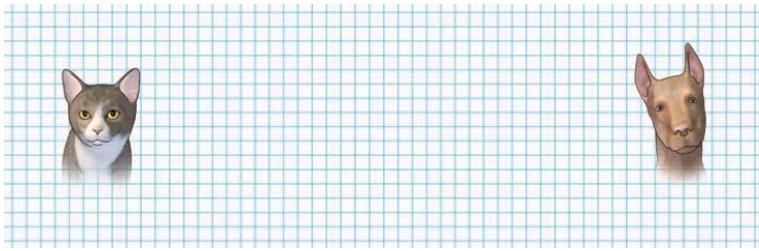
rods Photoreceptors in the retina that respond to lower light intensities and give rise to achromatic (colorless) sensations.

cones Visual receptors that respond to greater light intensities and give rise to chromatic (color) sensations.

fovea The area roughly at the retina's center where cones are plentiful and visual acuity is greatest.

optic nerve The bundle of fibers that proceeds from each retina to the brain.

4.27 The blind spot Close your right eye and stare at the picture of the dog. Can you see the cat without moving your eye? Move the book either closer to you or farther away. You should be able to find a position (about 7 inches from your face) where the cat's picture vanishes when you're looking at the dog. That's because, at that distance, the cat's picture is positioned on the retina such that it falls onto the blind spot. Note, though, that the grid pattern seems continuous. With this sort of regular pattern, your visual system is able to "fill in" the gap created by the blind spot.



This anatomical arrangement requires a space at the back of each eyeball to enable the axons of the ganglion cells to exit the eye on their way to the thalamus. These axons fill this space entirely, leaving no room for rods or cones. As a result, this region has no photoreceptors and is completely insensitive to light. Appropriately enough, it's called the *blind spot* (Figure 4.27).

Rods and cones differ in their structure, number, and placement on the retina; they also differ in their function. The rods are the receptors for night vision; they operate at low light intensities and lead to *achromatic* (colorless) sensations. The cones serve day vision; they respond at much higher levels of illumination and are responsible for sensations of color.

Why do we need two types of photoreceptors? The answer is clear when we consider the enormous range of light intensities encountered by organisms like ourselves as we go about our business during both day and night. In humans, the ratio in energy level between the dimmest stimulus we can detect and the brightest we can tolerate is roughly 1:100,000,000,000. Natural selection has allowed for this incredible range by a biological division of labor—so we have two separate receptor systems, one for vision in dim light and the other for vision in bright light.

The enormous sensitivity of the rods comes at a price: The same traits that make the rods sensitive to low levels of light also make them less able to discriminate fine detail. As a result, *acuity*—the ability to perceive detail—is much greater in the cones. This is the major reason why we point our eyes toward any target that we'd like to perceive in detail. This action positions our eyes so that the image of the target falls onto the fovea, where the cones are most closely packed and visual acuity is greatest.

Be aware that the differences between rods and cones also create situations in which we want to rely on the rods. That's why it's sometimes helpful to look at something "out of the corner" of your eye. Sailors and astronomers have known for years that when you're trying to find a barely visible star, it's best not to look directly at the star's location. By looking slightly away from the star, you can ensure that the star's image falls outside of the fovea and onto a region of the retina that's dense with the more light-sensitive rods. This strategy limits the ability to discern detail; but, by relying on the rods, it maximizes visual sensitivity to faint stimuli.

Rods and cones can also be distinguished in one further way—their chemistry. Inside each photoreceptor is a **photopigment**, a light-sensitive chemical pigment that allows the transduction of light energy into a neural signal. When light enters the receptor, the light energy changes the chemical form of the photopigment, setting off a chain of events that ultimately leads to an electrical signal. In this way, the light energy is translated into the electrochemical language of the nervous system. Inside the receptor, the pigment itself is then reconstituted so that it will be ready to react with light again when the next opportunity arises.

Rods and cones contain different photopigments. The rods contain *rhodopsin*, a pigment that breaks down more readily in response to light than the cone pigments do.

photopigment A chemical in the photoreceptors that changes its form in response to light, producing an electrical change that signals to the nervous system that light is present.



4.28 Brightness contrast Four (objectively) identical gray squares on different backgrounds. The lighter the background, the darker the gray squares appear.

Rhodopsin is part of the reason that rods can function at lower light levels. There are three different cone photopigments, and each cone contains one of the three types. The differences among the three pigments are crucial to the cones' ability to discriminate colors—a topic we'll turn to shortly. Rods, which contain just one pigment, are sensitive to differences in brightness (white versus gray, or a strongly illuminated red versus a weakly illuminated one); but they cannot discriminate among different hues. So, for example, the rods will respond in exactly the same way to a patch of red and an equally bright patch of blue. In effect, this response makes each of us nearly “color blind” at the visual periphery—that is, rather poor at telling colors apart if they fall on a retina position far enough from the fovea so that the position contains mostly rods and very few cones.

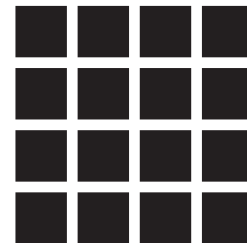
Contrast Effects

Earlier in the chapter, we discussed the fact that our sensory systems are keenly sensitive to *differences*—and so a noise sounds louder if it occurs in an otherwise quiet room; a room feels particularly warm if you've just come in from the cold. Similar effects can easily be documented for vision.

Notice, though, that these examples all involve changes as time goes by—so that the stimulus *now* is different from the one you experienced a moment ago. It turns out that the visual system is also sensitive to spatial contrast—the differences between the stimulus in view *here* and the one in view *there*. This is evident, for example, in *brightness contrast*—the effect that makes a stimulus look much brighter on a dark background than on a bright one (Figure 4.28). Brightness contrast can be documented in many settings, and so it plays a role in creating some illusions (Figure 4.29) as well as certain artistic effects.

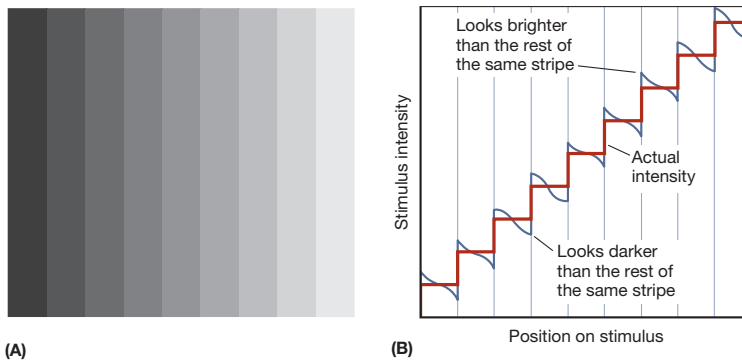
Contrast effects have an extremely important consequence: They make it easier for us to identify the objects we encounter. This point grows out of the fact that the objects we see are usually viewed against backgrounds that are at a different brightness level than the target object; hence, a change in brightness—from darker to lighter, or vice versa—typically marks a visual boundary, a point where one object stops and another begins. And, of course, these boundaries are immensely important for the visual system because they define the object's *shape*—and shape, in turn, is the information we generally use to identify an object.

Perhaps it's not surprising, then, that the visual system does more than just detect brightness boundaries. It actually *amplifies* them by a process often called *edge enhancement* which relies on brightness contrast and allows us to see the edges between objects more clearly. This exaggeration of edges happens with virtually all stimuli, but it's



4.29 The effect of distance between contrasting regions The white lines in this grid are the same color throughout, but they don't appear to be—each “intersection” seems to contain a gray spot. The uneven appearance of the white strips is caused by contrast. Each strip is surrounded by a black square, which contrasts with it and makes it look brighter. But this is not the case at the intersections, where the strips touch the black squares only at their corners. As a result, there's less contrast in the middle of the intersections and we see gray spots there.

4.30 Mach bands (A) These gray strips are arranged in ascending brightness, from left to right. Physically, each strip is of uniform light intensity, as shown graphically in red in (B), which plots position against physical light intensity. But the strips don't appear to be uniform. For each strip, contrast makes the left edge (next to its darker neighbor) look brighter than the rest, while the right edge (next to its lighter neighbor) looks darker. The result is an accentuation of the contours separating one strip from the next. The resulting appearance—the way the figure is perceived—is shown in blue in (B).



particularly obvious in the illusion we call *mach bands* (Figure 4.30A). In this figure, each separate strip of gray is uniform in its brightness. That is, the figure shows a homogeneous dark strip, then a uniform slightly lighter strip, then another uniform slightly lighter strip, and so on. However, most people don't perceive the strips as uniform. Instead, they perceive each strip as being slightly darker along its right-hand edge, where it meets its brighter neighbor. They also perceive each strip as slightly brighter along its left-hand edge, where it meets its darker neighbor. The resulting pattern is summarized in Figure 4.30B.

This illusion is produced by contrast effects like those we've already described. Specifically, when a light region borders a dark region, contrast between the two makes the light region look even lighter and makes the dark region look darker still. By accentuating the difference between the two adjacent regions, the contrast highlights the edge where the two regions meet.

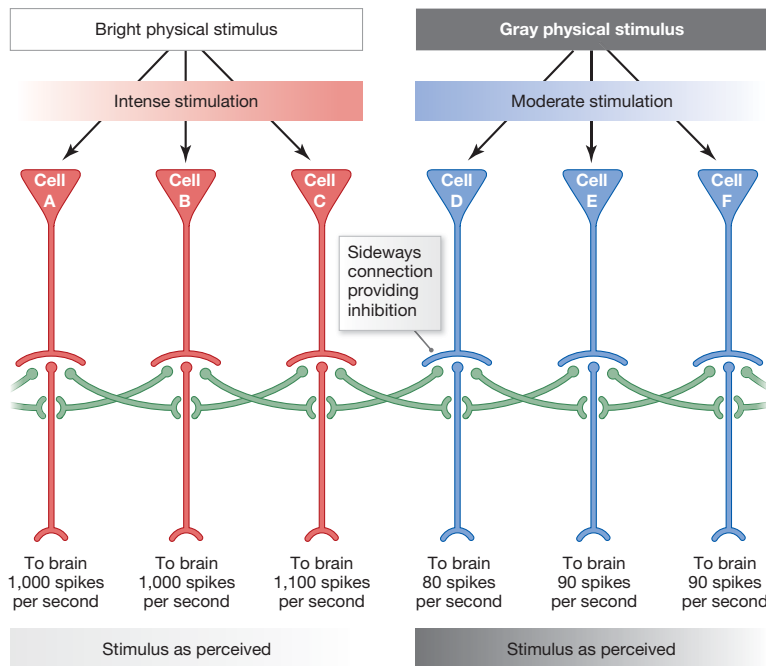
lateral inhibition The pattern of interaction among neurons in the visual system in which activity in one neuron inhibits adjacent neurons' responses.

We can take our explanation of this effect one step further because we can specify the events in the nervous system that lead to brightness contrast. The key is **lateral inhibition**—a pattern of interaction among neurons in which activity in one neuron actually decreases the responses in adjacent neurons. This is, in other words, inhibition exerted sideways. We can document this effect at many levels of the visual system; for example, recordings from single cells in the retina confirm that activity in one cell actually causes the immediately adjacent cells to fire *less* than they otherwise would.

To see how this pattern of interaction leads to edge enhancement, consider two cells, each receiving stimulation from a brightly lit area (Figure 4.31). One cell (Cell B in the figure) is receiving its stimulation from the middle of the lit area. It is strongly stimulated, but so are all of its neighbors, creating a situation in which all of the cells in this area are inhibiting each other. As a result, Cell B's activity level is *increased* by the stimulation but also *decreased* by the lateral inhibition it's receiving from nearby cells—including (in the figure) Cells A and C. This combination leads to only a moderate level of activity overall in this cell—and so the signal Cell B sends to the brain is weaker than it would have been without the inhibition.

In contrast, another cell (Cell C in the figure) is receiving its stimulation from the edge of the lit area. Cell C is therefore strongly stimulated, and so are its neighbors *on one side*. As a result, this cell is receiving inhibition from one side (by Cell B) but not from the other (Cell D), so it will be less inhibited than Cell B (which is receiving inhibition from all sides).

What's the result of all this interaction? Cells B and C initially receive the same input, but C is less inhibited than B, so it ends up firing more strongly than B and

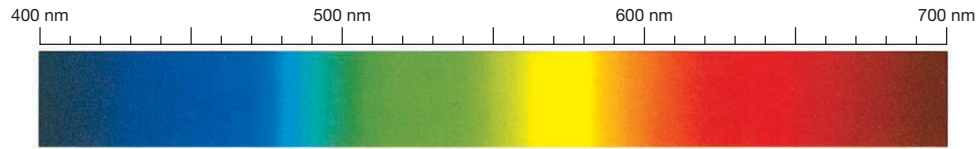


4.31 Response pattern to different colors: Lateral inhibition Cells B and C receive the same input. Cell B, however, is inhibited by its neighbors on both sides; Cell C is inhibited by neighbors on only one side. As a result, Cell C will send a stronger signal to the brain, emphasizing the “edge” in the stimulus. Likewise, Cells D and E receive the same input, but Cell D receives more inhibition. This cell will send a weaker signal to the brain, again emphasizing the edge of the dark gray patch. The spikes per second for each neuron are hypothetical figures, but they illustrate the sort of differences in firing rate that lateral inhibition can produce.

thus sending a stronger signal to the brain than B does. Of course, the same is true for all of the other cells (like Cell C) that receive their input from the edge of a surface, and for all cells (like B) that receive their input from the middle of the surface. The result is that all the cells detecting the edge of a bright surface end up producing a stronger response than that of the cells detecting the middle of the surface. This pattern will then lead to an exaggerated response along the surface’s edges, making these edges easier to detect.

The reverse happens for cells being stimulated by a patch that’s not as bright. Cells D and E both receive the same (weak) input. Cell E, though, is surrounded by cells that are only mildly activated, so it receives only gentle inhibition from its neighbors. Cell D, in contrast, has at least one very excited neighbor (Cell C), so it receives a large dose of inhibition. As a result, Cells D and E both receive the same input, but Cell D (because of the inhibition it receives) ends up firing less strongly than Cell E. Again, this leads to an exaggeration of the edge; and the weakest signal is coming from the cell at the edge of the dark patch.

These interactions among cells indicate exactly how the visual system enhances the brightness of boundaries it encounters—and, with that, why Mach bands appear as they do. Besides that, these mechanisms illustrate another important point. At the very beginning of this chapter, we asked whether we can think of the sensory mechanisms as passive recorders of the stimulus input or as mechanisms that somehow organize and interpret the input. The answer to these questions should be clear by now—and will become clearer as our discussion continues. Thanks to lateral inhibition, the visual system seems to be refining the stimulus information from the very start, emphasizing some aspects of the input (the edges) and understating other aspects (the areas being uniformly stimulated).



4.32 Hues The visible spectrum consists of light waves from about 400 to 700 nanometers.

Lateral inhibition arises from mechanisms just a synapse or two into the visual system; but even at this early level, the nervous system is “cleaning up” the input and doing far more than merely “receiving and recording” the incoming stimulus.

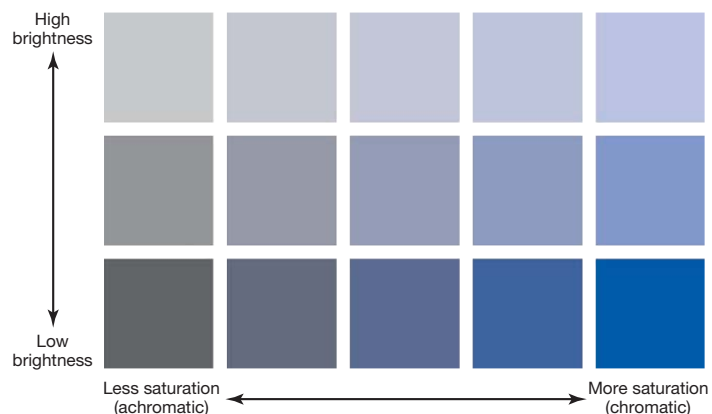
Color

Clearly, then, interaction among sensory elements can shape the sensory input. In particular, this process can highlight elements such as boundaries and moments of change that are of particular interest to the organism. This pattern of interaction is also evident when we consider a different aspect of vision—namely, the perception of color.

A person with normal color vision can distinguish over 7 million shades of color. But fortunately, this staggering number of colors can be classified in terms of just three dimensions. First, *hue* is the attribute that distinguishes blue from green from red; it’s also the attribute shared by, say, a bright orange, a middle orange, and a dark orange. This dimension corresponds closely to the way we use the word *color* in everyday life. Hue varies with wavelength (Figure 4.32), so that a wavelength of 465 nanometers is perceived as *unique blue*, a blue that’s judged to have no trace of red or green in it; a wavelength of about 500 nanometers is perceived as *unique green* (green with no blue or yellow); and a wavelength of 570 nanometers is perceived as *unique yellow* (yellow with no green or red).

Second, *brightness* is the dimension of color that differentiates black (low brightness) from white (high brightness) and distinguishes the various shades of gray in between. Black, white, and all of the grays are the *achromatic colors*; they have no hue. But brightness is also a property of the *chromatic colors* (purple, red, yellow, and so forth). Thus, ultramarine blue is darker (i.e., has a lower brightness) than sky blue, just as charcoal gray is darker than pearl gray (Figure 4.33).

4.33 Brightness and saturation Colors can be arranged according to their brightness. This dimension is easiest to recognize when looking at a series of grays (as in the leftmost column of this grid), which are totally hueless and vary in brightness only. But chromatic colors can also be classified according to their brightness, as in the other columns. As you move from left to right in this grid, brightness stays the same but saturation increases.



The third dimension, *saturation*, is the “purity” of a color—the extent to which it is chromatic rather than achromatic. The more gray (or black or white) that’s mixed with a color, the less saturation it has. Consider the bottom row of the grid shown in Figure 4.33. All five of these squares have the same hue (blue), and all have the same brightness. The patches differ only in one way: the proportion of blue as opposed to that of gray.

The Neural Basis of Color Vision

What is the neural basis of color vision? The answer turns out to have two parts: how the retina itself functions, and how the nervous system handles the information received from the retina.

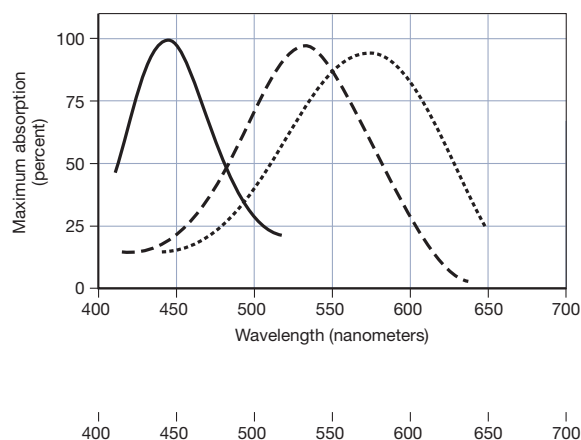
COLOR RECEPTORS

More than 200 years ago, Thomas Young hypothesized that humans have three types of color receptors; and he offered a theory of color vision building on these three elements. In 1866, Hermann von Helmholtz offered some refinements of this view. Today we know that, at least in broad outline, the *Young-Helmholtz theory* was essentially correct. Human color vision is **trichromatic**—based on three elements, each tied to one type of *cone*.

What are these “elements”? We’ve already mentioned that each of the three cone types contains a different photopigment. Each of these photopigments is sensitive to a broad range of wavelengths, but their patterns of sensitivity are plainly distinct (Figure 4.34). One pigment, and so the cones containing that pigment, is most sensitive to wavelengths in the short-wave region of the spectrum. Consequently, this pigment is sensitive to many inputs but especially sensitive to wavelengths typically perceived as blue. A second pigment is especially sensitive to wavelengths in the middle range (wavelengths typically perceived as green), and the third to wavelengths in the long range (typically perceived as orange or red; Bowmaker & Dartnall, 1980; MacNichol, 1986).

It’s important to realize that due to the broad sensitivities of these pigments, all three types of cones respond to most of the wavelengths in the visible spectrum. It’s therefore impossible to discriminate among wavelengths simply by noting which

trichromatic color vision The principle underlying human color vision. Color vision occurs through the operation of three sets of cones, each maximally sensitive to a different wavelength of light.



4.34 Sensitivity curves of three different cones in the primate retina The retinas of humans and monkeys contain three different kinds of cones, each with its own photopigment that differs in its sensitivity to different regions of the spectrum. One type of cone absorbs more of the shorter wavelengths (so it’s more sensitive to light in this spectral region); its sensitivity is shown as a solid line. A second cone type absorbs more of the middle wavelengths (dashed line), and a third (dotted line) absorbs more of the longer ones.

cones are responding, because generally all of them are. So once again, it appears that the nervous system relies on pattern coding; the input's wavelength is being specified by the relative rates of response by all three cone types. For an input of 480 nanometers, for example, the "short-preferring" and "middle-preferring" cones will respond equally, and their response will be about double the response of the "long-preferring" cones. This pattern of response specifies this particular wavelength. Likewise, an input of 580 nanometers will produce a response in the long-preferring cones that's roughly double the response in the middle-preferring cones, and there will be virtually no response from the short-preferring cones. This pattern identifies this specific wavelength. And so on for the millions of other response patterns, each of which identifies a specific wavelength.

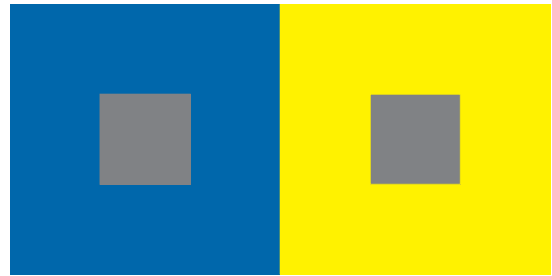
Of course, many of the colors you encounter involve a mix of several different wavelengths; but that's not a problem. Each of the wavelengths contained in this mix will trigger the neural response that would result if that wavelength were presented on its own, and so the total response for each cone type will simply be the sum of that cone's responses to each ingredient—each wavelength—in the mix. Here's an example: If the input contains wavelengths A, B, and C, the short-preferring cones' response to this stimulus will simply be the total of those cones' response to A when it's presented alone, plus their response to B when it's presented alone, plus their response to C. (And so if, say, the light is at an intensity in which wavelength A on its own would trigger the receptor to fire 70 times per second, and B on its own would trigger the receptor to fire 30 times per second, and C would trigger the cell to fire 10 times per second, the mix of A, B, and C will cause the cell to fire roughly 110 times per second.) The same goes for the middle-preferring and long-preferring cones; their responses, too, will simply be the sums of their responses to each of the individual ingredients in the mix.

Be aware, though, that it's the total response that matters—not how the total was achieved. Thus, if three wavelengths together cause the short-preferring cones to fire 110 times per second, it doesn't matter if the wavelengths on their own would have produced rates of 70, 30, and 10 (as in the previous paragraph), or if they would have produced rates of 20, 60, and 30 or 37, 15, and 58. All that matters is the sum. And this is crucial, because it's almost always possible to find different mixes of wavelengths that will produce the same three totals (again, one total for each of the cone types). This explains why artists can mix their pigments to produce virtually any color, and it's how a television or computer monitor produces the various colors that appear on the screen. In both of these cases, we're combining wavelengths so that we'll get the three totals we need to produce the desired perception.

COMPLEMENTARY HUES

The trichromatic analysis of color vision is consistent with many facts—including the central observation that there are just three cone types, each with its own photopigment. Other observations, however, don't seem to fit with the trichromatic view—such as the fact that, in important ways, colors seem to come in pairs. This pairing is evident, for example, in *simultaneous color contrast*—the chromatic counterpart of brightness contrast. Color contrast refers to the tendency of any chromatic region in the visual field to induce a *complementary color* in adjoining areas. For example, a gray patch tends to look bluish if it's surrounded by yellow, and yellowish if surrounded by blue; likewise, a gray patch looks reddish if surrounded by green, and greenish if surrounded by red (Figure 4.35). In this way, then, blue and yellow are "paired," as are red and green.

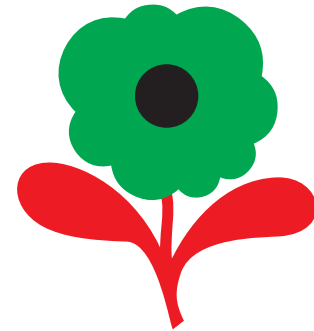
Color contrast can also be demonstrated in temporal relationships rather than spatial ones. Suppose that you stare at a green patch for a while and then look at a white wall. You'll see a *negative afterimage* of the patch—in this case, a reddish spot (Figure 4.36). In the same way, staring at a red patch will produce a green afterimage; staring at something blue will produce a yellow afterimage; and staring at yellow will produce a blue afterimage. In all cases, the afterimage has the complementary hue of the original stimulus. This effect again emphasizes the apparent pairing of colors—a pairing that trichromatic analyses leave completely unexplained.



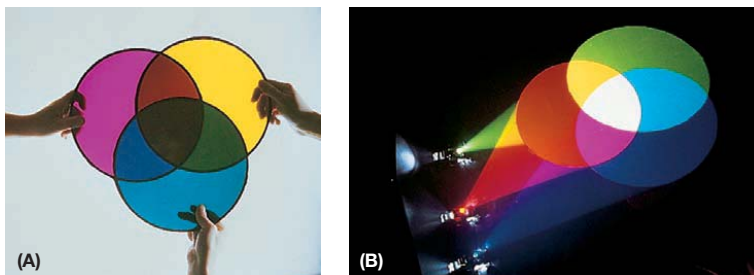
4.35 Color contrast The gray patches on the blue and yellow backgrounds are physically identical, but they don't look that way. To begin with, there's a difference in perceived brightness; the patch on the blue looks brighter than the one on the yellow—a result of brightness contrast. There's also a difference in perceived hue; the patch on the blue looks somewhat yellowish, while that on the yellow looks bluish. This is color contrast, a demonstration that hues tend to induce their antagonists in neighboring areas.

Another way to appreciate the importance of complementary colors is by mixing together colored lights. In these mixtures, “paired” colors seem to cancel each other; thus, if we mix blue and yellow lights, we produce a hueless white. The same is true if we mix red and green lights, or purple and yellow-green, or orange and blue-green. Here, too, it appears that colors are paired, such that each color has an “opposite” that cancels it—a relationship that, again, has no explanation in trichromatic theory.

As an aside, note that color mixing works differently when we mix *paints* or other pigments rather than lights (as in Figure 4.37). Why? Because of the physics. Here's an example: If a blue light is shining on a white surface, then the surface will reflect the wavelengths contained within that blue light. If a yellow light is also shining on the surface, then its wavelengths will be reflected too. So the full set of wavelengths reflected will be those from the blue light *plus* those from the yellow—which is why this is called an *additive color mixture*. In contrast, when white light shines on a *pigment*, only a certain band of wavelengths is reflected; the remaining wavelengths are absorbed by the pigment. Thus blue paint reflects the wavelengths between 420 and 520 nanometers, but it absorbs wavelengths outside this range; and so these other wavelengths are removed or “subtracted” from the reflected light. Yellow paint reflects wavelengths above 480 nanometers, and it absorbs those below. If the two paints are mixed together, then the only wavelengths reflected by the combination are those that aren't absorbed (i.e., not subtracted from the input) by *either* ingredient. This mixture turns out to be just the wavelengths above 480 nanometers and below 520; and that band of wavelengths is seen as green.



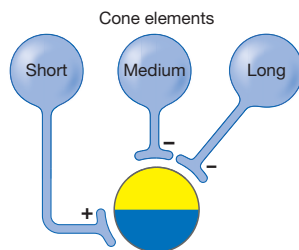
4.36 Negative afterimage Stare at the center of the figure for a minute or two, and then look at a white piece of paper. Blink once or twice; the negative afterimage will appear within a few seconds, showing the flower in its correct colors.



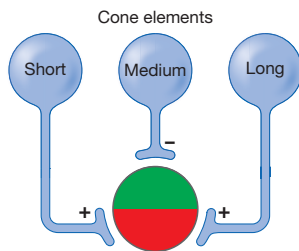
4.37 Different ways to mix color In subtractive color mixing, each constituent—here, each filter—subtracts certain wavelengths from the total light. In additive mixing, each constituent contributes wavelengths. Thus, in (A), subtractive mixing of three primaries yields black; in (B), additive mixing yields white.

opponent-process theory A theory of color vision that proposes three pairs of color antagonists: red-green, blue-yellow, and white-black. Excitation of neurons sensitive to one member of a pair automatically inhibits neurons sensitive to the other member.

(A) Blue-yellow opponent process



(B) Red-green opponent process



4.38 From receptors to opponent-process pairs A simplified presentation of a neural system in which the three receptor elements feed into two color opponent-process pairs. (A) The blue-yellow system is excited by the short-wave receptors and inhibited by the medium- and long-wave receptors. (B) The red-green system is excited by the short-wave and long-wave receptor elements, and it's inhibited by the medium-wave elements.

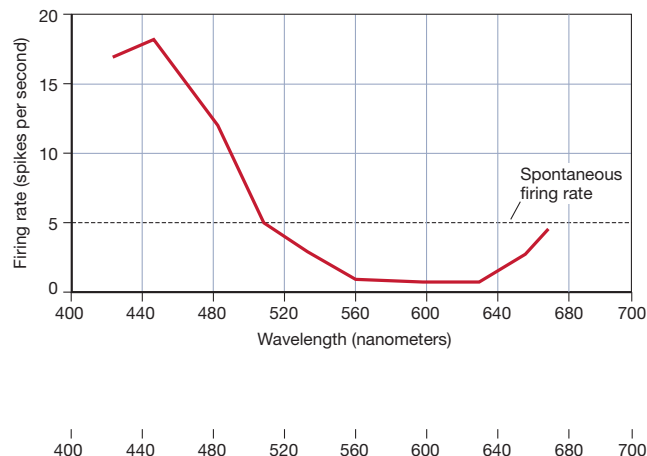
4.39 Opponent-process cells in the visual system of a monkey The figure shows the average firing rate of blue-yellow cells in response to light of different wavelengths. These cells are excited by shorter wavelengths and inhibited by longer wavelengths, analogous to the cells in the human system that signal the sensation “blue.”

THE OPPONENT-PROCESS THEORY

How should we think about the fact that colors seem to come in pairs? The answer lies in the **opponent-process theory**, first suggested by Ewald Hering but then developed by Leo Hurvich and Dorothea Jameson. This theory begins with the undeniable fact that we have three cone types, but it argues that the output from these cones is then processed by another layer of neural mechanisms that recode the signal on the basis of three pairs of colors—red versus green, blue versus yellow, and black versus white. These pairs are said to involve an “opponent process” because the two members of each pair are antagonists—that is, excitation of neurons on one side of these mechanisms automatically inhibits cells on the other side (Figure 4.38). As a result, each of the opponent-process mechanisms can be thought of as a balance—and if one arm of the balance goes down, the other necessarily goes up (Hurvich & Jameson, 1957).

How do these mechanisms shape our perception of color? According to the opponent-process theory, the psychological experience of hue depends on two of the opponent-process pairs—red-green and blue-yellow. If, for example, the input tips the red-green balance toward red and the blue-yellow balance toward blue, the perceived hue will be violet. If the input contains neither red nor green (so the red-green pair stays in balance) and the blue-yellow system tips toward blue, we perceive a pure blue. If both hue systems are in balance, there will be no hue at all, and the resulting color will be seen as achromatic (i.e., without hue).

This conception easily explains the apparent pairing of colors, because the pairing is built into the opponent processes themselves. It also explains why, according to most observers, there appear to be four primary colors (red, green, blue, and yellow)—even though, without question, our retina has only three cone types. But, in addition, evidence has directly confirmed the claims of the opponent-process theory by documenting that many of the neurons in the visual system behave exactly as the theory proposes. For example, certain cells increase their firing rate if the retina is stimulated by green light, but they decrease their rate if the retina is stimulated by red light. Other cells show the opposite pattern (increase for red, decrease for green). Still other cells show a similar pattern of responses for blue and yellow light (Figure 4.39; De Valois, 1965). All of this is exactly what we might expect if these cells embody the mechanisms proposed by the opponent-process theory.

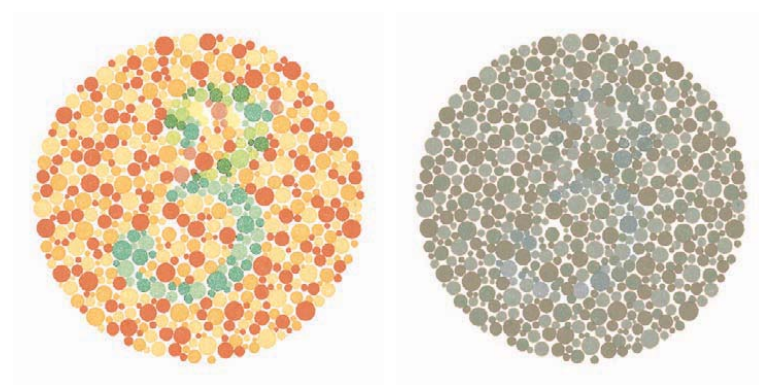


COLOR BLINDNESS

Not everyone responds to color like most of us do. Some form of color-vision defect is found in 8% of Caucasian males (but only 0.03% of females; the rate of color blindness is lower in other races). The deficiencies in color vision come in various forms. The great majority of people identified as color blind are actually missing one of the three visual pigments (and so they're "dichromats," not "trichromats"). Other forms of color blindness can involve a defective opponent process or a malfunction in brain circuitry needed for color vision (Hurvich, 1981). Most common is a confusion of reds with greens; least common is total color blindness, in which no hues can be distinguished at all. Interestingly, though, most of these problems are rarely noticed in everyday life, and color-blind people can spend many years without even realizing they're color blind. They call stop signs "red" and grass "green," just like anyone else does. And, presumably, they spend much of their lives believing that others perceive colors the same way they do. Their color blindness can be confirmed only with special tests like the one shown in Figure 4.40.

Color blindness can result from various injuries to the eye or brain, but this condition most commonly has a genetic origin. It's also much more frequent in humans than it is in other primates with color vision similar to our own. This finding has led some scholars to explore the evolutionary origins of color blindness. They argue that this supposed "defect" might actually have benefited some of our evolutionary ancestors—for example, in certain situations a color-blind hunter can spot prey that others might miss. (Because hues that appear "matched" to someone with normal color vision sometimes don't appear matched for someone who is color blind, some forms of camouflage—when the prey seems to be the same hue as the background foliage—will fail with someone who is color blind.) These situations might have produced a reproductive advantage for our color-blind ancestors, leading to an increased frequency in the relevant human genes.

Recent studies indicate that the genetics of color blindness are relatively complex and that many genes, on at least 19 different chromosomes, can contribute to color blindness. One of the genetic causes involves a gene mutation on the X chromosome, and this finding explains why color blindness is much more common in men than in women. Women have a pair of X chromosomes, so at least one of the chromosomes in this pair is likely to have a normal version of the relevant gene—leading to normal color vision. Men have an XY genetic pattern, and so only one X chromosome. If this chromosome contains the mutated gene, men have no "backup" gene on another chromosome—and color blindness is the result.



4.40 Testing for color blindness Plates used to test for color blindness. To pick out the number in the plate on the left, you must be able to discriminate certain hues. Those with normal color vision can do it and will see the number 74; color-blind people would see the version on the right.

How does the world look to someone who is color blind? For a long time, this question seemed impossible to answer, since most color-blind individuals have no way to compare their experience to that of an individual with normal color vision, and so no way to describe the difference. However, researchers discovered one unusual person (one of the rare women with a color-vision defect) who was red-green color-blind in one eye but had normal color vision in the other. She was able to describe what she saw with the defective eye by using the color language she had learned to use with her other eye. As she described it, with the color-blind eye she saw only grays, blues, and yellows. Red and green hues were altogether absent, as if one of the opponent-process pairs were missing (Graham & Hsia, 1954).

Perceiving Shapes

The perception of color enhances our appreciation of art and, more practically, allows us to distinguish a ripe fruit from a green one. Other aspects of vision are far more important. After all, a color-blind individual can live a perfectly normal life. But the same can't be said for an individual who can't tell a square from a circle, and can't tell whether the shape in front of her is that of an apple or that of a banana. These individuals (known as *visual agnosics*) are dramatically impaired in their functioning. We therefore need to ask how the visual system manages the perception of shape. This achievement turns out to be quite complex; so we'll begin addressing it in this chapter and then return to it in Chapter 5.

FEATURE DETECTORS

Recordings from individual nerve cells have allowed electrophysiologists to examine how particular cells in the visual system respond to certain stimuli. In these studies, researchers place a microelectrode into the optic nerve—or, in many studies, into the brain of an anesthetized animal. The animal's well-being is carefully monitored, both for ethical reasons and to allow the investigators to assess how neurons function in an intact, healthy organism. The animal's eye is then stimulated by visual inputs of varying brightness and different shapes, arriving at the eye from different locations (Figure 4.41). In this way, the investigator can learn which stimuli evoke a response from that cell.

Results from these studies show that the cells in the visual system—whether we're considering the rods and cones themselves, neurons in the optic nerve, or neurons in the brain—all have a preferred target, a certain type of stimulus that's especially effective in causing that cell to fire. We can think of the cells, therefore, as “detectors,” each one tuned for (and so likely to detect) its own set of targets.

What sorts of detectors does the visual system rely on? The answer depends on the species. Frogs, for example, need only a few bits of information about the world: “What's that large shape moving toward me? Just in case it's a predator, I'll take a leap to safety.” “What's that small, dark shape moving around? It might be a fly, so I think I'll flick my tongue at it.” Because they need so little information to survive, frogs have just a few detector types—and they're located on the retina, so the frog can quickly analyze the input and act on it (Lettvin, Maturan, McCulloch, & Pitts, 1959).

Unlike frogs, most animals—including the mammals—need more detailed information about the world around them. Their visual systems perform a more complex analysis, supported by a greater variety of detector types, located in the cortex as well as on the retina. Most of what we know about this visual analysis comes from the work

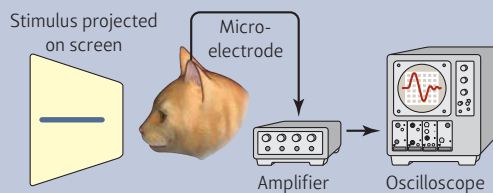
receptive field For a particular cell in the visual system, the pattern of retinal stimulation that most effectively causes the cell to fire. For some cells, this pattern is defined simply in terms of a retinal location; for others, the most effective input has a particular shape, color, or direction of motion.

feature detectors Neurons in the retina or brain that respond to specific attributes of the stimulus, such as movement, orientation, and so on.

4.41 SCIENTIFIC METHOD: How do individual cells in the visual cortex respond to different types of stimulation?

Method

1. An anesthetized cat has one eye propped open so that a series of visual stimuli—e.g., lines with different orientations—could be directed to particular regions of its retina.
2. A microelectrode was implanted in its visual cortex to monitor a single cell's firing rates in response to the lines.



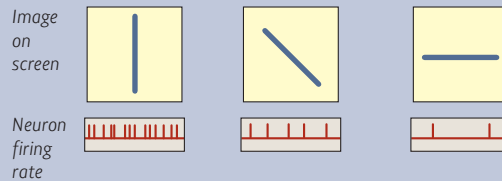
3. When the cell fired, its neural impulses were amplified, then displayed on an oscilloscope. (The procedure was repeated to monitor many individual cells' responses.)

Results

Some cells fired more rapidly in response to a vertical line.

These vertical-preferring neurons fired at only a moderate rate in response to a tilted line.

These cells didn't increase their firing rate at all in response to a horizontal line.



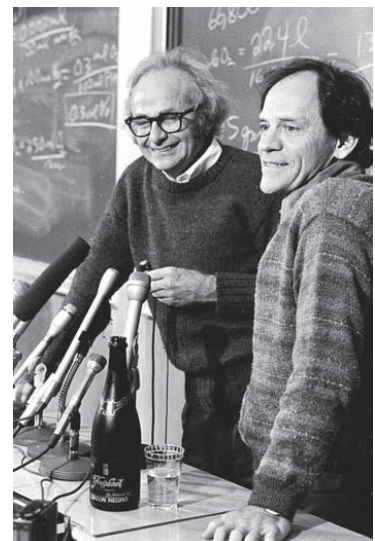
CONCLUSION: Each neuron in the visual cortex has a “target” stimulus that evokes especially rapid firing. These targets include low-level features, such as arcs or lines of a specific orientation.

SOURCE STUDIES: Hubel & Wiesel, 1959, 1968

of David Hubel and Torsten Wiesel, who won a Nobel Prize for their research (Figure 4.42). Working first with cats and then with primates, these investigators confirmed that each cell in the visual cortex responds to stimuli in only a limited region of space—or, equivalently, each cell in the retina responds to stimuli on only a limited region of the retina. This region defines that cell's **receptive field** (Figure 4.43). More important, this research made it plain that cells differ in the types of detectors they are. Some cells have receptive fields of a special size, location, and *shape*—and so they fire at their maximum rate only when the visual input is a line of a specific orientation at a specific retinal position. One such cell might respond to a vertical line at one position in the visual field, while another cell might respond to a line tilted to 45 degrees at the same position; still another cell might respond to a vertical line at some other position. In this way, and because the visual field is blanketed by receptive fields, lines of any orientation at any position will be detected by the appropriate type of cell (Hubel & Wiesel, 1959, 1968).

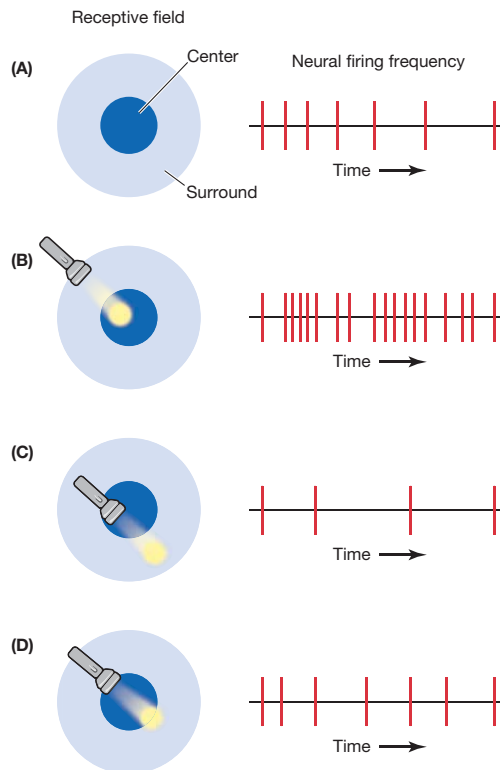
Other cells in the visual cortex are a bit more sophisticated. They also fire only in response to a line or edge of a particular orientation, but they're largely indifferent to the line's specific location within the visual field (see Figure 4.41). Cells like these serve as **feature detectors**, detecting certain elements within the visual pattern. Other cells, deeper within the visual system, presumably then assemble these now detected elements in order to detect larger configurations and more complex patterns.

Consistent with this suggestion, Hubel and Wiesel were able to locate other cells that responded only to more complicated inputs. For example, some cells responded maximally to corners or particular angles. Other cells responded to movement patterns, firing maximally only when they detected movement of the appropriate velocity and direction.



4.42 Torsten Wiesel and David Hubel Hubel and Wiesel won the Nobel Prize in 1981 for their groundbreaking work exploring the function of individual cells in the visual system.

4.43 Receptive fields on the cat's visual system Using the setup shown in Figure 4.41, stimuli are presented to various regions of the retina. The data show that different cells show different patterns of responding. For example, parts (A) through (D) show the firing frequency of a particular ganglion cell. (A) This graph shows the baseline firing rate when no stimulus is presented anywhere. (B) The cell's firing rate goes up when a stimulus is presented in the middle of the cell's receptive field. (C) In contrast, the cell's firing rate goes down if a stimulus is presented at the edge of the cell's receptive field. (D) If a stimulus is presented both to the center of the receptive field and to the edge, the cell's firing rate does not change from its baseline level. Cells with this pattern of responding are called “center-surround” cells, to highlight their opposite responses to stimulation in the center of the receptive field and the surrounding region.



DETECTORS FOR COMPLEX FORMS

It's easy to see how feature detectors might be useful. Let's say that a pattern of visual input reaches your retina and triggers a “horizontal-line detector” and a “vertical-line detector.” When these two detectors fire at the same time, this event might trigger a response in a “right-angle detector.” If at the same time you've also detected three other right angles, this combination might trigger a response from your “square detector.” Activity in this detector might then combine with activity in other detectors and eventually lead you to say, “Oh, look—there's my Intro Psych textbook.”

In this way, the feature detectors we've just discussed might be the starting point for a hierarchy of detectors that leads, step-by-step, from simple features to slightly more complex shapes to still more complex shapes. And eventually, the steps will lead to detectors that fire only in response to the sight of a complex object in the world—such as the letter Q, or your mother's face, or a sports car.

Is this explanation plausible? Could we have specific detectors for each of the countless things we recognize? For some targets, these detectors do exist—and, no surprise, they're usually detectors for stimuli that are especially significant for a species. For example, certain cells in a monkey's cortex have been shown to respond to pictures of a monkey's face, but not at all to pictures of other parts of a monkey's body. Other cells

seem to respond almost exclusively to pictures of a monkey's hand—whether the hand has an open palm or clenched fist or the fingers are pointed up or down (Desimone, Albright, Gross, & Bruce, 1984).

Still, it seems highly unlikely that such built-in mechanisms could account for all the forms that higher animals—especially humans—perceive and recognize. Simple creatures like frogs are able to recognize only a few patterns, so it's reasonable to think they might have specialized detectors for each one. In contrast, humans easily discriminate among a multitude of patterns; and this simple fact speaks powerfully against the idea that we might have specialized detectors for each of them—triangles, squares, apples, apple pies, champagne bottles, cabbages, kings—the list is endless. We know that the perception of any kind of form begins with a feature analysis; this process is plain in the functioning of the detector cells. But how do we integrate these features to create more complex forms? The answer to this question is surprisingly complex, and it's one of our main concerns in Chapter 5.

SOME FINAL THOUGHTS: THE ACTIVE PERCEIVER

Obviously, there's still much to say about how we come to know the world around us. We've looked at how sensory systems transduce the proximal stimulus, and how they code the incoming message into the various dimensions of our sensory experience. But we still need to ask how we come to recognize the various objects and events that we encounter every minute of our lives.

Even at this early stage of our discussion, though, we've answered a question we asked at the very start: When perceiving things, do we simply open our eyes and receive the information the world provides for us, recording this information faithfully and passively the way a camera does? Or do we take a more active role of shaping the input and interpreting and organizing it? By now it's clear that the evidence favors the second view: The complexities of signal detection remind us that even when detecting a simple stimulus—a light, a tone, a scent—we must often make a judgment, a decision about whether we detected an input or not. Likewise, thanks to mechanisms like lateral inhibition, it seems that we do shape the inputs we receive. We accentuate the most crucial bits (namely, edges) and deemphasize the less important bits. In a similar way, the detectors in our visual systems respond only to those aspects of the input that are likely to be useful. Creatures as simple as frogs need relatively little visual information, so their visual system is designed to pick out only a few features. As a result, they're essentially blind to any aspects of the input other than those few bits they must have. Our needs are more complicated; but even so, our visual system is attuned to an identifiable set of features. So, inevitably, our subsequent analyses are based on precisely this feature information. In these and other ways, our visual system does shape the visual input from the very start by selecting and emphasizing the aspects we're especially interested in.

As we'll see in Chapter 5, this is just the beginning of the active role we take in perceiving the world around us. At the most basic levels, our sensory systems are active receivers of information. And the level of activity involved in shaping and interpreting the input simply increases as we go deeper into the processes that make perception possible.

THE ORIGINS OF KNOWLEDGE

- The study of sensory processes grew out of questions about the origin of human knowledge. The empiricists argued that all knowledge comes through stimuli that excite the senses. However, the only way to get information about *distal stimuli* (the objects or events in the world) is through the *proximal stimuli* (the energies that impinge on a sensory surface). The empiricists therefore argued that much of perception is built up through learning by *association*.

PSYCHOPHYSICS

- Research in *psychophysics* seeks to relate the characteristics of the physical stimulus to both the quality and intensity of the sensory experience. One psychophysical measurement is the *absolute threshold*. Another measurement is the *difference threshold*, producing a *just-noticeable difference (jnd)*. According to *Weber's law*, the jnd is a constant fraction of the intensity of the comparison stimulus. Building on this principle, *Fechner's law* states that the strength of a sensation grows as the logarithm of stimulus intensity.
- Data in psychophysical procedures are influenced by a perceiver's sensory *sensitivity* as well as her *decision criteria*. These two factors can be assessed separately, though, via a *signal-detection* procedure.

A SURVEY OF THE SENSES

- *Sensory codes* are the rules by which the nervous system translates the properties of the proximal stimulus into neural impulses. Psychological intensity is usually coded by the rates of firing by the neurons and by the sheer number of neurons triggered by the stimulus.
- Other codes are for *sensory quality*. In some cases, qualitative differences within a *sensory modality* are best described by *specificity theory*—that different *sensory qualities* (e.g., red versus green) are signaled by different neurons, just as the different sense modalities are signaled by different nerves. More commonly, sensory coding is best described by *pattern theory*, which holds that certain sensory qualities arise because of different patterns of activation across a whole set of neurons.

- Certain properties can be observed in all of the sensory systems—including the phenomenon of *adaptation*—the tendency to respond less to a stimulus that has been around and unchanging for some time.
- The *vestibular sense* signals movements of the head, and helps us know which way is “up” and which is “down.” The receptors for this sense are in the semicircular canals in the inner ear.
- The *skin senses* include several distinct subsystems, and lead to the separate sensations of pressure, temperature and pain. Even within these systems, we must distinguish different types of receptors—for example, one type that fires when the temperature rises, and another that fires in response to a drop in skin temperature.
- The sense of *pain* depends on specialized receptors that respond to various forms of tissue damage and temperature extremes. However, the experience of pain is also influenced by other mechanisms, including the endorphins, and by neural circuits that provide a “gateway” blocking the transmission of some signals from the nociceptors.
- The sense of *smell* is triggered by receptors in the *olfactory epithelium*, which then send their neural signals to *glomeruli* in the olfactory bulb. The experience of a specific smell is coded by a pattern of activity across the glomeruli. Smell has many functions—helping animals to find food and avoid predators, and, in many circumstances, providing a means of communicating within a species. The chemicals used for these communications are called *pheromones*.
- The receptors for *taste* are located on the *papillae* found primarily on the tongue. There are five types of receptors, and each type is sensitive to a wide range of inputs. Once again, therefore, the qualities of taste (sweet vs. salty, sour vs. bitter) are coded by a pattern of responding across the five receptor types.

HEARING

- *Sound waves* can vary in *amplitude* and *frequency*, and set up vibrations in the eardrum that are then transmitted by the *auditory ossicles* to the *oval window*, whose movements create waves in the *cochlea*. Within the cochlea is the *basilar membrane*, which contains the auditory receptors that are stimulated by the mem-

brane's deformation. According to the *place theory*, the experience of pitch is based on the place of the membrane that is most stimulated; each place is especially responsive to a particular frequency and generates a particular pitch sensation. According to the *frequency theory*, the experience of pitch depends on the firing frequency of the auditory nerve. Evidence suggests that both theories are correct—the perception of higher frequencies depends on the place stimulated on the basilar membrane, and the perception of lower frequencies depends on firing frequency.

VISION

- Vision is our primary distance sense. Its stimulus is light, which can vary in *intensity* and *wavelength*. Some structures of the eye, such as the iris and the lens, control the amount of light entering the eye and form a proper proximal stimulus—the *retinal image*. Once on the retina, the light stimulus is transduced by the *rods* and *cones*. Acuity is greatest in the *fovea*, where the density of cones is greatest.
- Rods and cones differ markedly in function. The rods operate at low light intensities and are insensitive to differences in hue. The cones function at much higher illumination levels and are responsible for sensations of color.
- The various components of the visual system interact constantly, and these interactions actively shape and transform the stimulus input. One kind of interaction involves *contrast effects*, including brightness contrast. These effects serve to accentuate edges—as in the case of Mach bands. The physiological mechanism underlying this effect is *lateral inhibition*, a clear example of how the visual system refines the stimulus information by emphasizing some aspects of the input and understating others.
- Visual sensations vary in *color*; and color sensations can be ordered on the basis of their hue, brightness, and saturation. Normal human color vision is *trichromatic*, depending on three cone types. However, some facts do not fit with this

trichromatic conception, because colors come in pairs—as shown by the phenomena of complementary colors, color contrast, and negative afterimages.

- *Opponent-process theory* proposes that the output of the cones serves as input for a further layer of mechanisms that recode the signal into three opponent-process pairs: *red-green*, *blue-yellow*, and *black-white*.
- Shape perception depends on specialized *detector cells* that respond to certain characteristics of the stimulus, such as curves and straight edges. The optimal input for each cell—that is, a stimulus of a certain shape and size at a certain position—defines the cell's *receptive field*. In cats and monkeys, *feature detectors* seem to respond maximally when a line or edge of a specific orientation is in view. Other cells, deeper within the visual system, assemble these elements in order to detect larger configurations and more complex patterns.



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