Colorless

P., a 68-year-old retired office worker, had been rushed to the hospital after she suffered a stroke that affected part of the occipital lobe in both hemispheres. She was discharged following a few days in the hospital but continued to experience some lingering effects from the stroke: she had difficulty recognizing faces, including the face of her husband of 35 years (although she could easily recognize his voice), and the world appeared to be without color, as if she were watching a black-and-white movie. She said that the clothes in her closet all looked dirty, and she had difficulty deciding what she wanted to wear. Even more disturbing, all of her food looked gray, which made it difficult for her to recognize certain foods. Some she could identify by their size and shape—peas and bananas, for example—but an omelet might look like a steak, which meant she wasn’t always prepared for what something would taste like when she put it in her mouth.

When a neurologist tested her object-recognition abilities by showing her some common objects (e.g., a telephone, a coffee mug, and a pencil) and asking her to name them, P. made a few errors but for the most part seemed unimpaired. However, when the neurologist showed her a series of brightly colored objects, they all looked like pale shades of gray. And when she was given red, green, blue, and yellow cards of various brightnesses (e.g., bright, medium, and dark red) and asked to sort them into four same-color piles, she became frustrated and felt as if she was just guessing.

P.’s loss of color vision was not debilitating; she found ways to identify objects without depending on color—for example, she soon began to use her sense of smell to identify foods. But she found the world a less vivid sensory experience, and this change was depressing. She continued to go to art museums, a favorite activity before her stroke, but she focused on the sculptures because she found it too painful to view her beloved Impressionist paintings, which now looked drab and unappealing.
Color adds richness and beauty to the visual world, but that hardly explains why visual systems have evolved to perceive color. Without denying the purely aesthetic value of color, it's important to understand that color vision also serves many important practical purposes, both “natural” (e.g., letting us find red berries among green leaves or detect tawny-colored lions hiding in yellow grass) and “artificial” (e.g., enabling the use of traffic lights and the innumerable other technologies in which color perception plays a crucial role). Nevertheless, most of us take the practical aspects of color perception for granted, focusing instead on the subjective experience of color. From that point of view, vision without color is like eating without being able to taste flavors: you can certainly take in calories, but it's not much fun!

**Color vision** is the ability to see differences between lights of different wavelengths.

In this chapter, we begin our exploration of color vision by considering the wavelength composition of light and by looking at how the reflection of light from different surfaces can change that composition before it enters our eyes, thus providing information about the material properties of that surface. We then consider hue, saturation, and brightness (the qualities that describe how we perceive color) and follow that with a discussion of how colors mix, in which you'll see that colored lights mix quite differently from colored substances like paints. This will lead us into the core of the chapter: an investigation of the two physiological mechanisms that create our experience of color—trichromacy and opponency.

The final sections of the chapter address color contrast and color assimilation (both of which show that the perceived color of an object depends on the colors of nearby objects), color constancy and lightness constancy (our ability to see things as having the same color and lightness under different lighting conditions), and color vision deficiencies (sometimes called “color blindness,” in which people experience partial or total loss of the ability to see color).

Throughout the chapter, it will be important to keep in mind an idea first mentioned by Isaac Newton in his seminal treatise on light, *Opticks* (1704/1952), where he made the following observation about the subjective experience of color and its relation to the physical properties of light:

> The Rays to speak properly are not coloured. In them there is nothing else than a certain Power and Disposition to stir up a Sensation of this or that Colour…. So Colours in the Object are nothing but a Disposition to reflect this or that sort of Rays more copiously than the rest. (p. 125)

In other words, objects don’t “have” color any more than substances “have” odor (for a lively debate about this, see Byrne & Hilbert, 2003). Our perception of odors comes from the interaction between receptors in the nose and volatile molecules thrown off by substances—a specific experienced odor is evoked by specific types of molecules. Similarly, our perception of color comes from the interaction between receptors in the eyes and the wavelengths of light reflected from the surfaces of objects—a specific experienced color is evoked by specific wavelengths present in the light.

**Light and Color**

In Chapter 2, you learned that light is electromagnetic radiation with wavelengths in the range of about 400 to about 700 nm. This portion of the electromagnetic spectrum is called the **visible spectrum**. Within this range, people with normal vision perceive differences in wavelength as differences in color.

In discussing color vision, we’ll be concerned mainly with how we perceive light that is reflected from a surface into our eyes (and only occasionally with light that is transmitted directly from a source into our eyes, as when you look at a lightbulb or a campfire). It will often be convenient to refer to light of a particular color or to material things of a particular color, but you should always keep in mind—as Newton pointed out—that color isn’t in light or material things. Rather, color is a perceptual experience evoked by the wavelengths of light reaching our eyes.
Spectral Power Distribution

For any light, we can construct a graph that depicts the light’s spectral power distribution (SPD)—the intensity (power) of the light at each wavelength in the visible spectrum (see Figure 5.1). The SPD is a crucial determinant of the perceived color of the light.

Most light sources emit light that consists of a wide range of different wavelengths. Such light is called heterochromatic light (hetero, meaning “different”; chromatic, meaning “color”). Light that consists of only a single wavelength is called monochromatic light (mono, meaning “single”). The SPD of a monochromatic light is a vertical spike, as illustrated in Figure 5.1 (most laser pointers produce monochromatic, or nearly monochromatic, light).

Figure 5.1 compares the SPD of sunlight to that of light from two familiar artificial light sources, an incandescent bulb and a fluorescent bulb. All three of these light sources emit what could be called white light—that is, heterochromatic light that (1) contains wavelengths from across the entire visible spectrum and (2) has no really dominant wavelengths. The SPD of an idealized white light would be a horizontal line: a light in which all wavelengths across the visible spectrum have exactly equal power. We perceive white light as more or less colorless, which is why white light is also called achromatic light (a-, meaning “without”). The SPD of sunlight is quite close to that of an idealized white light. In contrast, the SPD of light from an incandescent bulb is more intense toward the yellow and red end of the spectrum, while the SPD of light from a fluorescent bulb has “spikes” at short and medium wavelengths that make fluorescent light somewhat more bluish than sunlight. You can easily see these differences by standing outside at night and looking at the windows of rooms illuminated by incandescent bulbs, which look distinctly yellowish, and by fluorescent bulbs, which look distinctly bluish.

**FIGURE 5.1 Spectral Power Distribution** Electromagnetic radiation varies enormously in wavelength across the spectrum (top). The visible part of the spectrum ranges in wavelength from about 400 to about 700 nm. A graph of the spectral power distribution of a light source (like the graphs for three light sources at the bottom of this figure) shows the relative amount (intensity, or power) of each wavelength in the light. For example, light from an incandescent bulb contains proportionately more long-wavelength (red) light than sunlight does. A fluorescent bulb contains narrow bands of high-intensity wavelengths within the blue and green regions of the spectrum. The vertical spike depicts the spectral power distribution of a monochromatic light with a wavelength of 500 nm.

**Definitions**
- **spectral power distribution (SPD)** The intensity (power) of a light at each wavelength in the visible spectrum.
- **heterochromatic light** Light that consists of more than one wavelength.
- **monochromatic light** Light that consists of only one wavelength.
- **achromatic light** (or white light) Light containing wavelengths from across the visible spectrum, with no really dominant wavelengths; perceived as more or less colorless (i.e., a shade of gray).
The SPDs shown in Figure 5.1 describe the wavelengths and intensities of the light emitted by light sources. In everyday life, however, we rarely look at light sources such as the sun and lightbulbs. Instead, we typically look at the objects around us that reflect the light from whichever light sources are present. This means that the perceived color of things depends on the SPD of the light source and on how things reflect light. The way objects reflect light depends on the molecular structure of the surface, which determines its spectral reflectance, the proportion of light at each wavelength that the surface reflects rather than absorbs (see Figure 5.2).

**FIGURE 5.2 Spectral Reflectance** A graph of the spectral reflectance of a surface shows the percentage of light at each wavelength that the surface reflects rather than absorbs. (a) The surfaces of carrots and tomatoes reflect proportionately more long-wavelength light than does the surface of a cabbage or a patch of blue paint, which reflect proportionately more medium- and short-wavelength light, respectively. (b) Black, gray, and white paper have similarly flat reflectance curves—indicating that they reflect about the same percentage of all wavelengths—but white paper reflects much more light overall, while black paper reflects very little light.

**Spectral Reflectance**

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Figure 5.2a shows that something we perceive as green, like a cabbage, reflects a greater percentage of the light in the “green” portion of the spectrum, in the range of 500–550 nm, and a lower percentage of most other wavelengths. Similarly, something we perceive as red, like a tomato, reflects more light with longer wavelengths and less light from the rest of the spectrum. Figure 5.2b shows that some surfaces—for example, white, gray, and black paper—have reflectance curves that are approximately horizontal lines, indicating that they reflect about the same percentage of all wavelengths. However, they differ in the overall amount of light they reflect, as indicated by whether their reflectance curve is high or low in the graph: black paper absorbs more than 90% of the incident light and reflects less than 10%, while white paper reflects 80% or more at almost all wavelengths.

**CHECK YOUR UNDERSTANDING**

5.1 What is the meaning of the term visible spectrum?
5.2 What is the difference between spectral power distribution and spectral reflectance?
5.3 True or false? In a graph like Figure 5.2b, if the gray paper were a darker gray, its reflectance curve would move up in the graph. Explain your answer.
Dimensions of Color: Hue, Saturation, and Brightness

In the previous section, we discussed the physical properties of light and of surfaces, which determine the wavelengths of the light that enters our eyes. In this section, we consider how those physical properties of light evoke subjective experiences of color.

The perceptual experience of color can be described in terms of three independent dimensions—hue, saturation, and brightness. **Hue** corresponds to the way we ordinarily use the word “color”—that is, to say whether something looks blue, green, yellow, red, or some other color, without specifying whether the color looks vivid or washed out or whether it looks bright or dim. In Figure 5.1, for example, it is the hue that varies from blue to red as you scan from left to right across the visible spectrum. Thus, hue is the characteristic most closely associated with the wavelength of light.

**Saturation** refers to the vividness, purity, or richness of a hue. A red velvet robe, for example, is typically a much more vivid (saturated) red than the pastel pink of a cherry blossom, although the robe and the blossom may have the same hue. Monochromatic hues like those in the color bars used to adjust your TV picture are shown maximally saturated—that is, as vivid as possible. You can decrease the saturation of monochromatic light by adding white light to it; if enough white light is added, the light will appear to be nearly pure white with just the faintest hint of a hue, but the hue itself will not have changed.

Brightness, as we’ve previously noted, refers to the perceived amount of light; brightness is what you change when you adjust the dimmer control on a lamp.

**Color Circle and Color Solid**

We can represent the three dimensions of hue, saturation, and brightness geometrically, in a way that captures our perception of the similarities among colors. A 2-D color circle can depict the two dimensions of hue and saturation, but to include the third dimension, brightness, we need a 3-D color solid.

In a **color circle** (see Figure 5.3), hue varies around the circumference and saturation varies along any radius; the most saturated hues are at the circumference and saturation decreases as you move toward the center. The sequence of hues around the circumference matches the sequence in the visible spectrum (see Figure 5.1), but the red and blue ends of the spectrum meet at the part of the circle labeled “Nonspectral purples” in Figure 5.3. These purple lights are mixtures of the shortest-wavelength violet and the longest-wavelength red—they’re called “nonspectral” because they don’t exist anywhere on the visible spectrum as single wavelengths, but can only be created as mixtures. White is also a nonspectral color: it can only be created by mixing together two or more wavelengths.

A **color solid** adds the vertical dimension to represent brightness, with brightness increasing as you move up. Figure 5.4 shows a color solid with the top tilted back. The central axis represents shades of gray light, since all the hues are equally represented at the center of the circle. Thus, the colors along this achromatic axis range from black at the bottom point to the brightest white at the top point. A color circle like the one at the cut can be produced at any given level of brightness by cutting horizontally through the color solid.

**FIGURE 5.3 Color Circle** A color circle represents two of the three dimensions of color perception: hue (around the circumference) and saturation (along any radius). The red and blue ends of the visible spectrum are joined across the range of hues labeled “Nonspectral purples”—purplish colors that are mixtures of red and violet, which are, respectively, the longest- and shortest-wavelength monochromatic lights we can see. These purplish hues are called “nonspectral” (i.e., heterochromatic) because they are created by mixtures of wavelengths, as opposed to the “spectral” (i.e., monochromatic) hues in the visible spectrum.
the color solid. Note that the radius of the color solid shrinks as you move up or down from the middle—that is, as you increase or decrease brightness. Since the radius represents saturation, a shrinking radius implies that saturation varies over a smaller and smaller range as brightness increases or decreases from its midlevel. This corresponds to our perception that as colors get very dim or very bright, they become less vivid.

**Color Mixtures**

Children playing with crayons soon learn that colors can be combined to make other colors. For example, a child who makes a scribble with a yellow crayon and then scribbles over it with a blue crayon sees that the result looks green. Painters know how to mix combinations of two or more of the paints on their palette to make a nearly infinite variety of colors. Theatrical lighting directors combine colored spotlights to create light that will evoke particular moods during a play. Inkjet printers mix just four different inks (three colors plus black) to create all the colors needed to print color photographs. Children with crayons, painters, and inkjet printers mix substances, whereas lighting directors mix light. The results of these two types of color mixing are generally quite different.

**Subtractive Color Mixtures: Mixing Substances**

As we have seen, the perceived color of a substance depends on its reflectance—the percentage of light it reflects at each wavelength, with the rest being absorbed. When two or more different-colored substances are mixed, as when a painter mixes paints, the reflectance curve of the mixture can be computed by multiplying the reflectances of all the substances in the mixture at each wavelength and plotting the results on a graph. (For the purposes of this discussion, we'll assume that the illuminant is white light—i.e., light containing approximately equal amounts of all wavelengths across the visible spectrum.) To see how this works, consider a mixture of blue paint and yellow paint. In Figure 5.5a, the illustration and the reflectance curve show that blue paint looks blue because it reflects mainly the shorter wavelengths (those toward the blue end of the visible spectrum), as well as some medium (green) wavelengths, and absorbs all other wavelengths (yellow, orange, and red). Figure 5.5b shows that yellow paint looks yellow because it predominantly reflects wavelengths from the yellow part of the spectrum, as well as some green, orange, and red wavelengths. In Figure 5.5c, we see that the mixture looks green because both the blue paint and the yellow paint reflect light from the green part of the spectrum, while the blue paint in the mixture subtracts (absorbs) all the yellow, orange, and red light, and the yellow paint in the mixture subtracts all the blue light. That’s why a mixture of substances is called a *subtractive color mixture*—because each substance in the mixture subtracts (absorbs) certain wavelengths that other substances in the mixture might reflect. (Paint, for example, is a mixture of substances called *pigments*, and each pigment reflects and absorbs certain wavelengths. After the pigments are mixed to make paint, each pigment continues to absorb the same wavelengths as before the pigments were mixed.)

**Additive Color Mixtures: Mixing Lights**

Now let’s consider how mixing lights differs from mixing substances like paints. Suppose a lighting director is using three equally bright theatrical spotlights, each of which emits light within a narrow range of wavelengths—say, red light, green light, and blue light. Figure 5.6 shows what happens when the three lights are projected on a white screen so they partially overlap. The screen equally reflects all the wavelengths that hit it, because the reflectance of a white surface is much the same at every wavelength. Thus, the proportions of wavelengths in the reflected light are the same as the proportions in the projected lights, and where the spotlights overlap, the reflected light contains the sum of the wavelengths in the overlapping region. This type of color mixture is called an *additive color mixture* because it results from adding wavelengths rather than subtracting them. Later in this chapter, in the section “Trichromatic Color Representation,” we’ll see why these
Dimensions of Color: Hue, Saturation, and Brightness

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additive color mixtures are perceived the way they are—for example, why a combination of red and green lights is perceived as yellow, while a combination of red, green, and blue lights is perceived as a shade of gray.

Figure 5.7 shows how you can use a color circle to predict the perceived color of an additive mixture of any two monochromatic lights. If you draw a line between the two hues in the mixture, the perceived color will fall somewhere on the line; exactly where will depend on the relative intensities of the two lights. For example, equal intensities of each hue will result in a perceived color at the line’s midpoint, while a greater intensity of one hue will shift the perceived color toward that hue. Thus, the spectral power distributions—wavelengths and intensities—of lights determine the perceived color of additive color mixtures.

Figure 5.7 shows the results for three different additive mixtures of pairs of lights. Note that the mixtures shown in the figure all involve fully saturated hues: the lines connecting the colors all begin and end at the circumference of the color circle, representing 100% saturation. It is clear that the hue resulting from any such mixture will be less than fully saturated, because it will fall inside the color circle, nearer to the fully unsaturated center.

What about mixtures of three monochromatic lights? The color resulting from such a mixture will fall somewhere within the triangle formed by connecting the three hues—exactly where depending on the relative intensities of the lights—and will again be less than fully saturated. Figure 5.7 shows such a mixture of three lights falling within a triangle connecting red, green, and blue.

Complementary Colors

In Figure 5.7, note the line connecting red and cyan. Since these two hues are exactly opposite each other on the circumference of the color circle, the connecting line runs through the center of the circle. Thus, a 50–50 combination of this pair (and of any other

A pair of colors 180° apart, such as yellow and blue, would be perceived as some shade of gray, depending on the intensity of the lights (e.g., the 75% green + 25% blue and 80% red + 20% green mixtures indicated in the figure). If the two lights have equal intensity, the perceived color of the mixture will be at the midpoint of the line, and if, in addition, two hues are opposite each other (i.e., if they are complementary colors, 180° apart), the perceived color will be at the center of the color circle (like the red + cyan mixture in the figure) and will therefore be a shade of gray. To predict the color of a mixture of three monochromatic lights, connect them to form a triangle, like the triangle formed by red, green, and blue. The color of the mixture will fall somewhere within the triangle, depending on the relative intensities of the three lights—for example, the 45% red + 45% green + 10% blue mixture. Any such set of three monochromatic lights makes a set of primary colors.

**Primary Colors**

Primary colors are any three colors that can be combined in different proportions to produce a range of other colors. As we noted above, the triangle formed by connecting red, green, and blue in Figure 5.7 defines a range of other colors that can be created by combining these colors in different proportions. Thus, red, green, and blue constitute a set of primary colors. In fact, any three hues in the color circle can be connected in this way to form a triangle enclosing other colors, which means that there is no unique set of primaries. Nevertheless, some sets are better than others, in terms of producing as many of the colors in the color circle as possible. The triangle formed by red, green, and blue, for example, has as large an area as a triangle in the color circle can have, because red, green, and blue are spaced equally around the circle; it therefore encompasses as large a range of other colors within the circle as possible. However, these three primaries are incapable of producing colors (such as a highly saturated cyan) that are outside the triangle. Red, green, and blue are the primaries conventionally used to produce additive color mixtures in color TVs and computer monitors. For technologies that use subtractive color mixtures (e.g., for color printing, as in inkjet printers), magenta, cyan, and yellow—which form as large a triangle as red, green, and blue—are conventionally used as primaries.

Why are primaries defined as sets of three colors and not, say, two or four? The simple answer is that human color perception is based on three types of cones, each with different sensitivities to different wavelengths of light, as discussed next in the section “Trichromatic Color Representation.”
CHECK YOUR UNDERSTANDING

5.4 What are the three perceptual dimensions of color and how are they depicted in a color solid? Which of these dimensions is lacking in a color circle?

5.5 Why are subtractive color mixtures called “subtractive” and additive color mixtures called “additive”?

5.6 Why do red, green, and blue make a better set of primary colors than cyan, green, and blue?

Color and the Visual System

To this point, we’ve explored some physical characteristics of light and of materials that reflect light and indicated how those characteristics relate to our perception of color. In particular, we’ve seen that the most important characteristics relevant to color vision are the spectral power distribution of a light and the reflectance of the material reflecting that light.

In this section, we’ll discuss how the light entering the eyes evokes patterns of activity in the visual system to produce the perception of color. Color perception is a two-stage process. In the first stage, referred to as trichromatic color representation, light evokes different responses from the three different types of cone photoreceptors in the retina. In the second stage, known as opponent color representation, the responses from the cones are combined and processed by a subset of retinal ganglion cells and by color-selective neurons in the brain. The observations that led to the formulation of these two types of color representation were first made during studies of color vision in the nineteenth century. For a time, they were seen as competing accounts of color vision, but studies in the mid-twentieth century showed that both are essential parts of the color vision system.

Trichromatic Color Representation

A trichromatic account of color vision was first proposed in 1802 by the English physician and scientist Thomas Young, who wrote: “As it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles [cones], each capable of vibrating in perfect unison with every possible undulation [wavelength], it becomes necessary to suppose the number limited.” He then suggested that the number of different “particles” was three, based on the observation that any visible color can be matched by the proper mixture of three primary colors. Some 50 years later, Young’s ideas were discussed and popularized by the great German scientist Hermann von Helmholtz. Thus, this is often called the Young–Helmholtz trichromatic theory.

Color Matching with Mixtures of Three Primary Colors

How do we know that a mixture of three primary colors can match any other color? First, we need to understand that this is a psychophysical question, not a physical one. The question is whether the right mixture of three monochromatic primary colors is perceived as identical in color to some other monochromatic light, not whether the mixture and the other light are physically identical. To show the perceptual equivalence of these lights, vision scientists conduct what are known as metameric color-matching experiments (Stiles & Burch, 1959). Metamers are any two stimuli that are physically different but are perceived as identical.

In a metameric color-matching experiment, an observer is shown two patches of light, called the test patch and the comparison patch, side by side on a perfectly white screen that reflects all wavelengths equally (see Figure 5.8). The test patch consists of a single wavelength with a fixed intensity—say, 590 nm. The comparison patch consists of an additive mixture of three monochromatic lights, with wavelengths of, say, 645, 526, and 444 nm.
which would be perceived as the colors red, green, and blue, respectively, and which function as the three primary colors in the experiment. The observer can turn three dials to adjust the intensities of the three lights in the comparison patch separately. The observer's task is to adjust the intensities so that the additive color mixture in the comparison patch appears to have the same color as the test patch. If the observer can do this, then the two patches constitute a metameric color match—that is, despite their physical difference, the two patches are perceptually identical.

In Figure 5.8, the observer has achieved a metameric color match with the test patch by setting the intensities of red, green, and blue at 228, 189, and 79, respectively (in an actual experiment, the observer wouldn't be working with numerical settings but would just turn the dials until she perceived a match). Figure 5.8 also shows two hypothetical previous attempts to achieve a match, one appearing a little too dark (corresponding to settings of 220, 180, and 70) and the other a little too light (corresponding to settings of 240, 200, and 90). Repeated color-matching experiments like this one have shown that people with normal color vision are, in fact, able to mix three primaries in this way to achieve metameric color matches with monochromatic light from across the visible spectrum.
spectrum. But does this imply the need for three types of cones—as Young proposed—or could a person with only one or two types of cones also match colors successfully? To answer these questions, we need to consider how cones work.

Cones and Colors

You already know from Chapter 2 that there are three types of cones, that each type contains a different photopigment, and that each photopigment has a particular spectral sensitivity. You also know that the three types of cones are referred to as L-cones, M-cones, and S-cones, according to whether their peak sensitivity is to a long, medium, or short wavelength, respectively. Figure 5.9 shows the spectral sensitivity function of the photopigment in each type of cone—that is, the probability that a photon of light with any given wavelength will be absorbed by that cone's photopigment (Stockman et al., 1993). You can see from the figure that the photopigment in each type of cone is most responsive to a particular range of wavelengths, but all three respond to a wide range of wavelengths, and their spectral sensitivity functions overlap considerably.

Principle of Univariance

Each type of cone varies in its sensitivity to different wavelengths of light, but it’s impossible to work backward from the response of a single cone to determine the wavelength of the light that caused the response. The reason for this is expressed by the principle of univariance as it applies to cones: the absorption of a photon of light causes a fixed response by a cone, regardless of the photon’s wavelength—in other words, the strength of the response generated by a cone when it transduces light depends only on the amount of light (i.e., the number of photons) transduced, not on the wavelength of the light (Baylor et al., 1987; Rushton, 1972). (We previously encountered an analogous idea in Chapter 3.)

FIGURE 5.9 Spectral Sensitivity of Photopigments

(a) Relative sensitivity. In this graph, the scale of the vertical axis is normalized, so the peak of each curve is at the same height (100%). The photopigment in S-cones is most sensitive to light with a wavelength of 443 nm and almost completely insensitive to wavelengths greater than about 550 nm. The photopigments in M-cones and L-cones both have some sensitivity across nearly the entire spectrum of visible light, but the sensitivity of M-cones is higher toward the middle wavelengths (peaking at 543 nm), while that of L-cones is higher toward the longer wavelengths (peaking at 574 nm). The photopigment in rods is most sensitive to light with a wavelength of 500 nm. (b) Absolute sensitivity. When the scale of the vertical axis isn’t normalized, it’s apparent that the photopigments in M-cones and L-cones are much more sensitive to their wavelengths of peak sensitivity than is the photopigment in S-cones. The photopigment in rods is the most sensitive of all—the peak absolute sensitivity of rods is about 100 times that of the peak sensitivity of M-cones (much too high to be shown on this graph).
while discussing how neurons in area V1 represent orientation—see Figure 3.9 and the accompanying text.) The spectral sensitivity functions show that cones differ in the likelihood that they will absorb photons of light of a particular wavelength, but once a photon is absorbed, its effect is the same for all wavelengths. For example, an M-cone’s response to a dim 543 nm light and to a bright 450 nm light could be identical, with the right choice of intensities. The principle of univariance means that color vision depends crucially on the relative responses of multiple cone types. Let’s take a look at why that’s the case.

If You Had Only One Type of Cone (or Only Rods)

Consider how a person with only one type of cone—say, M-cones—would perceive different wavelengths of light. Figure 5.10 shows the spectral sensitivity curve of M-cones. Suppose this person participated in a metameric color-matching experiment but was instructed to try achieving a metameric color match using only one of the monochromatic lights (instead of all three, as in the experiment described earlier). Also suppose that the

![Figure 5.10 If You Had M-Cones Only](image)

The table under the graph shows that a person with M-cones only could adjust the intensity of any single monochromatic comparison light to achieve a metameric color match with a 615 nm test light. The test light causes the M-cones to produce a response corresponding to the absorption and transduction of 145 photons/sec. In Experiment 1, the comparison light has a wavelength of 525 nm. The M-cones have a relative sensitivity of 89% to this wavelength. Thus, if the person adjusts the comparison light to an intensity of 163 photons/sec, the M-cones produce a response of 145 photons/sec (.89 x 163 = 145), matching their response to the test light. This means that the person can adjust the comparison light to perceptually match the test light. Experiments 2 and 3 show that such a match can also be achieved with two other lights, 640 nm and 475 nm. With the appropriate adjustments in intensity, any comparison light in the visible spectrum can produce the identical M-cone response of 145 photons/sec. A similar figure could be constructed for a person with only S-cones, only L-cones, or only rods. In all such cases, the person would be truly color-blind—that is, any two wavelengths could differ only in perceived intensity; everything would be perceived as shades of gray.
test patch consists of a monochromatic light with a wavelength of 615 nm and an intensity of 500 photons/sec. As you can see from the figure, the relative sensitivity of M-cones to this light is 29%; for the purposes of this example, let’s assume that this means that each M-cone absorbs and transduces 29% of the photons of this wavelength that strike it. Since the intensity of the test light is 500 photons/sec, each M-cone absorbs 145 photons/sec of this light (.29 × 500 = 145) and produces a response with a strength corresponding to the transduction of those 145 photons/sec.

Now suppose the person tries using a 525 nm comparison light to create a metameric color match to the test light. As you can see in Figure 5.10, the relative sensitivity of M-cones to light with this wavelength is 89%. Experiment 1 in the table in Figure 5.10 shows that if the person adjusts the 525 nm light to an intensity of 163 photons/sec, the M-cones will absorb and transduce the same 145 photons/sec and, by the principle of univariance, will produce the same response as the response to the test light. Since the lights produce the same response, the person has no way to perceive the difference in wavelengths: the test light and comparison light will look identical. Thus, by appropriately adjusting the intensity of a light that a person with normal color vision would perceive as green (525 nm), a person with M-cones only could achieve a metameric color match with a test light that a person with normal color vision would perceive as reddish orange (615 nm).

The table in Figure 5.10 shows that the same goes for a 640 nm comparison light (Experiment 2) and a 475 nm comparison light (Experiment 3). Indeed, a person with just one type of cone can create a metameric color match between any randomly selected test light and any arbitrary comparison light (as long as both lights are in the visible spectrum) by appropriately adjusting the intensity of the comparison light.

This hypothetical experiment sheds light on one of the questions we asked before: Could a person with just one type of cone match colors successfully? The answer is yes: to a person with only one type of cone, changes in the wavelength of light are indistinguishable from changes in intensity, with the degree of apparent change in intensity depending on the relative sensitivity of the cone type at the given wavelength. Such a person would be truly color-blind—everything would appear as some shade of gray—and matching colors would simply mean adjusting the intensity of one gray light until it looked like another gray light.

The principle of univariance also applies to rods and explains why night vision is color-blind (a fact we first mentioned in Chapter 2). Recall from our discussion of dark adaptation in Chapter 2 that rods are much more sensitive to light than cones; for this reason, only rods are active in low light. In effect, therefore, in low light people have only one type of photoreceptor: rods. If you now look back at Figure 5.9 and consider the spectral sensitivity curve for rods, you can see that the situation is the same as that for M-cones illustrated in Figure 5.10. That is, lights of different wavelengths can produce identical responses from rods. For example, the relative sensitivity of rods is about 50% both to light with a wavelength of around 465 nm and to light with a wavelength of around 545 nm. Thus, a person with normal vision will perceive two lights of these wavelengths as the same if their intensities are equal, even though in daylight, when cones are active, the person would perceive the first light as blue and the second as green. And just as in the M-cones example, the intensity of light with any other wavelength could be adjusted to produce exactly the same response from rods. This is why different wavelengths of light are experienced as different shades of gray at night, when vision is based only on rods. Under equal illumination, green surfaces might look brighter than red or blue surfaces—because the relative sensitivity of rods is higher in the green portion of the spectrum than in the red or blue portion—but they will not look different in color.

If You Had Only Two Types of Cones

Now let’s explore how a person with only two types of cones (say, M-cones and L-cones) would perceive different wavelengths. Figure 5.11 shows the spectral sensitivity curves for M-cones and L-cones. Suppose we conduct a metameric color-matching experiment with this person, again using a monochromatic test light with a wavelength of 615 nm, as in the experiment illustrated in Figure 5.10, and a monochromatic comparison light with a
wavelength of 495 nm. The intensity of the test light is fixed at 1,000 photons/sec. Since the relative sensitivity of M-cones to the test light is 29%, they absorb 290 photons/sec and produce a corresponding response. The relative sensitivity of L-cones to the test light is 62%, so they absorb 620 photons/sec and produce a different response. These two different signals coming from the part of the retina stimulated by this test light determine the perceived color.

A similar graph and table could be constructed for any combination of two types of cones and any test light and comparison light. Thus, a person with only two types of cones would have a form of color vision—that is, he or she would generally perceive differences in wavelength as differences in color.

As shown in the table below the figure, when the 495 nm comparison light has the same intensity as the test light—1,000 photons/sec—the M-cones absorb a greater number of photons than they do with the test light (380 versus 290 photons/sec), while the L-cones absorb many fewer photons than they do with the test light (200 versus 620 photons/sec). Because the responses of the two cone types differ for the test and comparison lights, they will look different. On the one hand, if the person reduces the intensity of the comparison light to 763 photons/sec, so the M-cones absorb the same 290 photons/sec that they do with the test light, the L-cones, of course, will absorb even fewer than before. On the other hand, if the person raises the intensity of the comparison light to 3,100 photons/sec, so the L-cones absorb the same 620 photons/sec that they do with the test light, the M-cones will absorb even more than before.

Clearly, there is no way to adjust the intensity of the comparison light so the M-cones and L-cones each absorb the same number of photons as they do with the test light. Thus, unlike the situation with a person who has just one type of cone, a person with two types of cones cannot adjust the intensity of a single arbitrary comparison light to match the color of a test light with a different wavelength. Such a person has a limited form of color vision—he or she will generally perceive two different wavelengths as two different colors,
Color and the Visual System

not just as a difference in intensity. (The reasons why color vision with just two types of cones is described as “limited” are discussed in the section “Color Vision Deficiencies” later in this chapter.)

Metameric color-matching experiments have shown that people with two types of cones can, however, match a monochromatic test light of any wavelength if they have a mixture of two monochromatic comparison lights to work with, instead of just one. For a person with two types of cones, there are, in effect, only two primary colors needed to match any other color. Furthermore, metameric color-matching experiments have also shown that people with normal color vision require three monochromatic comparison lights to match any monochromatic test light, indicating that, for them, there are three primary colors (e.g., red, green, and blue, as in the metameric color-matching experiments first described above).

The pattern is clear. The number of comparison lights required to produce a match with any arbitrary test light tells us how many cone types the observer has. Since most people require three comparison lights, the normal number of cone types (and of primary colors) must also be three, and this is why normal color vision is termed trichromatic.

Physiological Evidence for Trichromacy

Long after scientists had used metameric color-matching experiments like those described here to provide psychophysical evidence for three types of cones, definitive physiological evidence emerged to corroborate this idea. George Wald (who was awarded the 1967 Nobel Prize in Physiology or Medicine for his discovery of the basic cycle of visual transduction, described in Chapter 2) developed a method for measuring the amount of light at each wavelength absorbed by a foveal cone, which enabled the determination of the spectral sensitivities of the three types of cones (Brown & Wald, 1964).

The mosaic of the three types of cones within the human retina can be directly visualized using a technique called retinal densitometry (Roorda & Williams, 1999), which produces high-resolution images of the retina (see Figure 5.12). As indicated by this figure, the retina contains a fairly small proportion of S-cones (roughly 5%); the relative number of M-cones and L-cones, however, can differ greatly from one person to the next, even for people who have normal color vision.

Additional evidence of three different types of cones comes from photocurrent measurements done with monkeys, in which researchers directly measure the responses of individual cones (Baylor et al., 1987). An extremely thin electrode is used to measure electrochemical changes in a single cone that is stimulated with tiny beams of light of various wavelengths and intensities. If a large enough number of individual cones is assessed in this way, and the resulting measurements are plotted on a graph, three distinct patterns of sensitivity to light emerge, closely resembling the spectral sensitivity curves of the three different types of cones in humans (see Figure 5.9).

Meaning of Trichromacy

The trichromatic representation of wavelength can be thought of as a form of data compression. Rather than measure the amount of light at every wavelength at every point in the retina, the human visual system depends on the responses

**FIGURE 5.12 Visualizing Cones With Retinal Densitometry** The imaging technique of retinal densitometry produces images like these, providing direct evidence that people have three types of cones (the colors have been added to make it easier to distinguish the different types). As shown here, the proportion of S-cones tends to be about the same across individuals, but the proportions of M-cones and L-cones can vary greatly. These images were taken of a patch of retina about 0.3 mm from the fovea. [Republished with permission of the Society for Neuroscience, from Hofer et al., 2005. Permission conveyed through Copyright Clearance Center, Inc.]

<table>
<thead>
<tr>
<th>Retina of Person 1</th>
<th>Retina of Person 2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>S-cones</strong></td>
<td>6.4%</td>
</tr>
<tr>
<td><strong>M-cones</strong></td>
<td>44.3%</td>
</tr>
<tr>
<td><strong>L-cones</strong></td>
<td>49.3%</td>
</tr>
<tr>
<td><strong>S-cones</strong></td>
<td>4.6%</td>
</tr>
<tr>
<td><strong>M-cones</strong></td>
<td>27.6%</td>
</tr>
<tr>
<td><strong>L-cones</strong></td>
<td>67.8%</td>
</tr>
</tbody>
</table>
of just three types of cones to represent different colors. Clearly, some such compression is necessary, even though it necessarily results in a loss of information, as shown by the metameric color-matching experiments—that is, many pairs of lights that are physically different in their wavelength composition are perceived as identical. Evolution has resulted in an extremely efficient means of encoding color: just three types of cones, each with a spectral sensitivity function that spans most visible wavelengths, suffice to create fine enough distinctions in color for humans to thrive in a highly varied visual environment. Moreover, technological innovations exploit trichromatic color vision in printing and video color technology to create thousands of perceptually distinct colors with only a small number of inks or lights. This is why just three primary colors are sufficient to reproduce colors associated with wavelengths throughout the visible spectrum: if a mixture of the three primaries stimulates the three cone types in the same way as a given monochromatic light would, the visual system will be unable to discriminate that mixture from the monochromatic light.

CHECK YOUR UNDERSTANDING

5.7 What is a metameric color-matching experiment designed to test?

5.8 State the principle of univariance as it applies to cones.

5.9 The answer to the question of whether a person with only one type of cone could match any two colors successfully is yes. Explain why.

5.10 In general, how many comparison lights would a person with two types of cones need to match any given test light in a metameric color-matching experiment?

5.11 What are two sources of physiological evidence for trichromacy?

Opponent Color Representation

In the late nineteenth century, a debate arose about whether the trichromatic representation can account for all aspects of human color vision. At the center of the debate was the German scientist Ewald Hering, who pointed to several phenomena that were difficult to explain with a trichromatic approach to color vision (Hering, 1878/1964). Unfortunately, Hering’s arguments were largely ignored for several decades, not only because the trichromatic mechanism proposed by Young and Helmholtz worked perfectly for color-matching experiments, but also because of its elegant simplicity. It wasn’t until the late 1950s that Hering’s ideas were reexamined and clearly confirmed (Hurvich & Jameson, 1957).

Subsequent research has led to the current view of color vision as a two-stage process. In the previous section, we described the trichromatic representation, which correctly characterizes the first stage of color vision, up to the point where cones transduce light into neural signals. In this section, we’ll explore the second stage, the opponent color representation, which describes what happens after that point—that is, how retinal ganglion cells and color-selective neurons in the brain process the cone signals. The opponent color representation accounts for the puzzling observations made by Hering more than a century ago.

Four Basic Colors in Two Pairs of Opposites

Hering’s observations constituted psychophysical evidence for two important ideas: first, in some respects, the human visual system operates as if there were four basic colors, rather than the three implied by trichromacy; and second, these four basic colors can be divided into two pairs of colors, with the members of each pair being in some sense opposites, or “opponents”: a red–green pair and a blue–yellow pair. The observations that led to these ideas included the following:

• When people are given a stack of cards, each with a different patch of color, and are asked to sort the cards into piles of similar colors, they tend to sort them into four piles—which most people would call red, green, blue, and yellow—rather than the three piles one might expect if color vision were strictly trichromatic.
• Color afterimages have a peculiar feature involving the two pairs of opponent colors. You can use Figure 5.13 to observe this feature of afterimages for yourself: the colors in the afterimages will be the other member of each pair. These types of color afterimages suggest that the visual system intrinsically pairs certain colors, and this is hard to explain if we assume that the visual system operates only via a trichromatic representation, because you can’t make pairs with an odd number of colors.

• Colors often appear to be mixtures of two non-opponent colors but never appear to be mixtures of two opponent colors. For example, orange looks like a mixture of red and yellow, cyan looks like a mixture of green and blue, and purple looks like a mixture of red and blue—but we can’t even imagine a color that we would call reddish green or bluish yellow. Once again we see pairings of colors, and once again the trichromatic account can’t explain why that is.

Hering pointed out that in all these cases, there seemed to be four basic colors, not three, and that certain pairs of colors appeared to have an opponent character to them: red and green are in some sense opposites, and so are blue and yellow. These facts, Hering insisted, could not be accounted for by a trichromatic representation of color vision.

**Hue Cancellation**

In the 1950s, psychophysical experiments using the technique of hue cancellation were carried out to test the idea that some aspects of color perception are best explained by assuming that the visual system operates as if there were four basic colors consisting of two pairs of opponent colors, red–green and blue–yellow (Hurvich & Jameson, 1957). In a hue-cancellation experiment, a person is shown a monochromatic test light and instructed to neutralize, or cancel out, a perceived basic color in the light by adding its opponent color. For example, the person might be shown a monochromatic test light with a wavelength of about 550 nm, which would typically be perceived as a yellowish green. The person is asked to cancel perceived yellowness by adding an appropriate amount of blue light, because blue and yellow are opponent colors. The intensity of blue light needed to cancel the yellowness corresponds to the perceived amount of yellowness in the original 550-nm test light. Similarly, the person should be able to add a certain intensity of red light to the test light to cancel out the perceived amount of greenness.

**FIGURE 5.13 Color Afterimages** (top) Under good white light, stare at the blue, green, red, and yellow squares for 20 seconds or more, minimizing blinks and keeping your eyes fixed on the central point where the four squares meet (the longer you stare, the more vivid will be the afterimage). Then shift your gaze to the four gray squares and look at the afterimage there. You’ll see that, in the afterimage, the yellow and blue squares now look blue and yellow, respectively, and the same for the red and green squares. In both cases, the color of the afterimage is the other member of the opponent pair. (bottom) Repeat this procedure with the green, black, and yellow flag, first staring at the central white dot in the flag for at least 60 seconds and then switching your gaze to the gray, flag-shaped rectangle next to it, where you’ll see an afterimage with the usual flag colors (red, white, and blue, in place of the original green, black, and yellow, respectively). These colored afterimages provide evidence for opponent color representation and against a strictly trichromatic representation.

**hue cancellation** An experimental technique in which the person cancels out any perception of a particular color (e.g., yellow) in a test light by adding light of another color (e.g., blue).
Figure 5.14 depicts the results of hue-cancellation experiments for test lights with wavelengths across the visible spectrum. As you can see, the curves in this figure very closely match our perceptions. That is, from about 400 nm to the wavelength labeled “Unique green” (typically, about 489 nm), lights are perceived as having blueness but no yellowness; adding the appropriate amount of yellow light can cancel out the blueness. Above the “Unique green” wavelength, lights appear to have yellowness but no blueness, and adding the appropriate amount of blue light can cancel out the yellowness. From the “Unique blue” wavelength (typically, about 464 nm) to the “Unique yellow” wavelength (about 572 nm), lights are perceived as having greenness but no redness, with red light needed to cancel out the greenness. And redness but no greenness is perceived at wavelengths below “Unique blue” and above “Unique yellow.” We can make some sense of this split of redness perception by looking back at the color circle in Figure 5.3, where the red and blue ends of the spectrum meet in the “Nonspectral purples” range of hues, all of which are perceived as having redness.

The unique hues in Figure 5.14 are wavelengths that aren’t perceived as combinations, but as purely blue, green, or yellow (e.g., unique green is perceived as having no blue and no yellow). As you can see in the figure, the red–green curve contacts the zero line twice, with unique blue perceived at one point and unique yellow perceived at the other—each of these unique hues is perceived as having zero redness and zero greenness. In contrast, the blue–yellow curve contacts the zero line just once, where unique green...
is perceived. You can see that there is no unique red; this corresponds to our perceptions of red—even though the longest wavelengths all look reddish, they are still perceived as having a tinge of yellowness.

In Figure 5.14, all these perceptions are illustrated by the dashed vertical lines extending up from 450 nm, 600 nm, and the unique hues. At any wavelength except the unique hues, such a line would intersect exactly two of the curves, indicating the basic colors perceived as making up light of that wavelength. The points of intersection indicate the relative amounts of the two basic colors perceived as making up the light. For example, the line at 600 nm indicates that a light with that wavelength is perceived as containing some amount of red (but not green) and some amount of yellow (but not blue). In the case of the unique hues, one of the intersection points is at zero, indicating that these hues are not perceived as combinations.

Physiological Evidence for Opponency

Until the mid-1950s, all of the evidence in support of opponent color representation was psychophysical, based either on introspection (e.g., Hering’s observations) or on experiments like those just described involving hue cancellation. In the 1950s, techniques for measuring the responses of single cells in the retina and then the brain were developed and brought into wide use. First, single cones in the fish retina were found that responded in opposite ways to wavelengths from different parts of the visible spectrum, providing the first physiological evidence for opponency (Svaetichin & MacNichol, 1958). This was followed by measurements of neurons in the lateral geniculate nucleus of monkeys that also responded to color in an opponent fashion (De Valois et al., 1958; recall from Chapter 3 that the lateral geniculate nucleus, in the thalamus, receives signals from retinal ganglion cells, processes those signals, and sends them on to the primary visual cortex via the optic radiations). Later research using these techniques has confirmed the existence of neural circuits underlying the opponent color representations implied by the psychophysical evidence—that is, circuits supporting color vision with four basic colors grouped in two pairs of opposites, red–green and blue–yellow.

Figure 5.15 illustrates how such circuits in the retina are thought to work (Calkins, 2004; De Valois, 2004). Nerve impulses from the three types of cones are processed by networks of other retinal neurons (bipolar, horizontal, and amacrine cells—not shown in the figure), resulting in combinations of excitatory and inhibitory inputs to retinal ganglion cells (RGCs). These patterns of neural signals create four different types of “opponent color circuits” in which the RGCs function as “opponent neurons,” as described below, where + = excitatory; – = inhibitory; S = short-wavelength, or bluish-to-greenish, light; M = medium-wavelength, or greenish-to-yellowish, light; and L = long-wavelength, or yellowish-to-reddish, light:

- **+S–ML circuit.** The RGC in this type of circuit fires above its baseline rate in response to short-wavelength light (i.e., +S) and below its baseline rate in response to medium- and long-wavelength light (i.e., –ML). Figure 5.15a illustrates a +S–ML circuit.

- **+ML–S circuit.** The RGC in this type of circuit does the opposite, firing above its baseline rate in response to medium- and long-wavelength light and below its baseline rate in response to short-wavelength light. Figure 5.15b illustrates a +ML–S circuit.

- **+L–M circuit.** Here, the RGC fires above its baseline rate in response to long-wavelength light and below its baseline rate in response to medium-wavelength light. Figure 5.15c illustrates a +L–M circuit.

- **+M–L circuit.** The RGC in this type of circuit does the opposite, firing above its baseline rate in response to medium-wavelength light and below its baseline rate in response to long-wavelength light. Figure 5.15d illustrates a +M–L circuit.

This opponent color model accounts physiologically for the phenomena that are problematic for trichromatic representation. +S–ML and +ML–S neurons respond
oppositely to blue and yellow light, so their outputs support the perception of blue and yellow as basic and opposite colors. Similarly, +L–M and +M–L neurons respond oppositely to green and red light, so their outputs support the perception of green and red as basic and opposite colors. Thus, the model includes four basic colors, rather than three; and it includes a sense in which blue–yellow and green–red are paired opposites. In addition, it makes some sense of the fact that yellowish blue (or bluish yellow) and reddish green (or greenish red) aren’t possible color perceptions.

Color-Opponent Neurons in the Visual Pathway

The color-opponent RGCs described above respond with an increase in firing rate to one range of wavelengths and with a decrease in firing rate to the complementary range of wavelengths—for example, the RGC in a +L–M circuit (see Figure 5.15c) fires above its baseline rate in response to long-wavelength light and below its baseline rate in response to medium-wavelength light. The receptive fields (RFs) of these neurons are spatially uniform; that is, the neurons respond most strongly to a uniform patch of light having the preferred wavelength and are maximally suppressed by a uniform patch of light having the complementary wavelength.

In contrast, other color-selective neurons in the visual pathway—including RGCs, LGN cells, and cortical cells—have RFs that produce more elaborate patterns of response (Johnson et al., 2008). For example, the V1 cell depicted in Figure 5.16a has a single-opponent center–surround RF—it responds with an increase in its firing rate when the RF center is stimulated with long-wavelength (reddish) light and with a decrease in its firing rate when the RF surround is stimulated by medium-wavelength (greenish) light. Other single-opponent V1 cells have the opposite response pattern—they increase their firing rate in response to medium-wavelength light in the center and decrease it in response to...
Color and the Visual System

Single-opponent and double-opponent neurons have been identified in area V1 in monkeys. (a) A neuron with a single-opponent center–surround receptive field (RF) responds with an increase in firing rate when the RF center is illuminated by long-wavelength (reddish) light; its response is suppressed by medium-wavelength (greenish) light in the surround. The responses of these neurons provide information about uniform illumination across the RF. (b) A neuron with a double-opponent center–surround RF responds with an increase in firing rate to reddish light in the center and/or to greenish light in the surround; its response is suppressed by greenish light in the center and/or reddish light in the surround. The responses of these neurons provide information about the location of red–green edges—an increased response is evoked when an edge is located so that the center is stimulated by reddish light and a portion of the surround is stimulated by greenish light, because the excitatory signals from these parts of the RF outweigh the inhibitory signals from the portion of the surround stimulated by reddish light; and a suppressed response is evoked when an edge is located so that the center is stimulated by greenish light and a portion of the surround is stimulated by reddish light, because the inhibitory signals from these parts of the RF outweigh the excitatory signals from the portion of the surround stimulated by greenish light. (Data from Johnson et al., 2008.)

Color Afterimages and Opponency

Recall that the specific colors perceived in color afterimages were among the phenomena noted by Hering as not explainable by trichromatic representation (see Figure 5.13 and the accompanying text). Can opponent color representation account for such afterimages?

In Chapter 2, we discussed the process of dark adaptation and its converse, light adaptation, in which the visual system adjusts the sensitivity of photoreceptors to a level appropriate for the current intensity of ambient light. If the lighting becomes dim, the visual system becomes more sensitive; if the lighting becomes bright, the visual system becomes less sensitive. One of the primary mechanisms of dark and light adaptation is...
After a photopigment molecule absorbs a photon and undergoes the shape change referred to as photoisomerization (see Figure 2.19), some time must elapse before its shape changes back and the molecule again becomes light sensitive. We describe the state of the photopigment molecule during this period as bleached, meaning that it can't respond to light by absorbing photons with the wavelengths to which the molecule is sensitive in its unbleached state.

Color afterimages result from a kind of photopigment bleaching known as chromatic adaptation. If relatively intense light of one particular wavelength (or a narrow range of wavelengths) strikes the retina for an extended time, the photopigment molecules in the type of cones that are most sensitive to those wavelengths become bleached en masse, rendering the visual system temporarily less sensitive to those wavelengths (Burnham et al., 1957).

How would chromatic adaptation affect an opponent color circuit like the one illustrated in Figure 5.15c, and what would that mean for the perceived color of afterimages? Suppose you stare for 30 seconds at a brightly lit picture of a green square with peak reflectance of 500 nm. The photopigment molecules in the M-cones in the square portion of your retina where the retinal image of the square is projected will bleach more than those in the L-cones there, so the M-cones will be relatively less sensitive than the L-cones for a period of time. If during that time you look at a white surface, which would normally elicit equal responses from M-cones and L-cones (because white light contains all wavelengths equally), the L-cones in that part of the retina will respond more strongly than the M-cones because of the bleaching. The weakened response from the M-cones there means weaker inhibitory impulses transmitted to the +L–M opponent neurons with receptive fields there. The excitatory impulses from the L-cones to those +L–M neurons now outweigh the inhibitory impulses from the M-cones, and the neurons begin to fire, signaling reddishness, which you perceive as the color of a square afterimage on the white surface. When the M-cones recover from bleaching, the balance of excitatory and inhibitory impulses is restored, and white looks white again. A corresponding account can be given for the colored afterimages of green, blue, and yellow things.

Meaning of Opponency

In the section on the trichromatic representation of color, we saw that people with normal color vision have three types of cones, with three different photopigments that respond preferentially to different wavelengths of light. These physiological facts explain the results of psychophysical experiments in color matching, which show that we can mix three primary colors of monochromatic light to match light of any color.

Opponent color representation, in contrast, explains other psychophysical phenomena, such as color categorization, color afterimages, and the results of hue-cancellation experiments—all of which imply that, at some level, people operate with four basic colors grouped in two pairs. Physiological evidence for opponency comes from the detection of opponent neurons—retinal ganglion cells and neurons in the lateral geniculate nucleus and the visual cortex whose neural circuitry supports the four-colors-in-two-pairs aspects of color vision.

Why did the visual system evolve with an opponent representation of color? A likely explanation is that it's a matter of efficient transmission of information. To see why, note that the responses of M-cones and L-cones are very similar across a broad range of the visible spectrum, as indicated by the similarity of their spectral sensitivity functions (see Figure 5.9). That is, the responses of these two cone types, considered separately, would provide the visual system with much the same information. The +L–M and +M–L opponent color circuits use subtraction to send the visual system focused information about the difference in the responses of these two cone types, rather than making the visual system find the buried bits of useful information among all the redundancies. Similar difference information is provided by the +ML–S and +S–ML opponent circuits. Significantly, researchers have found that color opponency provides an extremely efficient code for representing the colors found in natural scenes (Lee et al., 2002), lending support to the idea that opponency is an evolutionary adaptation.
Color Contrast and Color Assimilation

A color viewed in isolation can be perceived very differently when viewed in juxtaposition to other colors, with the perception depending on the specific combination and spatial arrangement of colors. Figure 5.17a illustrates color contrast, in which the perception of a surrounded color is shifted toward the complement of the surrounding color. For example, in the leftmost column, the central red patch looks more red in the bottom panel, where it's surrounded by green (red is the complement of green), than in the top panel, where it's surrounded by pink. Color contrast provides further support for opponent mechanisms in color vision.

**FIGURE 5.17** Color Contrast and Color Assimilation  
(a) Color contrast: Colors look more vibrant when surrounded by colors close to the complementary color, as in the bottom row: red looks redder when surrounded by green (and vice versa), and yellow looks yellower when surrounded by blue (and vice versa).  
(b) Color assimilation: Identical colors in the central patches in each column look different because they take on some of the surrounding color. [Andrew Stockman and David H. Brainard]
**Color Assimilation**

The perception of a surrounded color as shifted toward a noncomplementary surrounding color; also known as the “spreading effect.”

Figure 5.17b illustrates the opposite effect, called **color assimilation**, in which the perception of a surrounded color is shifted toward a noncomplementary surrounding color. For example, in the leftmost column, the blue squares in the central patch look a bit red in the top checkerboard, where they’re surrounded by red squares, and a bit green in the bottom checkerboard, where they’re surrounded by green squares (the blue squares are identical colors in the two checkerboards)—that is, in each case the blue has taken on the color of the surrounding squares.

Thus, in color contrast, the difference in color between surrounded and surrounding elements is perceptually accentuated, whereas in color assimilation, the difference is perceptually reduced. (Color assimilation is also known as the **spreading effect**, because the color of the surrounding elements seems to spread into the surrounded ones.) In the next section, we’ll discuss another way in which the perceived color of an object can depend on factors other than the light reflected by the object into our eyes.

**Color Constancy**

Suppose you’re looking at a piece of blue paper lying on a tabletop and illuminated by the light from a lamp with an incandescent bulb. Suddenly, the bulb burns out, and you replace it with a compact fluorescent bulb. Under both types of illumination, you perceive the paper as the same shade of blue, which is not surprising because this paper predominantly reflects shorter wavelengths. But the wavelengths entering your eyes don’t depend only on the spectral reflectance of the paper but also on the spectral power distribution (SPD) of the illuminating light—that is, the relative intensities of all the wavelengths present in the light. Figure 5.18 shows the SPD of incandescent light and fluorescent light and the reflectance of the blue paper.

**Figure 5.18** Illustration and Surface Reflectance Determine the Wavelengths in Reflected Light. Incandescent light consists of a larger proportion of longer wavelengths than does standard fluorescent light, while fluorescent light contains narrow, high-intensity bands of medium and short wavelengths that aren’t present in incandescent light. As a result, the spectral power distribution (SPD) of light reflected from blue paper is quite different under the two different illuminants. Yet the paper is perceived as having the same color under both illuminants—an example of color constancy. (The SPD of some newer fluorescent bulbs is more similar to that of incandescent light.)
As indicated in Figure 5.18, the amount of each wavelength reflected into your eyes by the paper—that is, the SPD of that reflected light—is determined by multiplying the relative intensity of the illuminating light at each wavelength by the reflectance of the paper at each wavelength. And as you can see, the SPD of the light reflected by the paper in incandescent light is quite different from the SPD of the light reflected by the paper in fluorescent light. Yet you perceive little if any difference in the color of the paper after you replace the bulb. Figure 5.19 provides a striking visual illustration of how large the differences in the SPD of reflected light can be and still result in perception of the same colors. This tendency to see a surface as having the same color under illumination by lights with very different SPDs—that is, to base our perception of the color of an object on the reflectance of the object and not on the SPD of the light reflected by the object—is called color constancy.

At first blush, color constancy may seem like a perceptual error, a failure to perceive sometimes dramatic differences in the light reflected by an object. Consider, however, the adaptive advantage of color constancy. Reflectance is an intrinsic property that typically does not change, whereas the SPD of the light reflected from an object changes whenever the illumination changes. Perception of color based on reflectance may make it easier to identify edible objects like ripe red fruit and dangerous objects like venomous green snakes despite differences in illumination under different lighting conditions.

How does the visual system achieve color constancy? One way is by comparing the wavelength distributions in the SPDs of the light reflected from the various surfaces in a scene to estimate the SPD of the illuminating light and, on that basis, the reflectance of each surface (Maloney & Wandell, 1986). Our ability to do this depends to a great extent on the presence of multiple surfaces with varied reflectances, which is usually the case in everyday scenes. When perception is tested with artificial stimuli that contain just a few different-colored patches, color constancy can break down, as was demonstrated in a study involving the stimuli shown in Figure 5.20, where a surface containing a test button or test patch (A) is under different illumination than a surface containing two comparison buttons or patches (B and C), and participants have to decide whether B or C is closer in color to A (Radonjić et al., 2015). In trials with the stimulus shown in Figure 5.20a, color constancy was achieved: button B (with the same reflectance as button A) was perceived as closer in color to A. In trials with the stimulus shown in Figure 5.20b, however, color constancy failed: patch B has the same reflectance as patch A, but patch C, which reflects light with the same SPD as the light reflected by patch A, was perceived as closer in color to patch A.

Estimation of illumination and reflectance is not a deliberate, conscious process, but something that goes on without our being aware of it, and exactly how the visual system

**FIGURE 5.19 Color Constancy** Despite the differences in the spectral power distribution (SPD) of the light reflected from these two images of a multicolored cube, we correctly perceive the component tiles as having the same colors in each cube (i.e., as having the same spectral reflectance). Consider, for example, the tiles in the top front row. In each image, the rightmost tile looks blue and the adjacent tile looks yellow, correctly corresponding to their reflectance. But in fact the SPD of the light reflected into your eyes from the top of the “blue” tile under long-wavelength illumination is the same as the SPD of the light reflected into your eyes from the top of the “yellow” tile under short-wavelength illumination, and a surface reflecting light with that SPD, if seen in isolation, would look gray (the gray of the patch at bottom).
does this is not fully understood, though various theories have been proposed (Foster, 2011). One is that the visual system automatically determines the amount of each wavelength reflected from all the surfaces on average and uses this as its estimate of the SPD of the illuminant. If the SPD of the illuminant is known, then it is possible to determine the reflectance of a surface simply by dividing the amount of light reflected by that surface at each wavelength by the amount of light present in the illuminant at that wavelength. This method for achieving color constancy is often called *discounting the illuminant*.

Another way the visual system tends to achieve color constancy is through chromatic adaptation, which we discussed earlier in relation to color afterimages. As we saw in that discussion, cones adapt to continuous, intense stimulation by a particular wavelength, so that their response to that wavelength becomes weaker. For example, if you were to look at a scene illuminated by bluish light with an SPD like that of the light on the right of Figure 5.19, your cones would adapt by responding more weakly to short wavelengths. By adjusting your cones to compensate for the imbalance of wavelengths in the illuminating light (e.g., by making the cones less sensitive to the shorter wavelengths in the bluish light emitted by, say, a fluorescent lightbulb), chromatic adaptation “compensates” for non-white illumination, which helps you make more accurate judgments about the actual color of surfaces. That is, your eyes’ response to the wavelength distribution of the reflected light will be somewhat more uniform across the spectrum because of its reduced sensitivity to short-wavelength light.

### Lightness Constancy

In color constancy, when we correctly perceive the color of a surface under different illuminants, we’re perceiving how the surface reflects different wavelengths differently. But what about a surface that reflects all wavelengths about equally—that is, a surface...
we perceive as a shade of gray? Will such a surface appear to be a lighter shade of gray when illuminated by a very intense light, like sunlight, and a darker shade of gray when illuminated by a very dim light, like candlelight? The answer is no—the lightness of a gray surface appears about the same regardless of the intensity of the illuminant (Adelson, 1993). Here **lightness** refers to the perceived reflectance of a surface—where reflectance is the proportion of the illumination that the surface reflects—as distinct from its brightness, the perceived amount of light it might be reflecting at any one moment. The tendency to see a surface as having the same lightness under illumination by very different amounts of light is called **lightness constancy**, and it serves much the same purpose as color constancy: it lets us perceive an intrinsic property of a surface—its reflectance—despite changes in lighting conditions. You can demonstrate this for yourself by noticing that the paper of a book page looks the same shade of gray (i.e., white) regardless of whether you’re outside in bright sunlight or indoors under much dimmer light.

Figure 5.21 (left) illustrates lightness constancy in the type of scenario just described. If squares A and B were on an actual checkerboard, they’d be physically identical—that is, they’d have the same reflectance. In the figure, square B is brightly illuminated, and square A is in shadow. This means that they differ in brightness: square A is reflecting much less light than square B, yet the two squares tend to be perceived as the same shade of gray. In Figure 5.21 (right), the vertical gray bar, which reflects the same amount of light as square A, reveals the difference in intensity of the light reflected by squares A and B. The bar also demonstrates a very striking illusion—squares A and C appear to be very different shades of gray, yet they reflect light with exactly the same intensity.

If the illumination across a scene is uniform, lightness constancy can be explained by what’s known as the **ratio principle**, which says that the perceived lightness of a region is based not on the absolute amount of light reflected from the region, but on the relative amounts reflected from the region and its surround (Wallach, 1948). For example, the ratio between the black ink on this page and the white background will be the same under both dim and bright illumination, so the ink is perceived as black and the background as white, regardless of the amount of light in the illuminant.

But in Figure 5.21, the illumination isn’t uniform across the scene, which means that the ratio principle can’t explain why squares A and B are perceived as the same shade of gray. To address this problem, it has been suggested that the ratio principle be supplemented with a two-part anchoring rule: (1) In any given scene, the region that reflects the most light is perceived as white (or as the lightest shade of gray in the scene), and the lightness of every other region is perceived in relation to that anchor point. (2) If the scene consists of regions under different amounts of illumination (as in Figure 5.21, where a region that includes square A is in shadow), the visual system applies the anchoring rule separately in each illumination zone (Gilchrist, 2006). Thus, in Figure 5.21, square A

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**FIGURE 5.21 Lightness Constancy** In the image on the left, the intensity of the light reflected from squares A and B is different, yet they appear to be the same shade of gray. In the image on the right, the gray bar is a uniform shade of gray; the fact that the bar blends in with square A and contrasts sharply with square B shows how large the difference is in the intensity of the light reflected by the two squares. The bar also blends in with square C, demonstrating a powerful illusion: squares A and C, which look very different, reflect light with the same physical intensity.

[Edward H. Adelson.]
reflects the most light in its region (the region in shadow) and square B reflects the most light in its region (not in shadow); therefore, each square is the anchor point for its region, and the two squares are perceived as being the same shade of light gray.

Figure 5.22 illustrates an experiment using an illusion of depth perception to demonstrate the anchoring rule (Gilchrist, 1977). In Figure 5.22a, the white paper target is correctly perceived as attached to the near wall and is perceived as white, like the paper attached to the far wall. But in Figure 5.22b, the notches cut out of the target create the illusory perception that the target is attached to the far wall, and the target is perceived as dark gray. Again, the anchoring rule can be applied to explain these perceptions. Under the reasonable assumption that the near wall and the far wall have the same reflectance, observers' visual system “understands” that the illumination across the scene isn’t uniform but consists of two regions, a dimly illuminated near room and a brightly illuminated far room. In Figure 5.22a, observers see that the target reflects the most light in its region and that the white paper attached to the far wall reflects the most light in its region, so observers perceive each as its region’s anchor point and perceive both as white. In Figure 5.22b, however, the target is perceived as being in the far room. The brightly illuminated white paper attached to the far wall reflects the most light in that region and is perceived as the anchor point, and in relation to that anchor point, the dimly illuminated target is perceived as dark gray.

**FIGURE 5.22** An Illusion of Depth Perception Shows How an Anchoring Rule Can Be Used to Explain Lightness Constancy. In both setups, the white paper target and the black paper are attached to the dimly illuminated near wall, a white paper (with the same white as the target) is attached to the brightly illuminated far wall, and an observer looking through the peephole perceives that the scene consists of two rooms under different illumination (here, the ceiling and left side wall of the rooms have been cut away so you can see the interiors of the rooms). (a) The target is correctly perceived as attached to the near wall. It reflects more light than anything else in its region of the scene and is perceived as the region’s anchor point. Similarly, the white paper attached to the far wall is perceived as its region’s anchor point. And the two regions’ anchor points are perceived as having the same lightness, white. (b) The notches cut out of the target create the illusion that it’s attached to the far wall. The brightly illuminated white paper attached to the far wall is perceived as that region’s anchor point, and the dimly illuminated target—which seems to be part of the same region—is perceived, in relation to the anchor, as dark gray. (Research from Gilchrist, 1977.)
CHECK YOUR UNDERSTANDING

5.12 What were three observations made by Hering that could not easily be accounted for by a trichromatic representation of color vision?

5.13 In hue-cancellation experiments, what does the person try to do? How do these experiments support opponent color representation?

5.14 What is the difference between a +S–ML neural circuit and a +ML–S neural circuit? Between a +L–M circuit and a +M–L circuit?

5.15 What is photopigment bleaching and how is it involved in color afterimages?

5.16 Match the phenomenon with the corresponding perception.

<table>
<thead>
<tr>
<th>PHENOMENON</th>
<th>PERCEPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>A Color contrast</td>
<td>1 Two yellow patches with the same reflectance look identical in color when one patch is illuminated by blue light and the other patch is illuminated by yellow light.</td>
</tr>
<tr>
<td>B Color assimilation</td>
<td>2 Two identical patches of yellow look different when one patch is surrounded by blue and the other patch is surrounded by a more saturated yellow.</td>
</tr>
<tr>
<td>C Color constancy</td>
<td>3 Two gray patches with the same reflectance look like identical shades of gray when one patch is illuminated by bright light and the other patch is illuminated by dim light.</td>
</tr>
<tr>
<td>D Lightness constancy</td>
<td>4 The yellow squares in two checkerboard patterns are identical, but they look different when one checkerboard consists of yellow squares and red squares, and the other consists of yellow squares and green squares.</td>
</tr>
</tbody>
</table>

5.17 In Figure 5.22b, why did the experimenter create the illusion that the target was attached to the far wall?

Color Vision Deficiencies

We've all heard of people who are “color-blind,” but this term is actually a little misleading. Most people who have color vision deficiencies are not entirely insensitive to differences in wavelengths of light—that is, they aren’t entirely unable to see different colors—which is what color-blind would literally mean. In this section, we'll describe the most common deficiencies of color vision, which are inherited, as well as noninherited deficiencies that can result from brain damage.

Inherited Deficiencies of Color Vision

Inherited deficiencies of color vision occur when a person is born without one or more of the three types of cones in the retina. In most cases, these conditions affect males much more frequently than females, because the lack of M-cones or L-cones (but not S-cones) is caused by a specific defect in a gene on the X chromosome (Neitz & Neitz, 2011); men have one X and one Y chromosome, while women have two X chromosomes, effectively giving them a "backup" for a genetic defect on one X chromosome. There are two broad categories of inherited color vision deficiencies—monochromacy and dichromacy.
monochromacy A condition in which a person has only rods or has only rods and one type of cone; in either case, the person is totally color-blind, perceiving everything in shades of gray.

rod monochromacy A condition in which a person has rods only, with no cones.

cone monochromacy A condition in which a person has rods and only one type of cone.

dichromacy A condition in which a person has only two types of cones, instead of the normal three; in all such cases, the person has a limited form of color vision but cannot discriminate as many colors as a person with all three cone types.

ishihara color vision test A test using configurations of multicolored disks with embedded symbols; the symbols can be seen by people with normal color vision but not by people with particular color vision deficiencies.

protanopia A condition in which a person has M-cones and S-cones but lacks L-cones.

deuteranopia A condition in which a person has L-cones and S-cones but lacks M-cones.

tritanopia A condition in which a person has L-cones and M-cones but lacks S-cones.

Monochromacy: Total Color Blindness

A person with monochromacy sees everything in shades of gray. There are two inherited conditions that result in monochromacy, and both are rare: rod monochromacy and cone monochromacy. In rod monochromacy, a condition that occurs in about 0.002% of the population (20 per million), the person has no cones at all and must rely on rod vision all the time. (All the percentages given in this section are from Sharpe et al., 1999.) As a result, rod monochromats are not only unable to perceive color, but are also hyper-sensitive to light—typically, so hypersensitive that they must wear very dark sunglasses during the day (Sharpe & Nordby, 1990; recall the vignette about Knut Nordby at the beginning of Chapter 2). If you think back to the discussion in Chapter 2 of the differences between rods and cones, you’ll understand why this is so. Rods are much more light sensitive than cones, so people with normal vision use their rods to see in dim light (e.g., for night vision) and their cones to see in bright light. If rod monochromats try to see in daylight without sunglasses, their rods are overwhelmed by the amount of light—the rod photopigment is fully bleached and therefore not able to respond to light.

In Chapter 2, we also noted that the densely packed cones in the fovea of people with normal vision support high visual acuity; rod monochromats, with no cones at all, have relatively low visual acuity, making reading and other tasks that demand high acuity difficult.

The other type of monochromacy—cone monochromacy—occurs even less frequently than rod monochromacy. Cone monochromats have both rods and cones, but only one type of cone, which can be either S-, M-, or L-cones. Like people with normal vision, they use their rods to see in dim light and their cones to see in bright light; but like rod monochromats, they entirely lack color vision. Different wavelengths appear to them as different shades of gray (see the prior section “If You Had Only One Type of Cone”).

Dichromacy: Partial Color Blindness

More common, but still rare overall, are the three types of dichromacy, in which just one of the three types of cones is missing. As we saw in the section “If You Had Only Two Types of Cones,” people with two types of cones can discriminate between colors that a rod monochromat would see as equivalent, but they would confuse some colors that a trichromat could tell apart. The Ishihara color vision test can be used to determine whether someone has a type of dichromacy or other color vision deficiency (the top row of Figure 5.23 shows two of the many Ishihara test circles). The three types of dichromacy and their frequency of occurrence are as follows:

- Protanopia—the person lacks L-cones; affects about 1% of males and 0.02% of females.
- Deuteranopia—the person lacks M-cones; affects about 1% of males and 0.01% of females.
- Tritanopia—the person lacks S-cones; affects about 0.002% of males and females.

Most people with only two types of cones manage quite well; indeed, many dichromats are unaware of their condition. The differences between the subjective perceptual experiences of dichromats and trichromats are difficult to describe. To see why, imagine that you had four types of cones rather than three. You would look at a metameric color match produced by someone with normal trichromatic vision, and you would see the test patch and the comparison patch as different in color. In other words, you would be able to see more colors than a trichromat. But how could you describe what those colors look like? And how would you describe the experience of red to a monochromat without using color words to do so? Figure 5.24 shows a scene as it would look to a person with normal color vision (left) and how it would appear to a person with deuteranopia (right). If these two images look very similar to you, you might have some form of deuteranopia.
FIGURE 5.23 Ishihara Color Vision Test. The full form of the Ishihara color vision test consists of two dozen or more color plates like the two in the top row, in which the person being tested tries to detect a number. In the case of these two plates, people with normal color vision will see an "8" in the top-left plate and a "42" in the top-right plate; a person with a color vision deficiency may see a different number (or no number) in one or both of the plates. For example, if you see a "3" in the top-left plate, you may have some form of protanopia (missing L-cones), since the component circles that distinguish a "3" from an "8" are reddish colored, and L-cones are particularly sensitive to long-wavelength (reddish) light (the bottom-left plate shows what the top-left plate might look like to someone with protanopia). If you can’t see a "42" in the top-right plate, you may have some form of either protanopia or deuteranopia (missing M-cones). Typically, deuteranopes see only a "4" (as illustrated by the bottom-right plate), whereas protanopes see only a "2"—the components of the "4" reflect longer wavelengths than the components of the "2."

FIGURE 5.24 Color Perception With Deuteranopia. Individuals with deuteranopia are missing M-cones and have difficulty distinguishing red from green. They would perceive these two images as being very similar. [Richard Abrams]
Cortical Achromatopsia: Color Blindness from Brain Damage

Loss of color vision caused by injury to parts of the brain that are critical for representing color is called **achromatopsia**, and it occurs even less frequently than the inherited deficiencies discussed above. The vignette at the beginning of this chapter describes the case of P., whose injury included area V4, a part of the brain that is more active when people view color images than when they view black-and-white versions of the same images. As illustrated in Figure 5.25, researchers used fMRI to compare activity in the brains of people looking at multicolored patches to activity when they were looking at equally bright grayscale patches under otherwise identical conditions (Wade et al., 2008). Activity in several regions of the temporal and occipital lobes, including area V4, was greater when participants were looking at color patches, leading to the conclusion that these areas contribute to the perception of color. As discussed in Chapter 3, these areas are part of the ventral visual pathway—the “what” pathway—which represents information about the identity of objects, and color is certainly an important dimension of object identity.

**CHECK YOUR UNDERSTANDING**

5.18 What are the two main kinds of monochromacy? How do they differ?
5.19 Describe the three types of dichromacy.
5.20 Both the rod monochromacy of Knut Nordby and the cortical achromatopsia of P., resulted in total color blindness. What is the difference in the way their conditions originated?
APPLICATIONS: Color in Art and Technology

The use of natural pigments to reproduce the colors of objects began more than 30,000 years ago with the depiction of animals and humans in paintings on the walls of caves such as Chauvet and Lascaux in France. In more recent times, synthetic pigments have been developed to expand the range of colors in the paints and dyes used in fine art, mosaics, and tapestries, as well as in an enormous variety of manufactured goods. And the last few decades have seen the development of rapid and convenient methods for reproducing a wide range of colors in photographs taken using film, in printed materials, and in all forms of digital imaging.

Typically, artists mix paints and apply the mixtures to a canvas or other surface, and as we saw earlier in the chapter, these are subtractive color mixtures. In this section, we’ll see how artists have also used paint to produce a kind of additive color mixtures, and we’ll describe how color is produced by digital video displays using additive mixtures and by color printers using subtractive mixtures.

Pointillist Painting

In the late nineteenth century, pointillist artists such as Paul Signac and Georges Seurat began to experiment in their paintings with additive color mixtures. Rather than mixing pigments on a palette in correct proportion to create a desired paint color, these painters tried applying tiny flicks and dots of various colors close together on the canvas. The flicks and dots were supposed to blend together visually—if the viewer was standing far enough away—so that the light reflected from them would mix additively and the viewer would perceive the color represented by the mixture. For instance, an area on the canvas with an equal proportion of red dots and blue dots would be perceived as a rich purple. Figure 5.26 shows a painting by Seurat and a blowup of one part of the painting so you can clearly see the different colored flicks and dots.

One of the objectives in adopting this technique was to avoid the dimming effect of subtractive color mixtures, which are always less intense than the constituent pigments because of the subtraction of wavelengths (see Figure 5.5). In pointillist paintings, however, the brushstrokes don’t really disappear—that is, from a comfortable viewing distance of two to three meters, the individual flicks and dots are clearly visible across most of the painting. The visual effect isn’t true additive mixing but nevertheless results in a striking luminosity of a kind not previously achieved in painting.

**FIGURE 5.26** Pointillist Painting  George Seurat’s *A Sunday Afternoon on the Island of the Grande Jatte* (1884/86) is an example of pointillism—building up objects and surfaces from thousands of tiny dots and flicks (points) of color. The magnification on the right shows a detail of the painting, which clearly reveals the dots and flicks. [Seurat, Georges Pierre (1859–91), *Sunday Afternoon on the Island of La Grande Jatte*, 1884–86 (oil on canvas)/The Art Institute of Chicago, IL, USA/ Bridgeman Images]
Digital Color Video Displays

Digital color video displays such as digital television and computer screens use additive mixtures of three primary colors at each location on the screen to produce nearly the full gamut of colors you can see. They do this by taking advantage of the limited ability of the human eye to distinguish dots that are sufficiently small and close together (Wandell & Silverstein, 2003)—in a sense, these displays accomplish what the pointillist artists were trying to do.

The display screen of a digital color monitor consists of a large number of pixels (picture elements) arranged in a grid (see Figure 5.27a). For example, a display with a standard resolution of $1,024 \times 768$ is a grid 1,024 pixels wide by 768 pixels high, so that the display consists of a total of $1,024 \times 768 = 786,432$ pixels. As illustrated in Figure 5.27a, each pixel contains three subelements, which each emit light of a different primary color—red, green, or blue. As indicated in Figure 5.27b, the intensity of the light from each subelement can have any of 256 possible values (0–255). Each different combination of intensities from a pixel produces a different additive color mixture. Thus, the number of different colors that can be produced by each pixel is $256^3 = 256 \times 256 \times 256 = 16,777,216$. This is certainly greater than the number of colors we can actually distinguish as different.

At normal viewing distances, the pixels and their subelements cannot be seen individually by the human eye, and so the light from clusters of pixels blends together into

**FIGURE 5.27** How a Computer Screen Creates Colors (a) The screen of a color monitor is a grid of pixels (picture elements). Each pixel consists of three subelements, each of which emits (nearly) monochromatic light of one primary color—red, green, or blue. The pixels are too small to be seen individually, so we perceive additive mixtures of the light emitted from them. (b) The intensity of the light emitted by each subelement can have any of 256 possible values, from 0 (no light) to 255 (maximum amount of light). (c) With every possible combination of light intensities from the three subelements, each pixel can produce $256^3 = 16,777,216$ different colors, four of which are shown here. (d) Many computer graphics programs allow you to adjust color by specifying the intensity of each subelement individually. This Microsoft PowerPoint “Colors” dialog box shows the red-green-blue specifications for the lavender color illustrated in panel (c).
additive color mixtures. If our visual systems were acute enough to see the individual sub-elements, current color monitors would not work—that is, we’d see an array of red, green, and blue patches instead of additive color mixtures.

**Digital Color Printing**

Digital color printing is achieved by applying tiny droplets of different color inks to a material such as paper. In order to produce the desired patterns of color, the droplets must be applied precisely in the right locations and in layers with the right thickness (Wandell & Silverstein, 2003). Four ink colors are used: cyan, magenta, yellow, and black. As shown by the reflectance curves in Figure 5.28, the cyan ink mainly absorbs yellow and red light and mainly reflects blue and green; magenta ink mainly absorbs green and reflects blue and red; yellow ink absorbs blue and reflects green and red; and black ink absorbs all colors about equally. The thickness of the ink layer at each location determines how much of the light that ink absorbs: the thicker the layer, the more likely the ink is to absorb a photon of light in its absorption region.

When different inks are applied in layers one on top of the other, their subtractive effects combine. Suppose, for example, that a location is occupied by a thick cyan layer on top of a thin yellow layer. If a photon of red light strikes that location, it’s not likely to be absorbed by the yellow layer, because yellow mainly reflects red, but it’s especially likely to be absorbed by the thick cyan layer, because cyan mainly absorbs red and because the layer is thick; in contrast, a photon of green light will probably be reflected, because both cyan and yellow mainly reflect green. Given the known reflectance curves of the inks and the known ways in which the thickness of the ink layers affects the probability that light of a given color will be absorbed or reflected, precise control of the placement and thickness of the ink droplets allows the printing of any desired color image.

If you’re wondering why black ink is also used, given that shades of gray (including black) could be produced by thick overlapping layers of the other three inks to absorb light across the spectrum, the reason is economic: to avoid wasting ink. That is, it takes much less black ink to produce any desired shade of gray than it would take to combine the other three ink colors for the same effect.

**Figure 5.28** Reflectances of Inks Used in Digital Color Printing. Four different inks are used in digital color printing: yellow, magenta, cyan, and black. Their reflectance curves show that each of the nonblack inks absorbs light in one of the three regions of the visible spectrum and reflects light in the other two regions: cyan absorbs long-wavelength red light, magenta absorbs medium-wavelength green light, and yellow absorbs short-wavelength blue light. Black absorbs all wavelengths about equally. (Data from Wandell & Silverstein, 2003.)
5.21 Why did pointillist painters often avoid letting the dots and flicks of different-colored paint overlap and mix together?

5.22 If you looked at a digital video display through a magnifying glass powerful enough to let you see the individual subelements in the pixels, what color light would you see being emitted by each subelement? Would these colors necessarily look equally bright?

5.23 Suppose a digital color printer is malfunctioning so that it applies yellow ink in thicker layers than it should. How would that affect the perceived color at a location where a layer of yellow ink overlies a layer of cyan ink?

SUMMARY

- **Light and Color** The intensity of light at each wavelength is called the light's spectral power distribution. Light can be heterochromatic, monochromatic, or achromatic (also called white light). The percentage of light reflected by a surface at each wavelength is called the reflectance of the surface.

- **Dimensions of Color: Hue, Saturation, and Brightness** The perception of color can be described by three dimensions: hue, saturation, and brightness. A color circle depicts the two dimensions of hue and saturation; a color solid also depicts brightness. The color of a mixture of substances (e.g., paints) is called a subtractive color mixture because the light reflected from the mixture lacks all the wavelengths that are absorbed (subtracted) by any of the substances in the mixture. The color of a mixture of lights is called an additive color mixture because the mixture contains the sum of all the wavelengths that were present in the constituent lights. Pairs of colors that combine in equal proportion to yield a shade of gray are called complementary colors. Any three colors that can be combined in different proportions to yield a range of other colors are called primary colors.

- **Color and the Visual System** Two color representations work together in two stages to produce color perception. The first stage, trichromatic representation, involves three types of cones providing information about the wavelength composition of light. Metameric color-matching experiments provide psychophysical evidence that there are three types of cones. Physiological evidence for three types of cones comes from high-resolution images of the retina and from measuring how individual cones absorb different wavelengths of light. The second stage, opponent color representation, accounts for the fact that people tend to sort colors into four categories (red, green, yellow, and blue) and that these four basic colors consist of two pairs of “opposites,” red–green and yellow–blue. Hue-cancellation experiments provide psychophysical evidence for opponency. Physiological evidence for opponency comes from the identification of single neurons that respond to signals from the three cone types in an opponent fashion.

- **Color Vision Deficiencies** Color vision deficiencies can be inherited or can result from brain damage. Inherited deficiencies include monochromacies and dichromacies. Rod monochromacy and cone monochromacy result in total color blindness—everything is seen in shades of gray. In dichromacies, the person lacks just one of the three types of cones and has a limited form of color vision. Noninherited deficiencies can result from damage to parts of the brain involved in color vision, a condition known as cortical achromatopsia. Measurements of brain activity have identified area V4 as a region of the brain that may be important in color vision.

- **Applications: Color in Art and Technology** Pointillist artists applied tiny flicks and dots of paint close together on the canvas to create additive color mixtures. Digital color video displays create additive color mixtures via a grid of tiny pixels, each of which consists of three subelements, each emitting red, blue, or green light at any of 256 possible intensities. Digital color printers produce subtractive color mixtures by applying tiny droplets of cyan, magenta, yellow, and black ink in precisely droplets on the canvas to create additive color mixtures. Digital color printers produce subtractive color mixtures by applying tiny droplets of cyan, magenta, yellow, and black ink in precisely controlled locations and in layers with precisely controlled thickness.

