Color Perception Mechanisms

CHAPTER 10

10.1 INTRODUCTION

Color phenomena, such as we studied in the last chapter, do not result from the properties of light alone. They depend intimately on the way your photoreceptors respond to light and the way in which your visual system processes the signals from those receptors. As the philosopher Arthur Schopenhauer wrote in 1816:

Colors, their reciprocal relations and the uniformity of their appearance, all reside in the eye itself, and are nothing else than specific modifications of the activity of the retina. External causes act only as stimuli, to cause this activity.

To a certain extent, your visual system acts as a wavelength detector; if you look at monochromatic 575-nm light, you will identify it as yellow and easily distinguish it from 600-nm light, which you'll recognize as orange. That is, as long as the light is confined to points along the horseshoe curve of the chromaticity diagram, color phenomena are wavelength phenomena. But the fact that the curve is horseshoe shaped, and that the area inside the curve represents actual color phenomena, is a result of the processing within your visual system. What enters the eye is always just a collection of light waves of different wavelengths and intensities. Yet rather than seeing a mixture of 575-nm light and 474-nm light as yellow and blue, you see it as white, a color not in the spectrum. A mixture of 410-nm and 690-nm light appears as a new saturated color, also not in the spectrum—purple. A broad-band stimulus of long-wavelength light appears yellow, much like the monochromatic 575-nm light. These effects, indeed the whole of the region inside the horseshoe, as well as your ability to distinguish monochromatic lights, can be understood if your color perception mechanisms are understood.

But there are more color phenomena than those described by the chromaticity diagram. You seldom experience individual isolated colored regions. Look at the colors around you now—more than likely, each colored region is surrounded by others of different sizes, colors, and proximity. Such spatial attributes of a colored pattern affect your perception of the color of each component region. It is your visual system's *spatial* processing of color that accounts for this—closely analogous to the spatial processing of lightness discussed in Chapter 7. Our knowledge of lateral inhibition will stand us in good stead here. Similarly, the principles of receptive fields and channels are also quite general and will find applicability, here more colorfully than before.

10.2 TRICHROMACY OF COLOR VISION

The first step in your perception of color is the response of your rods and cones to the incident light. We've mentioned that these cells contain photochemicals (pigments) that resonate (recall Fig. 1.12). A plot of the response of rhodopsin, the rods' photochemical, to light of different frequencies is shown in Figure 10.1.

Suppose you had only one system of receptors, each having the same photochemical (for instance the one shown in Fig. 10.1). A large amount of light at one wavelength, λ_1, could then produce the same response as a small amount at λ_2. As your brain can be aware only of the *response* of the photoreceptor, it would not be able to distinguish between the lights of two different wavelengths.

Scotopic vision (Sec. 5.3D) relies on the rods alone. Because there is only one type of rod, you cannot distinguish colors in dim light. Hence under scotopic conditions, the world appears black, white, and gray—not colored (see the TRY IT).

Under bright light (photopic conditions), when only the cones are operating, you *can* distinguish colors. Therefore, there must be more than one type of cone. How many are required—two, three, a million? The insight of the physicist Thomas Young led him in 1801 to postulate *three* types of receptors. Young made his hypothesis of ***trichromacy*** based on the fact that there are three independent attributes to color: hue, saturation, and lightness. He knew that any system (including the visual system) could have three independent *output* signals only if it has at least three independent *input* signals. He guessed that these input signals arose from three different types of cone.

Later, Hermann von Helmholtz promoted Young's theory by drawing three hypothetical response curves, representing the response of Young's proposed receptors (Fig.

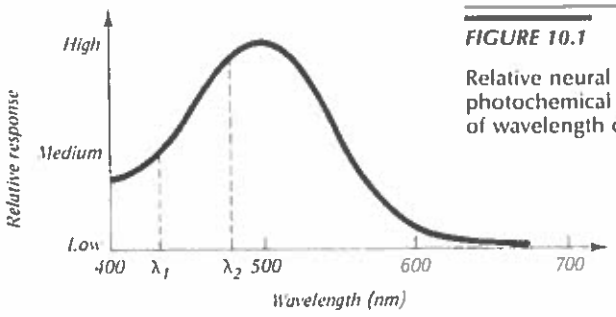


FIGURE 10.1

Relative neural response of the rod photochemical rhodopsin, as a function of wavelength of the stimulating light.

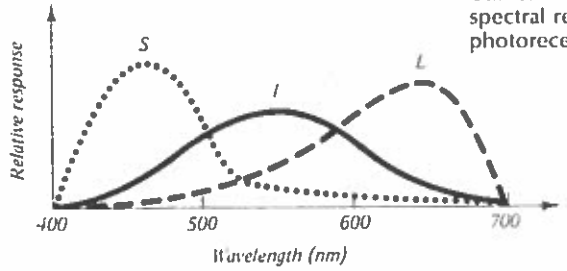


FIGURE 10.2

Curves based on Helmholtz's hypothetical spectral response curves of human photoreceptors.

10.2). Each curve has the general shape of a resonance curve, the difference between them being their resonant frequencies. One curve describes a receptor with best response to *short*-wavelength light (we'll call cones having this response S cones), one corresponds to *intermediate* wavelengths *(I)*, and one to *long* wavelengths *(L)*.

Spectral light (indeed *any* visible light) can excite all three receptor types, and so there are *three* signals associated with each color seen. For example, a spectral light of short wavelength will excite *S* cones most, *I* cones somewhat, and *L* cones least, as can be seen from the curves of Figure 10.2. This triplet of cone signals is (somehow) interpreted by the brain as "blue." No other spectral light can produce this relationship of all three cone responses, and thus no other spectral light looks like the blue we've chosen as an example. The same holds true for every *spectral* light; each causes a unique set of three cone responses.

Because the cone signals depend on the shape of these absorption curves, it is important that we determine the shape as closely as possible. What evidence will help us do that? Well, the evidence is plentiful but often indirect. Like Sherlock Holmes, we can piece it together, hoping that the pieces will fall into place and give a consistent picture of what the response curves are.

A. Overlap of response curves

The first deduction we can make is that the curves must *overlap* throughout the region of visible wavelengths (or equivalently, frequencies). One reason is that resonance curves are generally broad and cover a range of frequencies, as we saw for paints and pigments in the last chapter. Second, if there were a region of the spectrum where cones of only one type responded, you would be unable to discriminate colors based on wavelength alone, for the reasons we saw above. But you know that spectral light of each wavelength appears different from that of other wavelengths, so at least two cone response curves must overlap at any wavelength of visible light.

B. Spectral complementaries

Recall that all wavelengths contribute equally to broad-band white light. Such light will excite all three cone types approximately equally because there is short-, intermediate-, and long-wavelength light present. But we saw that an additive mixture of two complementary spectral lights can also yield the sensation of white. Thus the two complementary lights must produce equal photoreceptor responses, the same as broad-band white.

We can use this idea and the fact that the complements of green spectral lights are the nonspectral purples to determine where the S and *I* curves cross, and also where the *I* and *L* curves cross. Green spectral light has intermediate wavelength. Such light, with wavelength between the two crossover points, excites the *I* system most. Its complement has to excite *both* the S and the *L* system more than the *I* system to make the final excitations equal in all three systems. But *no* single wavelength light can do that! (Why?) Thus, the limits of the wavelength region with purple complements, that is, without monochromatic complements, must correspond to the two crossover points. These limits occur at about 490 nm and 565 nm (Fig. 9.9). Similarly you can argue that any spectral light having wavelength less than the *S* and *I* crossover point must have its spectral complement at a wavelength greater than the *I* and *L* crossover point, and vice versa. (These arguments hold rigorously if the curves of Fig. 10.2 are adjusted to have equal areas under each of them, ensuring that they have equal responses to broad-band white.) The revised curves of Figure 10.3 were drawn to incorporate the crossover points from the spectral complements.

The spectral complementary clue for people having one type of color deficiency ("color blindness," Sec. 10.5) also helps determine the crossover points. Color-deficient people who have only two of the three cone types can match white light with two spectral lights throughout the spectrum; there is no "gap" in their curves of spectral complementaries. Indeed, for these people, a certain *single* wavelength

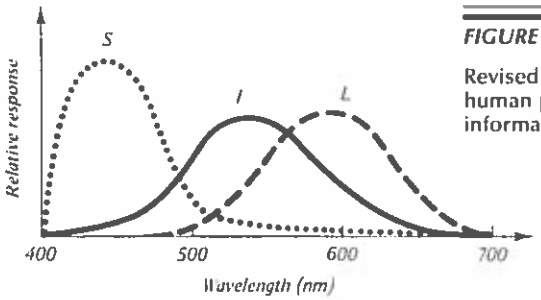


FIGURE 10.3

Revised spectral response curves of human photoreceptors, incorporating information about crossover points.

light (called a ***neutral point***) appears achromatic (gray or white). Since this wavelength excites the two cones equally, just as broadband white light does, it must be at the crossover point of their two cone response curves. For instance, those color-deficient people that have only *S* and *I* cones see broadband white and 495-nm light as identical. Thus the crossover point for their *S* and *I* cones occurs there, at about the same place as the prediction based on the spectral complementary data from normal observers.

C. Hue discrimination

Suppose you are looking at two spots of spectral light that differ only in wavelength. If the wavelength difference is not too small, you are pretty good at detecting the difference in hues. But if the wavelength difference is sufficiently small, you will not be able to distinguish the two hues. The *difference in wavelength* that is *just noticeable*, $\Delta\lambda$, is a measure of your ability to discriminate hues. This just noticeable difference depends on the wavelength you start with, λ; you may be able to distinguish two yellows with wavelengths only one nanometer apart, but two reds may have to differ by three nanometers to appear different. Figure 10.4a shows the results of such ***hue discrimination*** measurements. The dips in the curve at about 430 nm, 490 nm, 590 nm, and 640 nm show that as the light's wavelength gets close to these values, your hue discrimination improves. This implies that near these wavelengths the cone response curves must be steep, so that a small change in wavelength will result in a large (and thus noticeable) change in the cone responses. We've again revised the cone response curves (Fig. 10.4b) to take these hue discrimination results into account. Hue discrimination results for color deficients who have only two cone types also support the shape of the curves shown in Figure 10.4b.

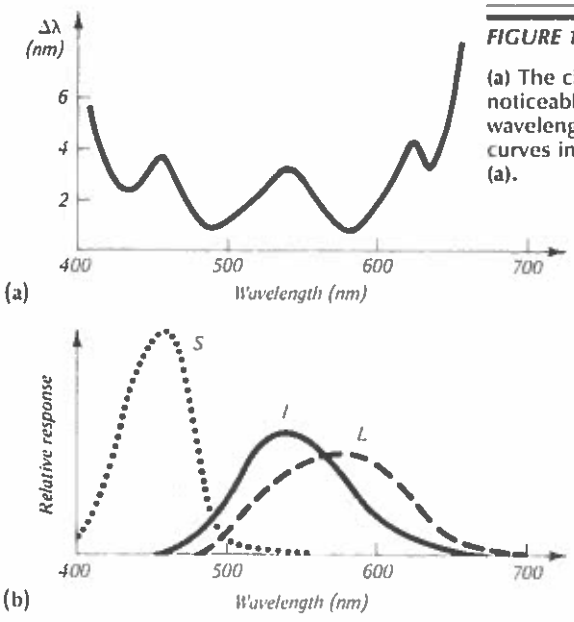


FIGURE 10.4

(a) The change in wavelength that is just noticeable, $\Delta\lambda$, plotted against the initial wavelength λ. (b) Revised cone response curves incorporating information from (a).

D. Microspectrophotometry

We can also get a clue from ***microspectrophotometry,**** that is, the physical measurement of the amount of light of each wavelength absorbed by each cone type. (This assumes that the signal produced by a cone is directly related to the amount of light absorbed by its pigment.) The absorption due to a single cone can be determined, one wavelength at a time, by carefully measuring the amount of light passing through it. Since there is also absorption in the part of the retina that supports the cone, this is separately measured (at a point between cones) and subtracted. For instance, if the cone and its supporting retina passed considerably less of the short wavelength light than the supporting retina alone did, the cone must have absorbed a lot of that short wavelength light.

Although many cones were measured in this way, only *three* types of absorption spectra were observed. This satisfied anyone who was still doubting Thomas; Thomas Young was correct about the number of types of cones. Further, the shapes of the curves agree very well with evidence from overlap, complements, and hue discrimination. The clues to our "mystery" fall into place! We have the cone responses (Fig. 10.5).

*Greek *mikros*, small, *phos*, light, *metria*, measure, plus Latin, *spectrum*.

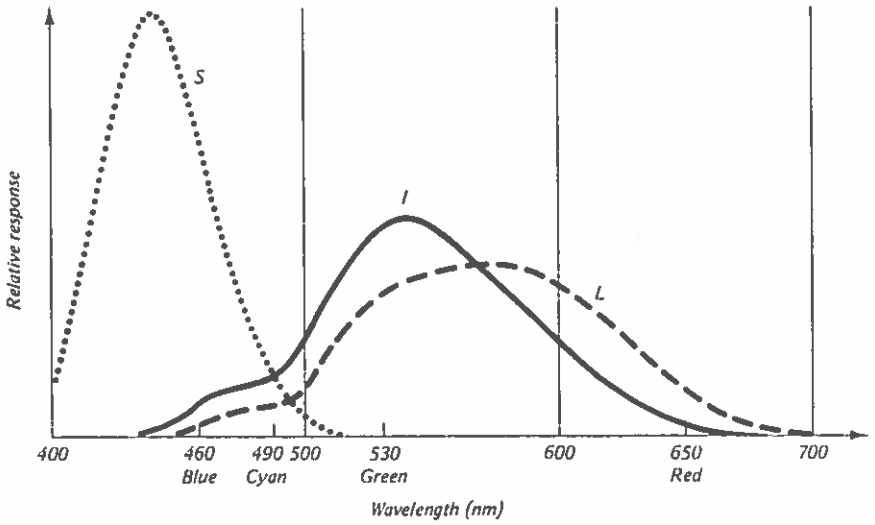


FIGURE 10.5

Spectral absorption of light by the three cone types, determined by microspectrophotometry. (We have modified these curves by including the short-wavelength absorption of the eyelens and macula, in order to make them comparable to the three previous figures.)

It is even possible now, by a new staining technique, to see the different cone types in the retina (Plate 10.1).

TRY IT

FOR SECTION 10.2
Scotopic vision and color

It's easy to demonstrate that you cannot distinguish hues under scotopic conditions. Have a friend arrange pieces of colored paper or unfamiliar colorful objects on a table and darken the room, while you sit with your eyes closed for about seven minutes. When you open your eyes, you will be properly dark adapted for the scotopic lighting conditions. You will not have previously seen the objects and so you cannot use past knowledge and memory to judge their hues. Notice that you cannot properly judge the hues of the papers and objects.

Because the peripheral parts of your retina contain chiefly rods, the TRY IT for Section 5.3D is closely related to this one.

10.3 COLOR MIXING AND MATCHING

The law of proportion according to which the several colors are formed, even if a man knew he would be foolish in telling, for he could not give any necessary reason, nor any tolerable or probable explanation of them.

Plato, "Timaeus"

In Section 9.4B we saw how different mixtures of lights could be metamers, that is, could appear identical to your eye although they might be of rather different spectral composition. One "tolerable and probable" explanation for this fact is that such mixtures produce identical triplets of cone signals. Now that we have the cone response curves (Fig. 10.5), we want to understand how they produce the color matching results.

For instance, suppose you want to match a 490-nm spectral cyan light, using as "primaries" 460-nm (blue), 530-nm (green), and 650-nm (red) lights. We saw in Section 9.4C that such a match can be made if you use a small negative amount of the red primary. What response does the cyan produce? From Figure 10.5 we see that it excites the *S* and *I* cones about equally, and the *L* cones about half as much. Now consider the response to the blue and green primaries. Again using Figure 10.5 we see that the blue excites the *S* cones a lot. We must therefore use enough green to excite the *I* cones the same amount. When we do that, the *L* cones will have a bit too much excitation. We can compensate for this by using a small *negative* amount of red, thus *decreasing* mainly the *L* cone response. Because the cone stimulation is then the same, the mixture looks like cyan—the match is verified:

460 nm (blue) + 530 nm (green)
− a little 650 nm (red)
≡ 490 nm (cyan)

This matching information is contained in Figure 9.10. You can similarly verify that other results in that figure agree with the cone response analysis.

PONDER

Verify this for matching a 630-nm light using these three primaries.

Thus, by considering the cone responses we can understand the matching of *spectral* colors. But what about the colors *inside* the horseshoe of the chromaticity diagram, for example, an additive mixture of 415-nm violet and 515-nm green? An equal mixture excites the *S* and *I* cones about equally, and the *L* cones slightly less. So the mixture appears like spectral cyan (*S* and *I* cones excited equally, and *L* cones about half as much) with some red mixed in (excess excitation of the *L* cones)—an unsaturated cyan, in agreement with the chromaticity diagram (Fig. 10.6).

PONDER

Verify from the cone response curves (Fig. 10.5) that 415-nm and 565-nm lights are complementary.

In sum, the information contained in the chromaticity diagram, both on and within the horseshoe, is consistent with that of the response curves of the three human cone types.

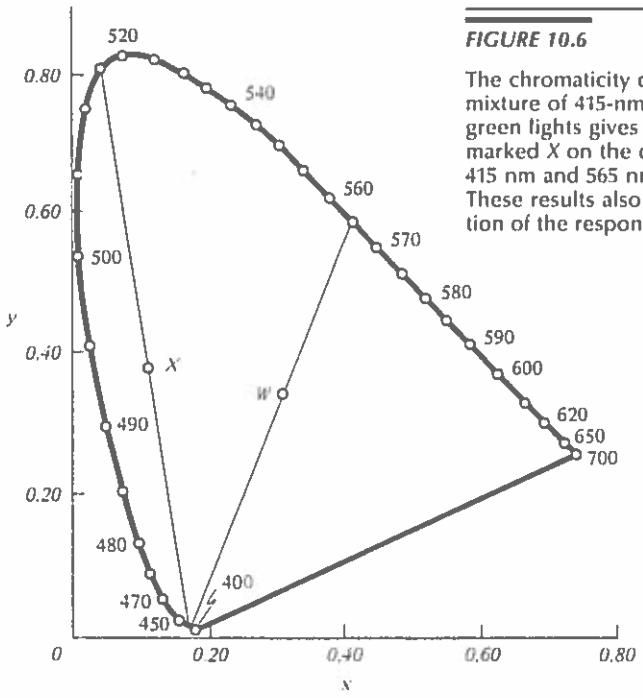


FIGURE 10.6

The chromaticity diagram shows that a mixture of 415-nm violet and 515-nm green lights gives an unsaturated cyan, marked *X* on the diagram. A mixture of 415 nm and 565 nm gives white, *W*. These results also follow from consideration of the response curves of Figure 10.5.

PONDER

What differences are there between complementary colors for bees and for humans? (Draw a bee line in Fig. 10.8 to determine a bee's spectral complementary to 480 nm. Compare your result with the complement of 480 nm obtained from the human chromaticity diagram of Fig. 10.6.)

10.4 OPPONENT PROCESSING

Most of the color phenomena we've been discussing up to now—such as detection, discrimination, matching—can be explained in terms of the response of the three cone types. But we have yet to understand the *appearances* of color mixtures. For example, an additive mixture of red and green does not appear reddish green, but instead yellow. A similar surprise is a subtractive mixture of cyan and yellow, which gives green, not a yellowish cyan. We must have a different set of primaries, other than the additive or subtractive primaries, in order to tell each other what colors *look like*. For this purpose, in fact,

Similar consistency is found in honey bees, which are trichromatic, but with their visible wavelengths ranging from ultraviolet to orange. Bees can be trained to respond whenever they experience a difference between two colors presented. In this way, color matching results have been obtained for the honey bee. These results agree quite well with the bee photoreceptor response curves obtained by recording nerve pulses from the bee's cones directly (Fig. 10.7). The bee chromaticity diagram (Fig. 10.8) shows the curve corresponding to the spectral colors to which the bee is sensitive, as well as the point we call "bee white"—broad-band light extending from 300 nm to 600 nm.

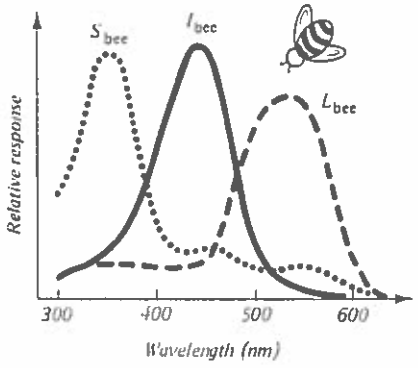


FIGURE 10.7

Spectral response curves of the three types of photoreceptor in the honeybee, as determined by directly measuring the neural response produced when light of various wavelengths is shined on the bee eye. The curves are somewhat idealized.

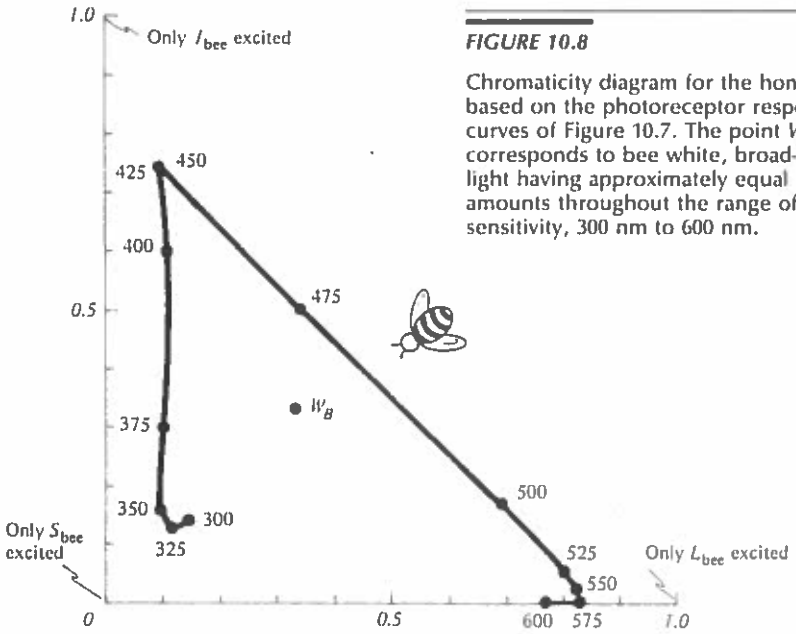


FIGURE 10.8

Chromaticity diagram for the honeybee, based on the photoreceptor response curves of Figure 10.7. The point W_B corresponds to bee white, broad-band light having approximately equal amounts throughout the range of bee's sensitivity, 300 nm to 600 nm.

you need *four* ***psychological primaries:*** *blue, green, yellow, and red.* All hues can be *verbally described* as combinations of these (e.g., orange looks yellowish red, cyan look bluish green, purple looks reddish blue, etc.). How can your brain process the output of the *three* cone types to obtain the psychological description in terms of *four* primaries?

To understand the appearance of colors, we must understand the neural signals that get to the brain. Conversely, to determine what signals get to the brain, we can study the appearance of colors. Only the last 30 to 40 years have brought the reconciliation of the trichromatic theory of Young and Helmholtz (for which we have already seen considerable evidence) with the apparently competing ***opponent colors*** theory of Ewald Hering.

A. Color naming

What's in a name?

One of the simplest approaches for studying the appearance of colors is to ask an observer to *name* the color of a spot of spectral light by rating its similarity to each of the four psychological primaries on a scale from 0 to 10. Figure 10.9 shows typical results for a normal color observer.

Note that there are some spectral ***unique hues*** that are described by just *one* psychological primary: blue (475 nm), green (500 nm) and yellow (580 nm). For example, unique yellow is what most people would call a pure yellow, without any red, green, or blue mixed in. But there is no spectral unique red—even at the longest wavelengths, the light appears slightly yellowish.

The most important point, however, is that you never experience a "reddish green" nor a "yellowish blue," though all other combinations of the psychological primaries are experienced. That is, there seems to be some opposition between yellow and blue, and between red and green—they are ***opponents.*** This opponency within these pairs extends to their presence in nonspectral colors; there is *no* color that simultaneously appears red and green, or simultaneously yellow and blue. You can't even imagine such a color!

B. Hue cancellation

The amount of subjective ***chromatic response*** for each spectral light can be determined more quantitatively by the technique of ***hue cancellation.*** To find the blue chromatic response for a certain wavelength light, say 430 nm (a deep blue), you add enough unique yellow to it so a color results that appears neither bluish nor yellowish. You find that the intensity of the 580-nm unique yellow must be *large* in order to cancel the blue in this light, so this blue is said to produce a *large* blue chromatic response. On the other hand, 490-nm light (which appears only *slightly* blue) requires only a *small* amount of the 580-nm yellow to cancel the blue there. The results of such hue cancellation are shown in Figure 10.10.

You're familiar with this type of cancellation technique, used in a simple balance (like that held by the statue of Justice). To find the

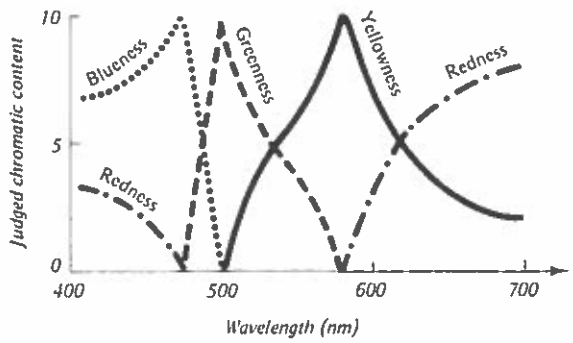
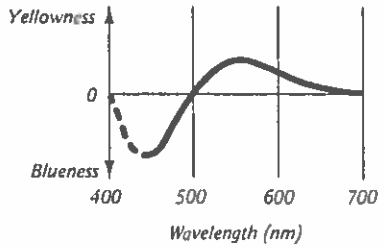
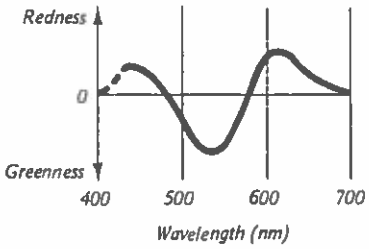


FIGURE 10.9

Typical color naming results for spectral lights. Subjects rated the apparent content of the four psychological primaries in each spectral light. For example, a 650-nm light appears primarily reddish and somewhat yellowish, but neither greenish nor bluish.



(a)



(b)

FIGURE 10.10

(a) Yellow versus blue (**y − b**) and **(b)** red versus green (**r − g**) chromatic responses for spectral lights determined using the hue cancellation technique. The two curves were separately determined. The values of the yellow chromatic response (plotted above the axis) are related to the amount of unique blue (475 nm) needed to cancel the yellow in all those wavelengths perceived as having yellow (above 500 nm). The blue chromatic response (plotted below the axis, to emphasize its opponency to yellow) is related to the amount of unique yellow (580 nm) needed to cancel the blue in all wavelengths perceived as having blue (below 500 nm). Likewise, the red and green responses are plotted above and below the axis. The red response was canceled using unique green (500 nm). A 700-nm light was used to cancel the green chromatic response. (The green chromatic response curve does not depend significantly on the choice of "red" wavelength used for cancellation.)

weight on one pan, you add a known weight on the other until the scale is level. Similarly in hue cancellation, to find how much blue is in a certain spectral light, you add yellow until the blue is canceled. Of course, it is as if there are *two* pan balances in the visual system; after one opponent pair has been balanced by this technique, the other pair may not be balanced.

PONDER

What hue name(s), chosen from the four psychological primaries, would describe the resulting color after you canceled the blue in the 430-nm light?

You can use Figure 10.10 to describe the appearance of colors. Thus, the curve of Figure 10.10a shows that a 550-nm light appears fairly yellowish, and a 430-nm light quite bluish, whereas a 500-nm light (unique green) appears neither.

C. Neural connections

How can the signals originating in the three cone types get mixed, or processed, to yield signals corresponding to the subjective responses described by Figure 10.10? As we saw in Chapter 7, signals to the brain are often comparisons between different receptor responses. Figure 10.11 shows hypothetical connections, two of which involve *differences* between signals from the different types of cone. These correspond to ***chromatic channels*** and explain the observed chromatic responses. Similar connections are directly observed by electrophysiological measurements on goldfish and monkeys.

Consider, for instance, the ***yellow minus blue*** chromatic channel ***(y - b)***, which compares the long-wavelength part of a light with the short-wavelength part. When light excites either the *L* or *I* cones, there is *excitation* in the cells of the ***y - b*** channel. If, however, light excites the *S* cones, there is *inhibition* of the ***y - b*** cells. If the net result is excitation, the light appears yellowish. A net inhibition makes the light appear bluish.

Likewise, for the ***red minus green*** chromatic channel ***(r - g)***, a net excitation leads to the sensation of red, a net inhibition leads to the sensation of green. (Note that an excitation of the S cones leads to a red sensation, hence the short-wavelength end of the spectrum, "violet," appears to have some red in it as shown by Fig. 10.9.)

We've stressed that there are three attributes of any color and that there are three cones. Unless there is a third channel, your brain could be aware of only the two attributes of color represented by "red-greenness" and "yellow-blueness." This third opponent channel—the ***white minus black*** channel ***(w - bk)***—relays *lightness* information. The ***w - bk*** channel has a positive response whenever *any* of the three cone types is stimulated. The opponent nature of this channel is slightly different from that of the chromatic channels, though. Inhibition in this channel does not result from excitation of any cone type. There is inhibition in all three channels due to adaptation and lateral effects. The spatial processing discussed in Chapter 7 involves such effects in ***w - bk*** channels. (Color television, interestingly enough, also employs two chromatic channels and one gray-scale channel. The latter is necessary so the signal can be used by black and white sets. Reception of the two chromatic channels is controlled by knobs sometimes labeled "color" and "tint.")

So, we find a reconciliation between the once apparently competing ideas of trichromacy and opponency; the initial photoreceptor stage is trichromatic, but the signals from that stage are subsequently processed through three opponent channels (two chromatic channels and one achromatic). Each chromatic channel accounts for two hue responses. Thus there are four fundamental hue responses and hence four psychological primaries.

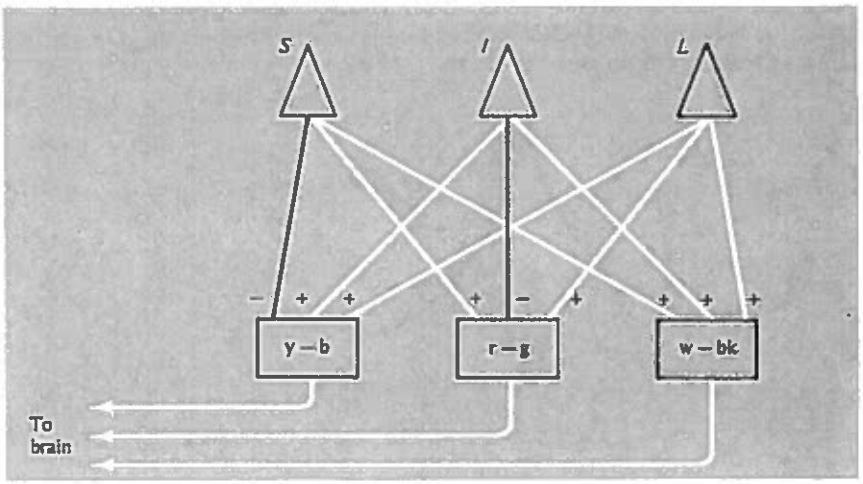
D. Chromaticity diagram

We saw in Section 10.3 that the relative stimulations of the *L*, *I*, and *S* cones determine the location of any color on the chromaticity diagram. But the relative stimulations of the cones also determine the responses in the opponent channels. It is possible, then, to relate the activity in the chromatic opponent channels ***(r - g*** and ***y - b)*** to the chromaticity diagram. (The activity in the ***w - bk*** channel, related to the lightness, is not contained in the diagram.)

The two lines on the chromaticity diagram of Figure 10.12 divide it into regions corresponding to the activities in the chromatic chan-

FIGURE 10.11

Highly schematic hypothetical connections between the cones and the cells of the two chromatic channels, **r − g** and **y − b**, and of the achromatic channel, **w − bk**. Excitation is denoted by + and inhibition by −.



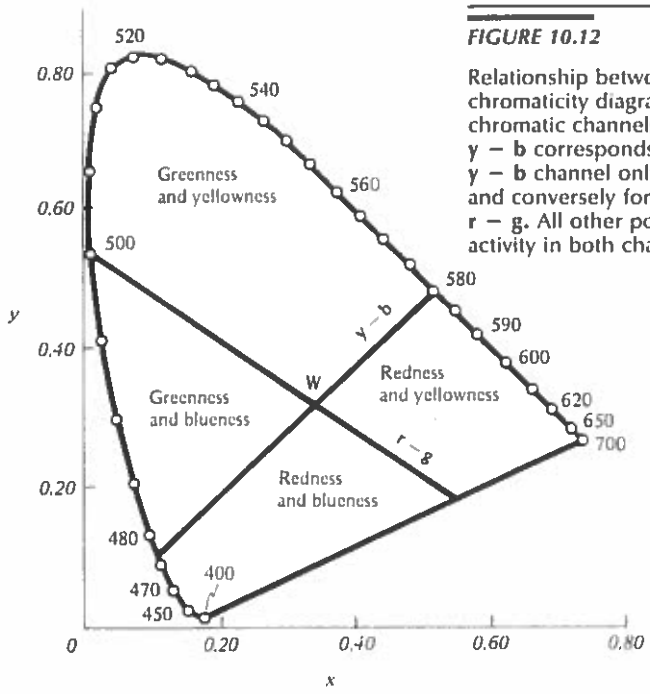


FIGURE 10.12

Relationship between points on the chromaticity diagram and response of the chromatic channels. The line marked **y − b** corresponds to activity in the **y − b** channel only (no **r − g** activity); and conversely for the line marked **r − g**. All other points correspond to activity in both channels.

nels. The neutral point, *W*, is where there is as much blue response as yellow and as much red as green. Thus, the lines must cross there. From Figure 10.10, you see that spectral light of 580 nm or 475 nm does not lead to activity of cells in the ***r - g*** channel. Since any color lying on the line connecting these two points looks like a mixture of these lights, *any* color falling along this line appears neither reddish nor greenish—this line denotes *no* response in the ***r - g*** channel. Colors above this line have an inhibitory signal in the channel; such colors appear greenish. Colors on the other side of this line appear reddish.

The line that passes through the *W* point and 500 nm (unique green) corresponds to no activity in the ***y - b*** channel. Colors falling along this line appear neither yellowish nor bluish (though they may appear reddish or greenish). Colors to the right of this line yield excitation in the ***y - b*** channel and thus appear yellowish, whereas colors to the left of this line yield inhibition and appear bluish. Notice that this line does not strike the horseshoe at the lower right. This reflects the fact that the unique red is not spectral, but the complement of 500 nm, that is 500c. (Notice from Fig. 9.9 that the complement of unique blue, 475 nm, is *not* unique yellow, 580 nm, as opponent processing would predict, but 575 nm instead. We may take this discrepancy as a measure of the error accompanying these measurements.)

Thus, any point on the chromaticity diagram can be identified by the amount of activity in the two chromatic channels and vice versa. These two channels carry all the chromaticity information.

*10.5 COLOR DEFICIENCY

A person is called ***color deficient*** when his color matches are not the same as those for most of us. (The term "color blind" has fallen out of favor primarily because most color-deficient people do see color, only somewhat differently from most of us.)

While color matching is the most reliable and revealing test for color deficiency, it is simpler and faster to have the subject look at colored plates similar to those of Plate 10.2, which appear different to normals and color deficients. For example, normals can see two digits in Plate 10.2a, but some color deficients can see only one.

Little is known directly about the way in which the visual system of a color deficient differs from that of a normal color observer, and you should consider the explanations presented here as simply informed guesses. For instance, some color deficients lack the use of one or more cone type. This might result from any of a number of causes: the nonfunctional cones may simply be missing; they may be present but lack connections to subsequent nerves; perhaps the cones are connected to subsequent nerves meant for *another* cone type; maybe the cones are present but are filled with the "wrong" photopigment, either a modified one, or one used in other cones; or any combination of these (and yet other!) reasons. There may even be problems in the neural processing of the opponent channels. All this makes it difficult to be definite about conclusions concerning color deficiency.

One thing is clear, though: different people require a different number of colors to match any light. Thus we can group those requiring, one, two, or three such colors as ***monochromats***, ***dichromats***, and ***trichromats***,* respectively.

A. Monochromacy

By suitably adjusting the intensity of only *one* spectral light, a monochromat can match a light of any color. These unfortunate people can be considered truly color *blind*, in that they cannot distinguish any wavelength from any other—like watching a color TV program on a black and white set. (This relatively rare color deficiency is often linked with other visual problems, such as inability to see fine detail.)

A standard photocopier is monochromatic, as you can see from Figure 10.13 and the TRY IT.

*Greek *mono*, one; *di*, two; *tri*, three; plus *chroma*, color.

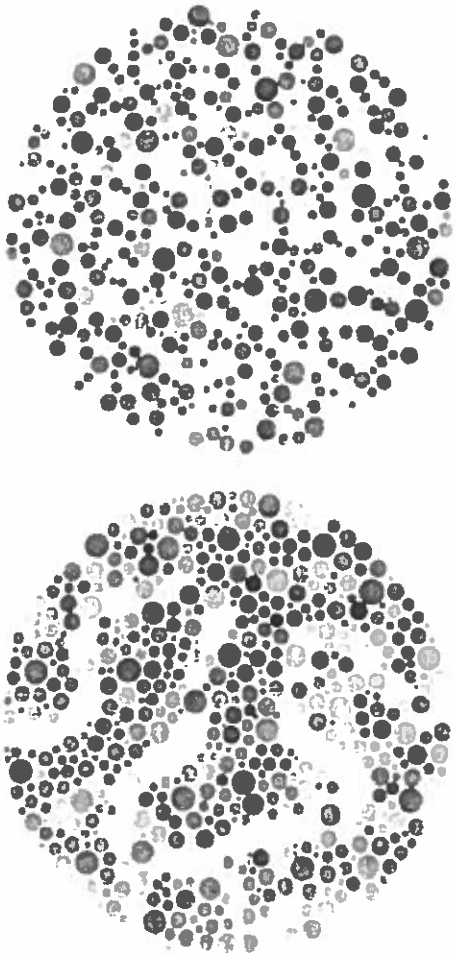


FIGURE 10.13

Photocopy of Plate 10.2 made using a Savin photocopier. The photocopier cannot "see" the numerals, but it can "see" the serpentine path.

There are two main types of monochromats, depending on which single photoreceptor responds to light. ***Cone monochromats*** have functional cones, but of only one type (or they lack the two chromatic channels). They can see under photopic conditions. On the other hand, ***rod monochromats*** lack all cone function and respond using their rods alone. They have great difficulty in seeing under photopic conditions. Lacking foveal cones, their acuity is usually quite poor, and they must avert their eyes slightly when they want to look at something.

TRY IT

FOR SECTION 10.5A

Color blindness of a photocopier

You can investigate the color blindness of a standard photocopier using colored pens, colored photographs, or the color deficiency plates of Plate 10.2. First photocopy a multicolored picture. To which colors is the machine most sensitive? Least sensitive? If you can make two colors that photocopy the same, you can construct a pattern of dots (similar to the plate) that is discernible by you, but not by the photocopier. Next photocopy the color deficiency testing plates, as we did for Figure 10.13. The plates are matched in lightness for humans, but may not be so for your photocopier. Thus, the machine may be able to distinguish some of the patterns. What kind of color deficiency is most like that of the machine?

B. Dichromacy

Dichromats require only *two* colors to match any color. Some of these people may have only two of the three *cone* types fully functioning. There are three main classes of such dichromats, corresponding to each of the possible nonfunctional (or relatively insensitive) cone types. Other dichromats may have only one of the two *chromatic channels* functioning. There would be two classes of such dichromats.

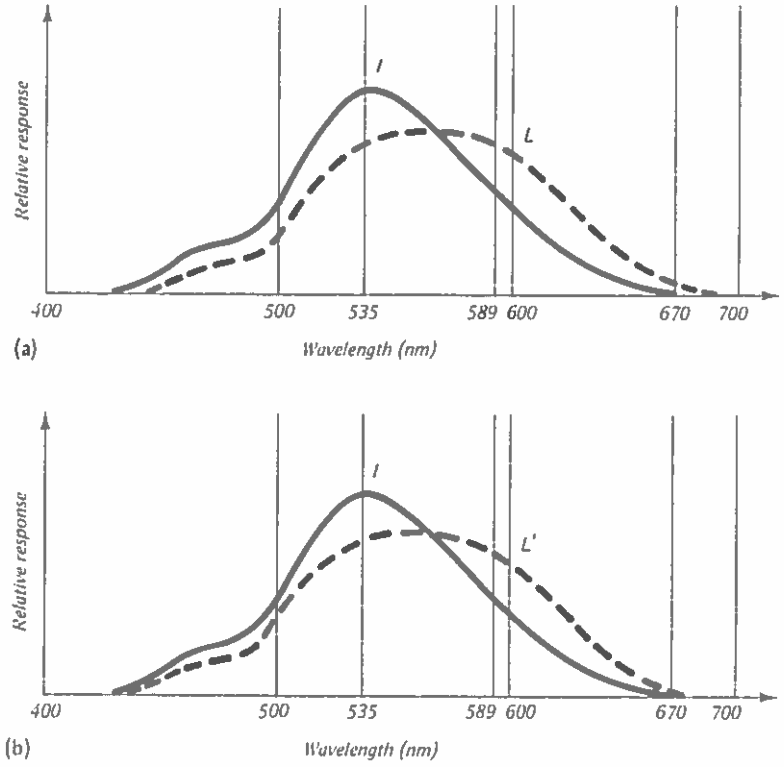
A useful test for understanding dichromacy is that of finding the *neutral points* (Sec. 10.2B). If only two cone types are functional, the wavelength of a neutral point marks the crossover point of these two cones; if only one chromatic channel is functional, a neutral point occurs where its two opponent colors balance.

PONDER

A dichromat with only two cones functioning has a second (nonspectral) neutral point in the purple. Why?

FIGURE 10.14

Rayleigh test. (a) *L* and *I* cone response curves for a normal observer, as in Figure 10.5. (The *S* cones do not respond at the wavelengths used in this test.) (b) A protanomalous observer may have the *L* curve shifted to shorter wavelength, *L'*.



The responses of the *L* and *I* cones can be compared by the ***Rayleigh test.*** The subject adjusts the relative intensities of particular green and red lights until the sum appears identical to a certain yellow. (In practice, 670-nm and 535-nm lights are used to match a 589-nm light.) If both *L* and *I* cones respond normally, a certain, "normal" ratio of the two lights' intensities is required for the match (Fig. 10.14a). If, however, one type of cone is not functioning, say the *L* cones, then the subject can make a match using a variety of relative intensities. He need only keep the total excitation in the *I* cones the same, since the *S* cones do not respond appreciably in this wavelength range. In fact, given many chances, the subject will not show consistency in his settings.

An analogous test for the *S* and *I* cones would reveal information about the relative response of these cones. But, because the composition and color of the macula lutea (Sec. 5.2B) varies considerably with age and from person to person, such a matching test at short wavelengths is less reliable.

A further test is that of hue discrimination. As we saw in the Section 10.2C, hue discrimination is good ($\Delta\lambda$ small) at wavelengths where the cone response curves are steep, and poor ($\Delta\lambda$ large) where they are fairly flat. If a cone type, and hence the steep regions of its response curve, is missing, there are fewer wavelength regions where hue discrimination is good. Their location tells indirectly which cone types are present.

With these tests in mind, check to see that the results in Table 10.1 are consistent if ***protanopes*** lack the *L* cones, ***deuteranopes*** lack *I* cones, and ***tritanopes*** lack *S* cones.

What would happen if a subject had the photoreceptors and pigments of a normal person, but lacked one of the chromatic channels, say the ***y - b*** channel? Such a person would respond using his ***r - g*** channel, and would consequently have *two* neutral points: about 580 nm (i.e., near unique yellow) and about 470 nm (i.e., near unique blue). This behavior is similar to that of a few observers called ***tetartanopes.***

PONDER

Suppose a subject lacks the r - g channel instead. Where would his neutral points be? Would his response differ from a deuteranope's?

C. Trichromacy

Trichromats (including normal color observers) require *three* colors to match an arbitrary color. As such, trichromats must have three cone pigments. Their differences in color vision may arise from pigments with slightly different response curves than those of the normal pigments. Alternatively, the connections between one type of cone and the subsequent nerve cells may be defective.

The Rayleigh test is particularly useful for describing ***anomalous trichromats.*** Suppose the *L* cones of a trichromat were shifted to wavelengths shorter than normal (Fig. 10.14b). The shifted cones then have their sensitivity at the 535-nm green increased by a small percentage, compared to normal cones; however, their sensitivity at the 670-nm red is reduced by a large percentage. To compensate, such an observer requires *extra red* in his Rayleigh match with the 589-nm yellow. (This kind of color deficient would also have reduced sensitivity at long wavelengths, due to the shifted *L* cone curve.)

Anomalous trichromats are usually classified as ***protanomalous*** (excessive red in the Rayleigh

TABLE 10.1 The symptoms of the principal types of color deficiency

	Number of colors needed for match	*Approximate wavelength of neutral point(s) (nm)*	*Approximate wavelength of peak sensitivity (nm)*	*Reduced sensitivity at long wavelengths?*	*Rayleigh test excess*		*Percentage of males affected**
					green	*red*	
Monochromacy							
Rod monochromacy	1	all	505	yes	inconsistent		.003
Cone monochromacy	1	all	three types	some may be	inconsistent		very small
Dichromacy							
Protanopia	2	495 and red-purple	540	yes	inconsistent		1.0
Deuteranopia	2	500 and purple	560	no	inconsistent		1.1
Tritanopia	2	570 and blue-purple	555	no			very small
Tetartanopia	2	580 and 470	555 (?)	no			very small
Trichromacy							
Protanomaly	3	none	540	yes		yes	1.0
Deuteranomaly	3	none	560	no	yes		4.9
Tritanomaly	3	none	560	no			very small
Neuteranomaly	3	none	555	no			very small
Normal	3	none	555	no			91.

*Greatest percentages of occurrence are reported for males.

match), ***deuteranomalous*** (excessive green in the Rayleigh match), and ***tritanomalous*** (normal Rayleigh match but yellow-blue problems), but there is a continuous range of variation. Indeed, there is not even a sharp division between anomalous trichromats and dichromats.

Some of the problems associated with these trichromats may arise in the neural processing beyond the photoreceptors. Indeed, a fourth type of anomalous trichromacy, ***neuteranomaly,*** is believed to involve normal cone responses but relative ineffectiveness of the ***r - g*** channels compared to that of the ***y - b*** channel. One symptom of this deficiency involves the neuteranomalous observer's wavelength settings for unique blue and yellow, which are the same as for normal observers on the average, but show great variation; because his ***r - g*** chromatic response curve is reduced, it is indistinguishable from zero for a *range* of wavelengths (Fig. 10.15).

In short, it seems that anything and everything can go wrong in a color vision system. One, two, or all three cone responses may be lacking; a chromatic channel may be nonfunctioning or may not respond efficiently; the photoreceptor pigments present may not have the normal response curves, or they may be combined differently in the chromatic channels; or there may be a combination of these defects. Further, each set of symptoms exhibited in Table 10.1 may be achieved by more than one such physiological defect.

Are there any "cures" or techniques that can help color deficients, such as there are for people with focusing problems? In some cases, yes. One technique is to have the color deficient wear a red filter over *one* eye (in the form of an eyeglass lens or a contact lens). Suppose a color deficient, who had a neutral point in the cyan region of the spectrum, wears such a lens. Although to him a broad-band gray and a certain cyan appear *identical* in the uncovered eye, they appear *different* in the covered eye. Thus, the red filter over one eye has converted physical information of color difference into binocular information, which the subject can detect. With practice, the deficient comes to associate such binocular information with different colors—permitting a greater range of distinguishable colors.

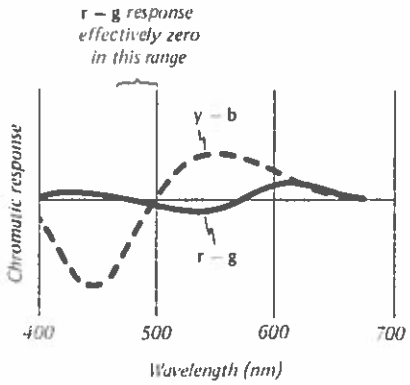


FIGURE 10.15

Hypothetical chromatic response curves of a neuteranomalous observer showing reduced response in the r − g channel.

10.6 SPATIAL PROCESSING OF COLOR

In Chapter 7 we saw several fundamental effects of lightness perception: simultaneous lightness contrast, edge enhancement, lightness constancy, etc. In this section, we'll see that these spatial effects have counterparts "in living color" that come about because of similar neural processing in the chromatic channels.

A. Chromatic lateral inhibition

Even though the four small squares in Plate 10.3 are objectively gray (use a mask to check this), they appear different colors because of their surrounding regions. Notice that the yellow region makes the gray appear somewhat blue, the green region makes the gray appear red, and so on. Such ***simultaneous color contrast*** suggests that there is lateral inhibition (Sec. 7.4). That is, there must be a *spatial* opponency ("center minus surround") of the chromatic channels, in addition to their chromatic opponency ("red minus green," for example). Indeed, some cells of the chromatic channels are opponent both in color and in space, and hence are called ***double-opponent cells.***

A double-opponent cell of the ***r - g*** channel (Fig. 10.16) has the cones of the center connected in the usual ***r - g*** fashion. The surround is connected in the opposite way, ***g - r*** (e.g., stimulation with red here leads to inhibition in the pooling cell). Thus, the stimulus that leads to the greatest excitation of the pooling cell has long-wavelength light striking the center and intermediate-wavelength light striking the surround. Likewise, a double-opponent cell of the ***y - b*** channel would have the familiar ***y - b*** response from the center and a ***b - y*** response in the surround.

Consider such a cell of the ***r - g*** channel whose center is viewing an area just inside the gray region surrounded by the green in Plate 10.3 (Fig. 10.17). The gray stimulates both the *L* and *I* cones in the center, leading to no net excitation there. The green in the surround, however, primarily excites the *I* cones there, leading to excitation of the ***g - r*** in the surround, and hence to a net *excitation* in the pooling cell. This excitation is interpreted as red because it stimulates the pooling cell in the same way that a central red stimulation would. The gray square therefore appears slightly reddish. If the surround had been red, instead of green, there would have been net *inhibition* in the pooling cell and the gray square would appear slightly greenish, in accord with what you see in Plate 10.3. A similar process occurs for the double-opponent cells of the ***y - b*** channel.

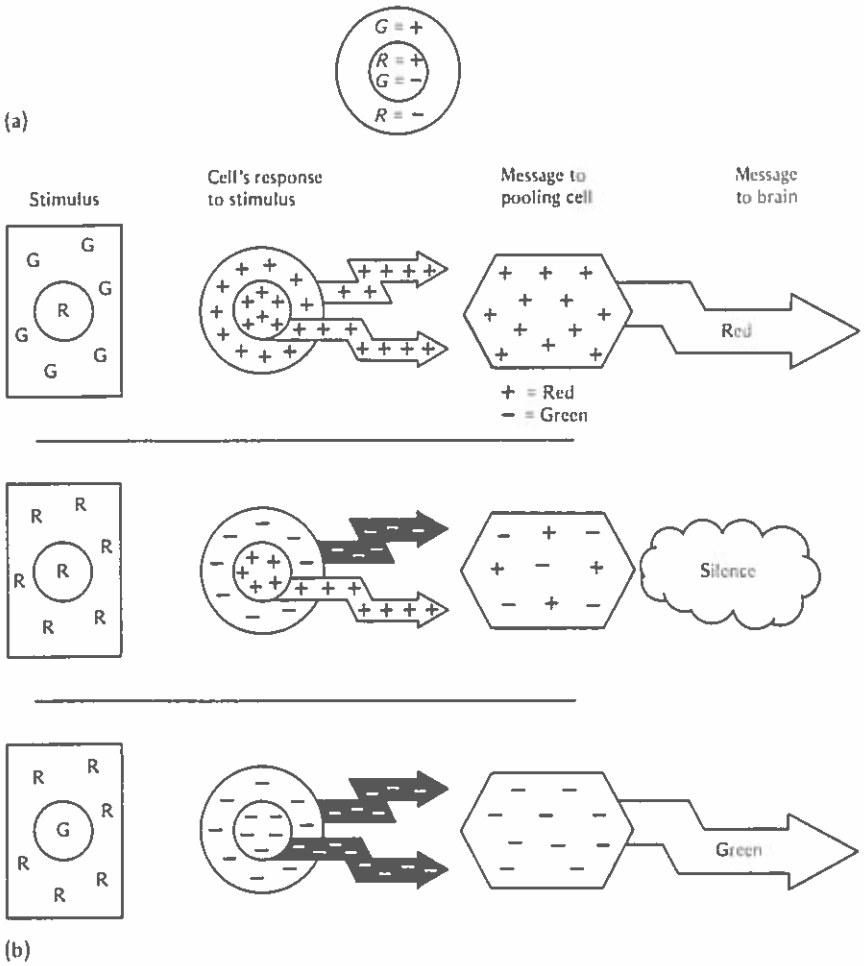


FIGURE 10.16

(a) Receptive field of double-opponent cell of the **r − g** channel. Long-wavelength light in the center excites the pooling cell, while intermediate-wavelength light there inhibits the cell, as in Figure 10.10b. In the surround, however, intermediate-wavelength light excites the pooling cell, and long-wavelength light inhibits it (Figure 10.10b with redness and greenness interchanged). **(b)** Examples of this cell's response.

PONDER

The gray square surrounded by light yellow appears somewhat dark. Why?

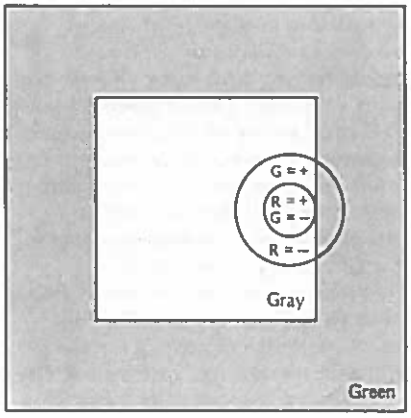


FIGURE 10.17

An **r − g** double-opponent cell explanation of simultaneous color contrast. The green in the receptive field's surround leads to excitation of the cell, and thus to some perception of redness in the objectively gray region.

In general, any large colored region tends to make its neighboring regions appear more like the color opponent of the original region. For example, a green region when surrounded by yellow appears more bluish, that is, more like cyan. The TRY IT shows how you can further verify that the appearance of a color is influenced by colors nearby.

Although the basic phenomena of simultaneous color contrast were fairly well known to artists for centuries, it was only in 1839 that the director of the Gobelins tapestry works, Eugène Chevreul, formulated the relevant principles somewhat scientifically. He had been receiving complaints about the quality of the colors in the tapestries. He found no deficiencies when he thoroughly checked the dyes, so Chevreul considered the *perception* of color. He discovered that he could make colors appear more saturated and bright by changing the *designs* of the tapestries. For instance, a yellow surrounded by dark blue appears more saturated and lighter than if it were surrounded instead by orange. The brilliance of the Impressionists' color was achieved using these ideas, by the placement of large dabs of complementary colors adjacent to one another. The painter J. M. W. Turner may have used this principle in reverse: it is said that he made last-minute modifications in the colors in his paintings to diminish the effectiveness of the colors in his rivals' paintings, hung nearby. More recently, color contrast has been used by many artists—for example, the saturation of the green region in Plate 5.2 results, in part, from the red surrounding it.

The effects of edge enhancement that we saw in Chapter 7 have counterparts in color as well. For example, in "Side Show *(La Parade)*," Georges Seurat paints one side of an edge extra bluish and the other side extra yellowish, thereby making the two regions each appear more saturated (a chromatic analogue of the Craik-O'Brien effect). Although most of the Impressionists disdained intellectual approaches toward color, Seurat had an obsession with color theories and principles and was greatly influenced by Chevreul among others.

TRY IT

FOR SECTION 10.6A

Simultaneous color contrast

In the middle of a piece of colored construction paper, cut a small hole (about 2 mm across) to form a mask. Hold the mask at arm's length, close one eye, and look through the hole at colored objects. Compare the colors you see with and without the mask. Notice that the mask tends to make the region in the hole appear more like the color complementary to that of the mask.

B. Color constancy

Objects tend to retain the same perceived color even though the coloration of the overall illumination may change. This ***color constancy*** certainly is both useful and a biological necessity. An edible berry may be distinguishable from a poisonous one only by its color, so it is essential that this color persist, no matter what the illumination (blue noon sky, red twilight, gray clouds, etc.)—there must be color constancy if the berry eater is to survive.

Like lightness constancy (Sec. 7.4A), color constancy involves lateral inhibition. For example, an overall excess in red illumination is "ignored" by the double-opponent cell of the ***r - g*** channel (Fig. 10.16), because the increased stimulation of the receptive field's center and inhibition in its surround cancel each other. To look red, the berry must reflect *more* red light than the average, so that the center of a double-opponent cell viewing the berry can be excited, but not the surround. Hence colors depend on the *relative* amount of colored lights. The first TRY IT shows how you can demonstrate these effects.

Color constancy isn't perfect, however, and may be affected by your overall state of adaptation, even achromatic adaptation, as the second TRY IT shows.

First TRY IT

FOR SECTION 10.6B

Colored shadows and Hering papers

You can demonstrate simultaneous color contrast with ***colored shadows.*** *Place an object, such as a beer can, some distance in front of a white screen. Use two lamps or slide projectors as point sources to form two nonoverlapping shadows of the can on the screen. Now hold a red filter in front of one of the lamps, so that the lamp illuminates the can and screen with red light. Notice the color of the shadow regions on the screen. One of them receives light from the red lamp only and appears red as you might expect. The other shadow region receives only white light but appears cyan. (You may have to wait a few moments.) This is because the regions surrounding that shadow receive red (and white) light, and by simultaneous color contrast, make the shadow appear cyan; the shadow is less red than the average illumination. What would be the color of the shadow if you replaced the red filter by one of another color? Try it!*

This phenomenon was first observed by Count Rumford in the eighteenth century without lamps or slide projectors. He used a candle as one (slightly yellowish) source and the (bluish) noon sky as another. To balance the intensities of the two lights, he brought the candle close to the screen. What color were the shadows he produced? Try it!

Another way to demonstrate that a color depends on a comparison of the light coming from different regions involves a sequence of achromatic regions ranging from black through gray up to white (Fig. 7.4b). (Hering originally used small pieces of achromatic papers of various lightness, which are now called ***Hering papers.****) View that figure under strong red light; be sure to eliminate all other illumination. Notice that (after a few moments) the intermediate gray region in the middle of the scale still appears gray. The upper region, reflecting more long-wavelength light than the average, appears red. The lower region, reflecting less long-wavelength light, appears cyan, or green. Your perception of color is determined by the relative amount of light at different wavelengths, not the overall amount.*

Second TRY IT

FOR SECTION 10.6B

Dependence of color on your state of adaptation

That color depends on you, as well as on the light coming to your eyes, is easily demonstrated by taking advantage of the fact that you have two eyes. Find a picture with lots of different colors, or arrange a variegated scene. By alternately closing one eye and then the other, compare how these colors look to each of your eyes. Most people will notice no difference between the eyes (although there are very rare people with color deficiency in only one eye—if you are such a person, rush to your nearest psychophysicist and volunteer as a subject). Now close one eye, and stare at a bright white light (not the sun!) with the other for half a minute. Move your eye around, so no one spot on the center of your retina receives more light than its neighbors. Having adapted one eye in this manner, repeat the original experiment; closing first one eye, and then the other, look at the colored scene. Compare the colors as viewed by your two eyes now. Note that the colors change even though you have adapted to achromatic (white) light. What would you expect to happen if you adapt by staring at a bright colored light? Try it!

C. Spatial assimilation

Even though the red background in Plate 10.4 is physically uniform throughout, the red in the central square appears slightly yellowish, while the red in the outer portions appears slightly bluish. Simultaneous color contrast would make the red in the central square appear bluish (in contrast to the yellow dots there) and the red in the outer portions appear yellowish (in contrast to the blue dots there). The effect shown in the plate, in which the color of a region ***assimilates*** that of neighboring regions (rather than taking on the opponent hue), is called the ***von Bezold spreading effect.*** If two colors are in adjacent large areas, they will affect each other via contrast. However, if they are small, intermingled areas, they produce assimilation, as in partitive color mixing (Sec. 9.5B).

Although the mechanism for assimilation is not fully understood, one idea is plausible—the receptive fields of the double-opponent cells of the chromatic channels come in a variety of sizes. The large receptive fields contain the color information while the small ones primarily relay information about fine detail. Cells with large receptive fields do not see the dots as separate, so the red area in the center appears somewhat yellowish. You can still see the dots as separate because the cells having small receptive fields relay the spatial information.

Because contrast and assimilation depend on the size of the patterns involved, the colors of a given region will change as you change your distance from it. When you stand very close to a painting like the one shown in Plate 7.2 you can see each dot and its color as individual or there may be contrast effects due to nearby dots that affect the color. From an intermediate distance, however, you still see a dot as individual but its color is affected by that of neighboring dots via assimilation—the colors tend to mix partitively. If you view the painting from a greater distance, you see the partitive mixture, but you can't resolve the individual dots. It is unfortunate that some museums hang pointillist paintings in rooms so small that you can't move far enough from the painting for some of these changes to occur.

10.7 TEMPORAL PROCESSING

We can extend the parallel between achromatic (Chapter 7) and chromatic processing by discussing the temporal response of the chromatic system. Many of the temporal phenomena of the earlier chapter have analogies in color. In addition, because the temporal properties of the response to different colors can themselves differ, we'll find temporal phenomena in color that have no counterpart in achromatic vision.

A. Standard negative afterimages

Adapt (Sec. 7.5) to Plate 10.5 to form a negative afterimage. Note particularly the colors in the afterimage. Where you adapted to yellow, you now see blue (and vice versa), and similarly for cyan and red. Notice here that the afterimage of a color is its *complement*. As in black and white, the color afterimages do not transfer between your eyes. (Try it!)

The explanation for such color afterimages is a simple extension of that used for achromatic afterimages. Consider the cones in the area of your retina responding to the yellow region during adaptation. The yellow light stimulates (and thus desensitizes) your *L* and *I* cones much more than it does your *S* cones. Therefore, when you subsequently look at the white piece of paper, your *S* cones respond vigorously whereas your desensitized *L* and *I* cones do not. The resulting excess of *S* cone response makes the afterimage appear blue in that region.

As you continue to observe the afterimage carefully, it fades and its *color* changes slightly. This is because your different cones (and chromatic mechanisms) recover from adaptation at different rates.

Negative afterimages can be used to explain the phenomenon of ***Bidwell's disk*** (Fig. 10.18). When the black and white sectored disk is rotated *counterclockwise*, the red bulb appears properly *red*, whereas rotating the disk *clockwise* makes the bulb appear *cyan*. While rotating clockwise, first the notch reveals the red bulb, and then the *white* region covers the bulb. The brief exposure of the red bulb desensitizes your *L* cones primarily; when you then view the white region, the standard cyan afterimage results. At the proper rotation speed, the afterimage can last much longer than the presentation of the bulb, and so your impression is that the bulb is cyan. When the disk is rotated counterclockwise, the notch revealing the red bulb is immediately followed by the *black* sector. By the time the white region comes into view, your *L* cones have recovered, so you don't see a negative afterimage. The bulb thus appears red.

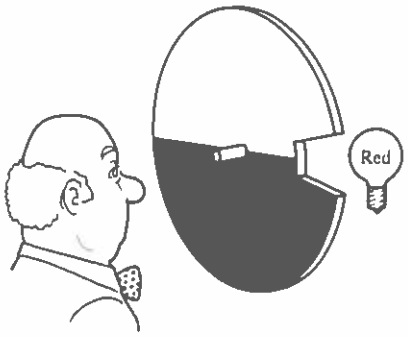


FIGURE 10.18

Bidwell's disk. As the black and white sectored disk rotates, its notch intermittently reveals a bright red light bulb, whose apparent color depends on the direction of rotation.

B. Positive afterimages

When producing a *positive* afterimage in the first TRY IT for Section 7.7A, you undoubtedly used a colored stimulus, for example, the blue sky. That the positive afterimage retained the original colors (at least initially) demonstrates that your chromatic channels have persistence. Our discussion of TV and movie presentation and flicker is just as valid for your chromatic response as it is for lightness, as you know if you watch color TV.

Notice that the color of the afterimage *changes* as you wait. As in the negative afterimage case, your different cone types recover at different rates, leading to a changing set of signals as time goes on.

*C. Other temporal effects

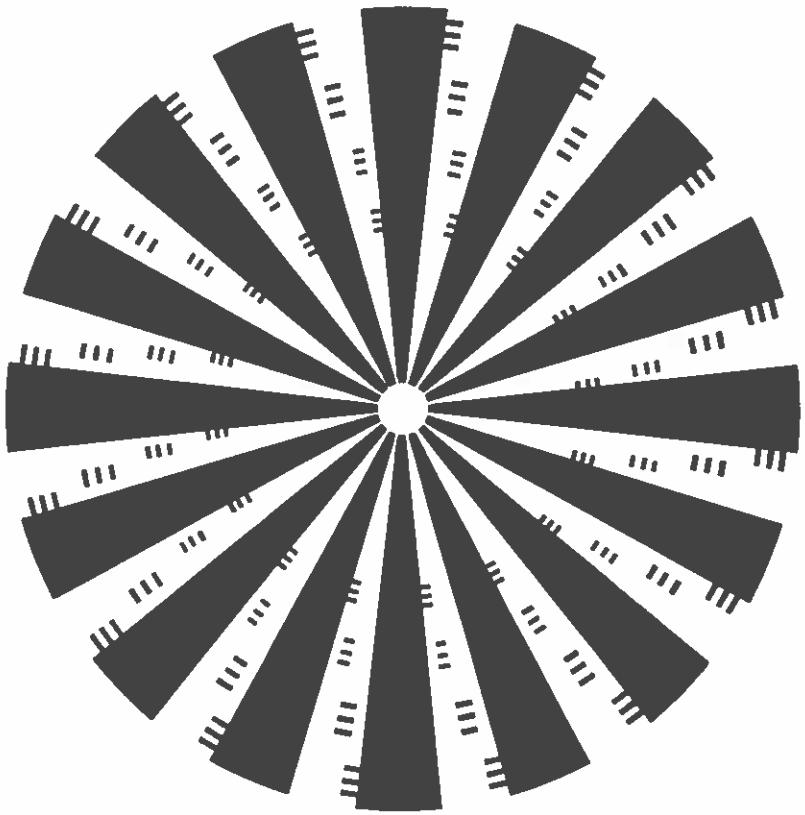
Because the different chromatic mechanisms respond at different rates, it is possible to elicit color responses by presenting black and white stimuli with the proper temporal behavior. An example is ***Benham's disk*** (Fig. 10.19), which was invented by a toymaker in the nineteenth century who noticed colors appearing in concentric rings when the disk was rotated at the proper rate (he mounted his on a toy top—see the first TRY IT). Consider what happens as the disk turns and white light, reflected by the disk, strikes your retina. Figure 10.20 shows the sequence of white and black produced at various positions while the disk is rotating. A receptive field pointed at any one of these places, therefore, can have a different sequence of white and black stimulation on its center, compared to that on its surround. Because the persistence exhibited by a receptive field's center may differ from that of its surround, such unusual intermittent stimulation can lead to an imbalance in chromatic response between the center and surround. This imbalance is interpreted as color. (For a related effect, see the second TRY IT.)

Like your cones, the different color sensors in a television camera also have different temporal response properties, as can be verified when the TV camera sweeps across a very bright spot, such as a stadium light; there is often a colored streak across your color TV tube, because the different sensors each respond, and decay, at different rates.

We've discussed how eye movements can translate spatial variation of a stimulus into temporal variation in signals (Sec. 7.6). These variations induced by eye movements can produce subtle colors even when the stimulus is black and white, as in Figure 10.21. Such ***Fechner's colors*** can also be experienced as your eye scans any black and white pattern having fine detail such as Figure 7.17.

FIGURE 10.19

Modern version of Benham's disk. When rotated at 33⅓ rpm, colors appear in the concentric bands: red on the inner set, blue on the outer set.



First TRY IT

FOR SECTION 10.7C

Benham's disk

You can easily see colors from Benham's disk. Photocopy Figure 10.19, and use a black felt tip pen to get good blacks, if required. (Just like the visual system, photocopiers process edges, often at the expense of large, uniform regions. Since the photocopier does not have a brain to fill in the solid regions, you, armed with your black pen, must do it.) Place the copy on a phonograph turntable and set it rotating at 33 rpm, well illuminated by incandescent light or daylight. Notice the colors in the bands produced by the rotating disk. If you can change the speed of your turntable, try 45 rpm and note any change in colors.

Second TRY IT

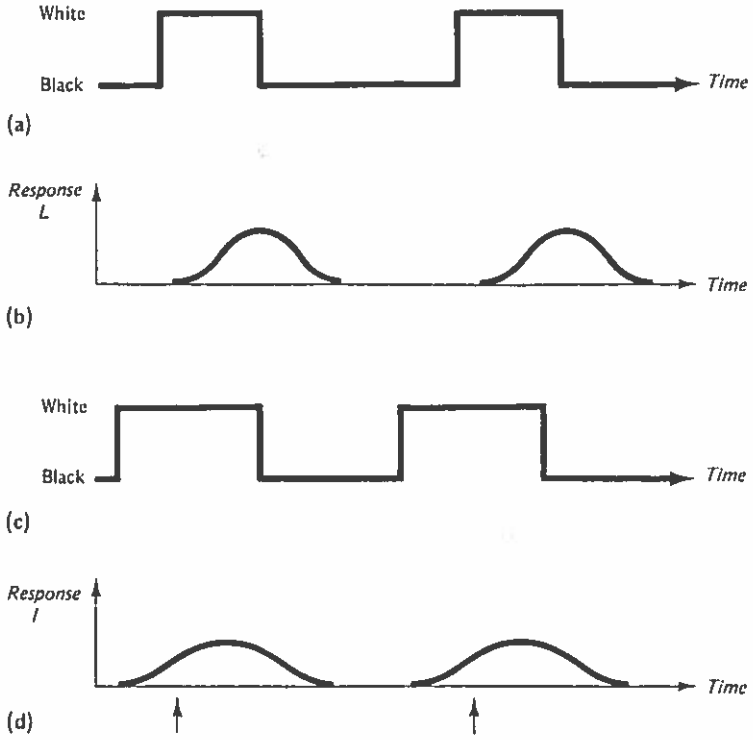
FOR SECTION 10.7C

Latency and color

Under bright, white light, hold this book on your lap and look at Plate 10.6. Shake the book back and forth as quickly as you can, as you would shake a pan when making popcorn. The red square appears locked to the cyan, and the two move together, as you would expect.

Dim the room lights until you can just barely recognize the colors, and then shake the book as before. Note now how the cyan area appears "rubbery"—the red square seems to slosh back and forth within it.

Under bright light the cones and channels respond rapidly. Thus, they can "keep up" with the moving squares of the plate. Under dim light, however, there can be significant differences between the latencies of your response to the red compared to the cyan. (Recall the Pulfrich phenomenon, Sec. 8.5C.) As you shake the plate, then, one region is processed more slowly and appears to lag behind the other.



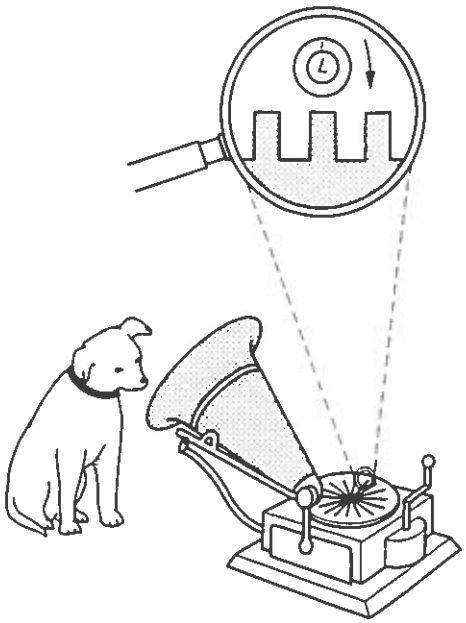


FIGURE 10.20

One effect that may contribute to the Benham's disk illusion. **(a)** Stimulation and **(b)** response versus time for the *center* of a receptive field centered at the point shown in the inset. **(c)** Stimulation and **(d)** response for the *surround* of the same receptive field. The receptive field is of the **r − g** channel. For the sake of simplicity we take it with *L* cones in its center and *I* cones in the surround. Suppose the *L* cones respond faster than the *I* cones. Then, the intermittent stimulation would lead to the responses shown. Because at certain times the signals from the center and the surround are not balanced (arrows), your **r − g** channel responds and you see color at that point on the disk.

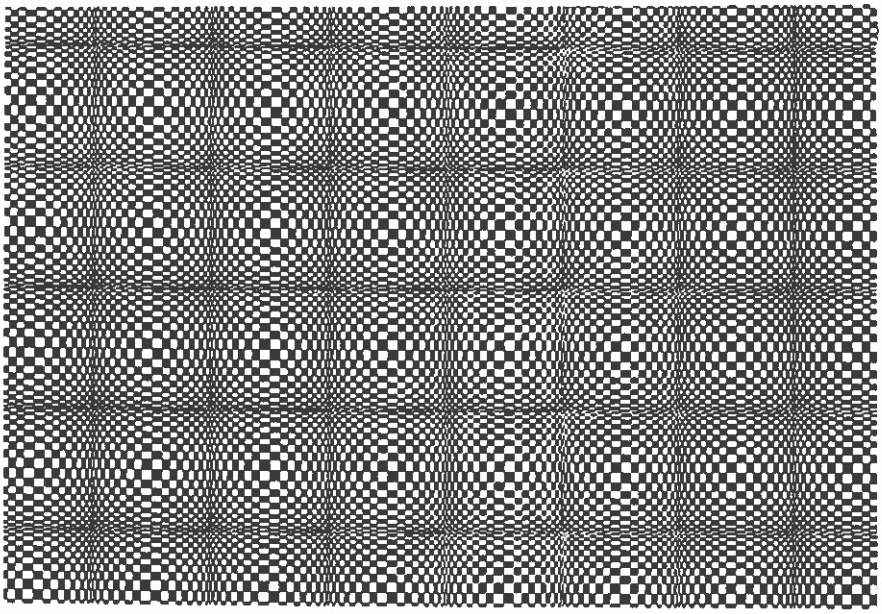


FIGURE 10.21

Fechner's colors. As your eye scans across the black and white pattern, the spatial pattern is translated into a temporal pattern of stimulation. Because the different cones and chromatic channels respond at different rates, their signals are not always balanced. Consequently, you may see unsaturated colors in the pattern.

*10.8 CONTINGENT AFTEREFFECTS AND MEMORY

A curious example of an aftereffect is the ***McCulloch effect*** (Plate 10.7). After prolonged adaptation, alternating between the vertical red bars and the horizontal green ones, vertical white bars will appear slightly greenish while horizontal white bars appear reddish. Because you adapt to as much red as green, there cannot be a standard *color* afterimage—after all, what color would such an afterimage be? There cannot be a standard *pattern* afterimage because you move your eyes while adapting. Also, the aftereffect can last much longer than a standard afterimage. With adaptation of about 10 minutes, you should be able to experience the aftereffect for hours or even weeks! (Try it! You needn't be concerned about the prolonged aftereffect. If it bothers you, you need only take the antidote—rotate the book 90° and adapt again.) Check to see that the effect transfers.

How can we explain the McCulloch effect? Presumably it involves cells in the visual cortex that respond to *both* color (in the usual opponent combinations) *and* form. Here is one possible explanation: Adaptation to the plates selectively desensitizes cells of the ***r - g*** system that also respond well to vertical lines. Later, when you look at the black and white vertical bars, those cells respond less than the ***g - r*** cells that also respond well to the vertical bars. This imbalance in response after adaptation is then interpreted as green. Naturally, the analogous process occurs with the horizontal bars, only here it is the ***g - r*** cells that are desensitized.

A similar aftereffect links color to *motion*. You adapt alternately to an *upward*-moving grating of red and black horizontal bars, and a *downward*-moving grating of green and black horizontal bars. Then, an upward-moving, black and white grating appears slightly greenish whereas a downward moving grating appears slightly reddish. This suggests that there are cells sensitive to both motion and color.

Contingent aftereffects such as these are common; any two aftereffects we've mentioned before can be linked together as in the examples here.

Knowledge and memory can also affect color perception. For example, if you're looking at a well-lit lemon, you'll have no problem seeing that it is yellow. If the lights are dimmed, you'll continue to see yellow even under scotopic conditions, where the cones cannot give color signals. The reason you still see yellow is poorly understood, but it most probably involves higher processing in the brain that links lemons and yellowness based on past experience. Such ***memory color*** is thought to play a role in color constancy.

A related experiment further supports this view. A piece of gray paper, when cut into the shape of a leaf, will appear slightly greenish even when viewed under photopic conditions. Try it!

SUMMARY

That all colors have three attributes demands that there be three cone types in the normal color observer. Based on information of ***spectral complementaries***, ***hue discrimination*** and ***microspectrophotometry***, the rather broad and overlapping ***spectral response curves*** of the *S*, *I*, and *L* cone types are found. Every color produces a triplet of responses in these cones, and colors that produce such identical response triplets are metamers even though their physical characteristics may differ. The response curves are consistent with such color matching data as summarized, for instance, in the chromaticity diagram.

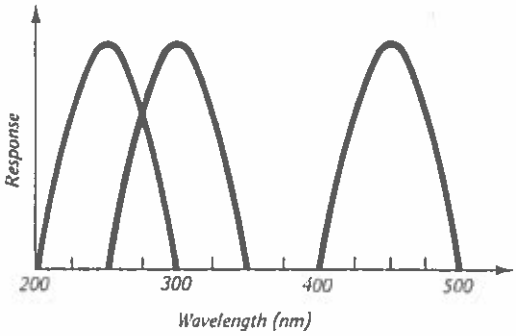
The signals from the initial (cone) stage are processed through ***opponent channels*** to form signals coding ***red minus green (r - g)***, and ***yellow minus blue (y - b)***, ***chromatic responses***. The evidence for chromatic opponency comes from ***color naming***, ***hue cancellation***, and electrophysiological measurements. Because your perception of color is related to the activity in the opponent channels, you need ***four psychological primaries*** to describe the appearance of any hue: blue, green, yellow, and red. A third, ***achromatic*** opponent channel, ***white minus black (w - bk)***, carries lightness information.

The three broad classes of ***color deficiency*** are ***monochromacy***, ***dichromacy***, and ***anomalous trichromacy***, reflecting that either one, two, or three colors are needed to match an arbitrary color. Such deficiency may result from ***missing pigments***, ***shifted pigments***, ***missing chromatic channels***, ***ineffective chromatic channels***, or a combination of these problems. Color deficiency can be revealed by matching data, a ***Rayleigh test***, ***hue discrimination***, ***overall sensitivity***, or through patterned ***color plates***.

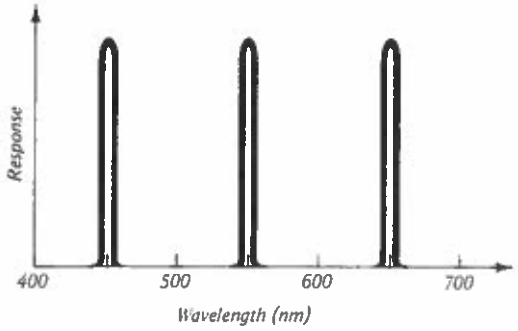
Lateral inhibition within a chromatic channel can result from ***double-opponent cells***, having a general center-surround structure. Such cells can account for ***simultaneous color contrast***, ***chromatic edge enhancement***, and ***color constancy***. ***Spatial assimilation*** of color (such as the ***von Bezold spreading effect***) occurs when small areas of one color affect another to make it appear more *like* that of the small areas. ***Negative afterimages*** in color are the ***complement*** of the color used for adaptation and can explain the phenomenon of ***Bidwell's disk***. ***Positive afterimages*** illustrate persistence of the chromatic response. Because there are different response times for different colors, temporally modulated black and white patterns can produce colors, as in ***Benham's disk*** and ***Fechner's colors***. Different aftereffects can be produced simultaneously to form ***contingent aftereffects***, such as the ***McCulloch effect***. ***Knowledge*** and ***memory*** can influence your perception of color.

PROBLEMS

P1 Suppose a Venusian is trichromatic and has the response curves in the figure. (a) What wavelength ranges can a Venusian detect? (b) What wavelengths can a Venusian detect but a normal human cannot? (c) What wavelengths can a normal human detect but a Venusian cannot? (d) Where is a Venusian's overall sensitivity probably greatest? (e) Suppose Venusian white contains broad-band light between 200 nm and 500 nm. The Venusian spectral complements are rather peculiar. One color will have several complements, while another has none. Approximately for what ranges of wavelengths does the Venusian have spectral complementaries? (f) What is the Venusian spectral complement of 425 nm? Of 450 nm?



P2 Suppose that, like Earthlings, Martians have three different color-sensitive pigments in their retinas. The sensitivities of the Martian pigments are shown in the figure. (a) What wavelengths can a Martian detect but a human cannot? (b) What wavelengths can a normal human detect, but a Martian cannot? (c) Does a Martian have any spectral complementaries?



P3 A Martian (with color-sensitive pigments as described in P2) is watching a show about street lights, on Earth color TV. One of the lights discussed is the sodium light that emits only 589 nm. The Martian is impressed by the effectiveness of this light in illuminating streets. That night he rushes out to a country road that is illuminated by sodium lights. To his chagrin, everything appears dark—it seems to him that the lights are not even turned on! Explain why the Martian could see objects illuminated by sodium light in the TV program, but not on the country road.

P4 How does the stimulation of your *L*, *I*, and *S* cones differ for two lights that differ in: (a) brightness, (b) hue, and (c) saturation?

P5 (a) What is an advantage of having significant overlap of the cone response curves? (b) What is a drawback of such significant overlap?

P6 (a) Use the bee's chromaticity diagram (Fig. 10.8) to determine the bee's spectral complement of 500 nm. (b) Use Figure 10.7 to check your answer by analyzing the bee's cone responses to the two lights. Describe how each cone is stimulated by 500 nm and by its complement.

P7 What (if it exists) is the spectral complement of 650-nm light for (a) a human, (b) a bee?

P8 Why are *two* light beams required to determine the cone absorption curves by microspectrophotometry?

P9 (a) What is meant by a psychological primary color? (b) Name all of them. (c) Which are opponent to which? (d) What is a unique hue? (e) Which unique hue does not lie in the spectrum?

P10 (a) How is hue cancellation used to determine the chromatic response in the chromatic channels? (b) Suppose only the red chromatic response due to a 650-nm light is to be canceled. What wavelength should be used? (c) What hue name would describe the color after the red is canceled?

P11 (a) How many colors does a normal person need to match an arbitrary color? (b) How many does a protanope need? (c) A tritanomalous observer? (d) A cone monochromat? (e) A neuteranomalous observer?

P12 (a) What is a neutral point? (b) What kinds of color deficients have them?

P13 A person who is color deficient and described as deuteranomalous might be missing: (a) rods, (b) cones, (c) one visual pigment, (d) two visual pigments, (e) no visual pigment, just one modified. (Choose one.)

P14 Describe two different physiological defects that might cause a person to be deuteranopic (neutral points at about 500 nm and in the purple). Specifically state what is missing, nonfunctional, or ineffective.

P15 How does placing a colored filter over *one* eye help some color deficients? Why won't placing identical filters over *both* eyes help?

P16 Suppose you have two strips of uniformly colored paper, one a dark blue and one a light blue. If you place them edge to edge, neither will seem to be uniform any longer. (a) Describe and explain the apparent nonuniformity. (b) Repeat for a yellow and a blue strip of paper.

P17 (a) Why does the color produced in the last part of the TRY IT for Section 9.4B look desaturated? (b) Does it look more desaturated than it did before you rotated the paper? Why? (Think about edge information.)

P18 By analyzing the response of a double-opponent cell of the $\mathbf{y} - \mathbf{b}$ channel, explain why the gray square that is surrounded by blue in Plate 10.3 looks yellowish.

P19 If a gray hat is brought into a room illuminated by blue light, it may still look gray. Explain this by considering

what happens to a double-opponent cell of the **y − b** channel.

P20 Small yellow dots on a blue background make this background look desaturated. On the other hand, a blue region surrounded by a large yellow region looks very saturated. (a) What are these two phenomena called? (b) What accounts for the appearance of the blue background when the small dots are present? (c) What accounts for the appearance of the blue region when it is surrounded by yellow?

P21 Mention and explain two instances where the human eye may see complementary colors that are not "really" there.

P22 You view a blue book for a minute, then shift your gaze to a white piece of paper. (a) What color do you then see? (b) What is this effect called? (c) What accounts for it?

P23 Suppose the red bulb in Figure 10.18 were replaced by a yellow bulb. (a) What color would you see when the disk rotates counterclockwise? (b) What color would you see when it rotates clockwise? (c) Explain why you see these colors.

P24 What are Fechner's colors and what causes them? Would you experience them under retinal stabilization?

P25 A subject adapts alternately to a *rightward*-moving grating of blue and black vertical bars, and a *leftward*-moving grating of yellow and black vertical bars. After adaptation, she is shown a vertical, *leftward*-moving black and white grating. What color does it appear to her?

P26 How may memory color play a role in color constancy?

HARDER PROBLEMS

PH1 From the bee's photoreceptor response curves (Fig. 10.7), deduce and draw a bee's hue discrimination curve as best you can.

PH2 Use the Martian photoreceptor response curves (shown in P2) to answer the following: (a) One type of dichromat is a color-deficient person who is missing the *I* cone. Does a Martian dichromat of this type have a neutral point? (b) Devise a color plate analogous to Plate 10.2 that would reveal such deficiency in a Martian. What colors would you use for the pattern? What colors would you use for the background? (c) Devise another simple test that could tell you quickly if a Martian were deficient in this way. (One such test involves having the Martian look at a certain light.)

PH3 Use the Martian sensitivity curves of P2 for the following. (a) Construct a chromaticity diagram for the Martian. The horizontal axis should denote the relative excitation in the Martian *L* photoreceptor, while the vertical axis should denote relative excitation of the *I* photoreceptor. Mark on the chromaticity diagram the points corresponding to 450 nm, 550 nm, 650 nm, as well as to broad-band white (*W*). (b) What point (if any) corresponds to 500-nm light? (c) Use a *Y* to mark the point corresponding to broad-band yellow. (d) Show that, for Martians, this yellow is the complement of 450-nm blue. (e) Is *Y* complementary to 400-nm blue? Why or why not?

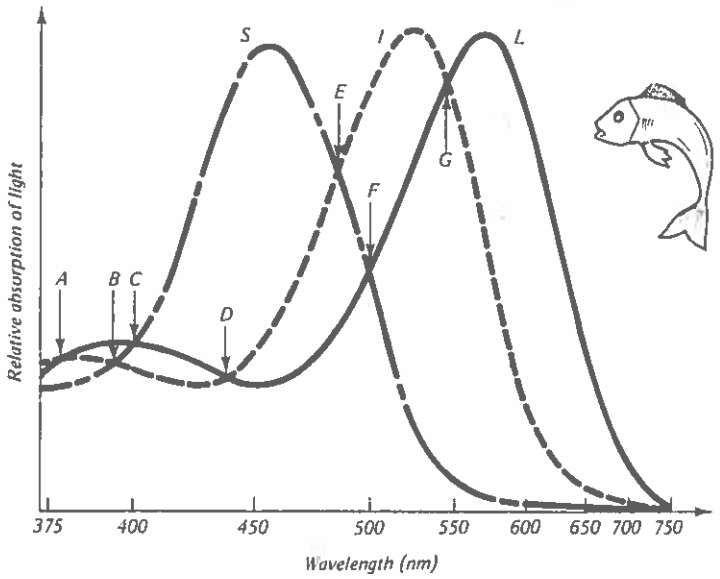
PH4 The relative absorptions of the three retinal cones of the cichlid fish *Cichlasoma longimanus* are shown in the figure. Note the large number of crossover points of the curves, which we've labeled *A* through *G*. Because of all these crossover points, the fish's spectral complementaries are strange. (a) For these fish, wavelengths above 550 nm (*G*) have spectral complements lying only between *D* and *E*. Explain why these complements lie in this, and no other, region. (b) Are there spectral complements, and if so, where, to wavelengths lying between *C* and *D*? Explain. (c) Repeat (b) for wavelengths lying between *E* and *F*. (d) Repeat (b) for wavelengths lying between *A* and *B*. Compare your result with your previous results and comment.

PH5 Using a cone response analysis similar to that of Section 10.3, state the approximate hue and saturation of a mixture of equal amounts of 470-nm and 600-nm light. Use a chromaticity diagram to check your answer.

PH6 What two different wavelengths would you use to make a unique red—one with neither blue, yellow, nor green chromatic response? Explain your answer using Figure 10.10.

PH7 Suppose in some spectral region, ranging from some point *A* to another point *B* on the horseshoe curve of the chromaticity diagram, only *two* photoreceptors respond. (a) Show that any spectral light in the region can then be matched by a suitable additive mixture of *A* and *B* only. (b) What is the shape of the horseshoe curve between *A* and *B*? Identify this region in Figure 10.6 and give approximate wavelengths at the limits of the region, *A* and *B*. (c) Show that your result is consistent with Figure 10.5.

PH8 (a) One way to distinguish between the three kinds of cone monochromat is to have the monochromat match a given broad-band stimulus with each spectral light, one at a time, and measure the amount of each spectral light needed for the match. How would this allow you to determine which kind of monochromat the subject was? (b) Another technique would be to measure absolute sensitivity to light of various wavelengths. Again, how would this



information allow you to determine which kind of monochromat the subject was?

PH9 Draw the hue discrimination results you'd expect from a deuteranope.

PH10 (a) Suppose a certain color deficient has his *L* cone response curve shifted to longer wavelengths. Would he require extra red or extra green to form a Rayleigh match? (b) What kind of color deficient might this describe? (c) What other symptoms might he have?

MATHEMATICAL PROBLEMS

PM1 Use the hypothetical photoreceptor response curve of the figure to answer the following. (a) About how much light at 650 nm will produce the same photoreceptor response as 100 units of 550-nm light? (b) About how much light at 450 nm must be added to 50 units of 600-nm light to produce the same response as 150 units of 500-nm light? (c) About how much light at 625 nm must be added to 100 units of 500-nm light to match 100 units of 450-nm light? Interpret this result.

PM2 Use the photoreceptor response curves of the figure to analyze the following matching experiment. A 500-nm test light is to be matched using three "primaries" of 450 nm, 550 nm, and 650 nm. (a) About how much light at 450 nm will produce the same *S* photoreceptor response as 100 units of 500-nm light? (b) About how much light at 550 nm will produce the same *I* photoreceptor response as 100 units of 500-nm light? (c) About how much light at 650 nm will produce the same *L* photoreceptor response as 100 units of 500-nm light? (d) Notice that the 550-nm light you used in (b) also produces a response in the *L* photoreceptor. How much 650-nm light would you need to produce the same response in the *L* photoreceptor as that produced in it by the 550-nm light of (b)? (e) Use your results from above to determine how much light at 450, 550, and 650 nm (when presented together) will match the 100 units of 500-nm light.

PM3 (a) Show that, if only two receptors respond to light in some region of the visible spectrum, the horseshoe curve on a chromaticity diagram must be a straight line in that region. (b) Using Figure 10.5, find where the corresponding straight-line region on the chromaticity diagram lies.