

CHAPTER 14

COLOR VISION

14.1. CONES AND COLOR VISION

Color vision first begins in the retina with three different classes of cones. Each class of cone contains a different photopigment due to some slight differences in the opsin molecule. Because of these structural differences, each type of photopigment absorbs light over a specific, fairly broad range of wavelengths.

14.1.1. Spectral sensitivity functions.

For each class of cone, it is possible to make a graph showing how much light is absorbed by the photopigment as a function of wavelength. The resulting plot is one form of *spectral sensitivity function*. Although each cone photopigment absorbs light over a different range of wavelengths, and peaks at different wavelength, the ranges overlap to a large degree.

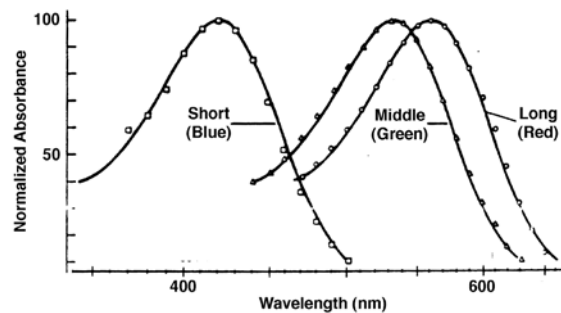


Figure 14-1. Absorption spectra for the three classes of human cones. The vertical axis represents the ability of the cone photopigment to absorb light at each wavelength within the visible spectrum as represented on the horizontal axis.

"Red cones" absorb long wavelengths, "green cones" absorb medium wavelengths, and "blue cones" absorb short wavelengths.

14.1.2. Cones and color blindness.

Color blindness is a fairly common condition, occurring in about 2% of the population. The most common cause of color blindness is the lack of one or more cone photopigment(s) or an altered absorption spectrum in one or more of the photopigments.

Color blindness is an inherited characteristic. It is far more common in males than in females. This is because the cone photopigment genes are located on the X-chromosome (men have only one X-chromosome, but women have 2 X-chromosomes, greatly increasing the chances of having a "good" one).

14.2. COLOR DISCRIMINATION

We only have 3 types of cones. Moreover, the spectral sensitivity curves for the three cone types overlap, with the result that just about any wavelength of light will activate more than one class of cones. Given these observations, how is it that we are able to distinguish so many colors?

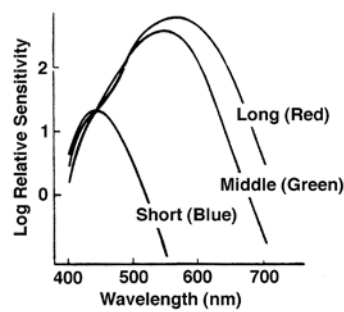


Figure 14-2. Another form of spectral sensitivity function plots the responsiveness of the three classes of cones (i.e., how easily they are stimulated to hyperpolarize) as a function of wavelength.

Thinking back to the chemical senses, where taste and odor quality were represented by relative amounts of activity across a population of neurons, the answer becomes clear. Color must also be represented by a population code. Because the relative amounts of activity in the different classes of cones are different for each wavelength of light, we are able to use this information to identify many colors and to discriminate small gradations of those colors along the entire visible spectrum.

Review: Two different ways to encode information in the nervous system.

- Specificity code, or labeled line code:* an individual neuron conveys unambiguous information, independent of activity in other neurons.
 - Population code:* information is conveyed by relative amounts of activity in different neurons.
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14.2.1. The trichromatic theory of color vision.

The idea that three different types of photoreceptors participate in a population code for color is often referred to as the "*trichromatic theory*" of color vision.

In addition to the existence of the three different classes of cone photopigments, considerable support for the trichromatic theory comes from observations of human color perception. For example, experiments in which subjects are shown different colors and asked to

match them by mixing only three pure wavelengths of light in various proportions show that humans can, indeed, match any color using only three wavelengths of light - red, green and blue.

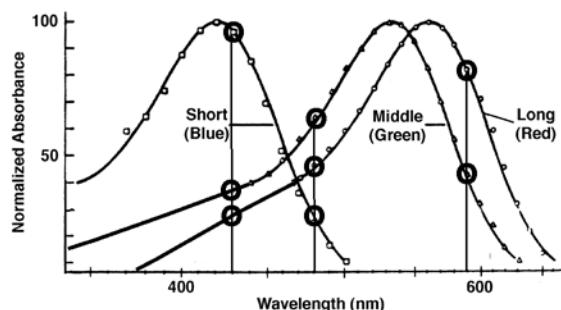


Figure 14-3. Almost any wavelength of light will be absorbed by more than one class of cones, at least to some degree. A shorter wavelength (left) will affect blue cones the most, followed by green, then red cones. A mid-range wavelength (center) will affect the green cones the most, followed by red, then blue.

14.3. RETINAL NEURONS AND COLOR VISION

14.3.1. Color-opponent receptive fields.

The receptive fields of ganglion cells innervated by cones have a center-surround organization just as do those innervated by rods. However, in the case of the cone pathway, the center and surround may be *color-opponent*. This means that the ganglion cell is excited by one color (e.g., yellow) in the center of the receptive field, and inhibited by the "opposite" color (e.g., blue) in the surrounding area.

Clearly, color-opponent fields could increase our perception of color contrast just as on/off fields increase our perception of light-dark contrast.

Color "opposites" include blue and yellow, as well as red and green. Because there are no "yellow cones", the blue-yellow contrast mechanism presumably depends on combining information from the red and green cones and comparing it with information from the blue cones.

14.3.2. The opponent-process theory of color vision.

Some perceptual phenomena, including color opposites, cannot be explained solely on the basis of the trichromatic theory. Not only is each color perceived as having an "opposite". We also perceive colored after-images after looking at a colored area in the visual field. If we look at a colored pattern and then look away, the after-image will be the color "opposite" of the object we were looking at.

The trichromatic theory and opponent-process theory of color vision are not mutually exclusive. Each illustrates a different aspect of the processes that take place when we perceive color. The creation of color-opponent cells by retinal circuitry may represent the first stage of the comparisons that must take place in order to measure relative amounts of activity in the red, green and blue cone outputs.

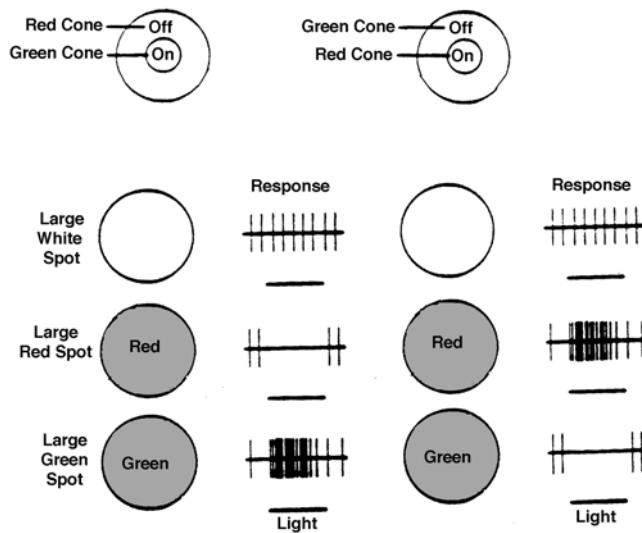


Figure 14-4. Examples of two retinal ganglion cells with color-opponent receptive fields (red-green). Both cells respond moderately to a large spot of white light, because it contains both red (which turns off the cell on the left and turns on the cell on the right) and green (which turns off the cell on the right and turns on the cell on the left). A large red spot fills the surround of the cell on the left and completely suppresses its response; it fills the receptive field center of the cell on the right and stimulates multiple action potentials. For a large green spot, the situation is reversed.

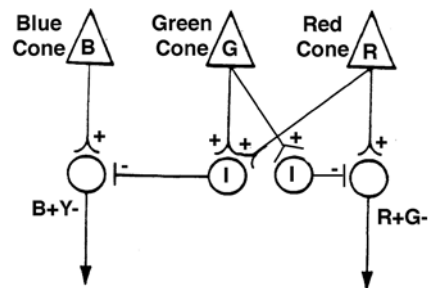


Figure 14-5. Hypothetical neural circuit for creating color-opponent receptive fields. B+Y- is a blue-on center/yellow-off surround cell; R+G- is a red-on center/green-off surround cell. + indicates an excitatory input, - an inhibitory input.