Color Perception

Robert Kentridge, Charles Heywood, and Jules Davidoff

Introduction

Color is the name we assign to the experience elicited by an attribute of a surface, namely, its spectral reflectance. Color sensations have a reliable, though complex, relationship to the spectral composition of light received by the eyes. The visual system tackles a series of computational problems in the course of processing wavelength. Variation in the wavelength of light is isolated from variation in its intensity. The spectral reflectance properties of surfaces are isolated from the effects of the spectral composition of light illuminating them (matching surfaces with the same reflectance properties in different parts of the visual scene or under different illuminants are the two problems of color constancy). Finally, the resulting continuous color space is partitioned into discrete color categories. In addition, it will become clear that wavelength signals can be used in the course of perceiving form or motion, independent of their role in the subjective experience of color.

Wavelength-Dependent Differences Within the Visual System

Color percepts derive from light that varies in both wavelength and intensity. A single type of photoreceptor in the eye responds with differing efficiency to light over a wide range of wavelengths. Consequently, a visual system in which there is only a single type of photoreceptor inevitably confounds wavelength and intensity. A visual system containing photoreceptors that differ in their spectral response can, in principle, disambiguate wavelength and intensity by comparing the responses of different types of receptors.

Receptors

Wavelength-selective processing can be traced from differentially wavelength-sensitive cone types in the retina to the lateral geniculate nucleus (LGN) and then on to striate cortex and extrastriate areas beyond it. There are three cone types in the human retina, with peak sensitivities at 560 nm, 530 nm, and 430 nm and referred to as L, M, and S (long-, medium- and short-wavelength-sensitive) cones, respectively. In some people one or more of these cone types are missing; hence, color sensations that would normally be perceived as distinct are confused, and the individuals are “color-blind.” The functions relating the sensitivities of these cone types to the wavelength of stimulating light can be inferred by comparing the wavelength sensitivities of color-blind and normal observers or by examining the effects of adaptation to light of one wavelength on sensitivity to light of other wavelengths. Figure 1 shows the relative absorption efficiencies of the three cone types and the typical pattern of behavioral sensitivity to intensity modulation.

The output of cones provides information about an object’s state, for example, allowing ripe and unripe fruit to be discriminated. The peak sensitivities of photoreceptors appear exquisitely matched to maximize the discriminability of the foliage or fruits that form the diets of a number of species of primates (Sumner and Mollon, 2000). Studies of the genetic coding of cone pigments indicate that human trichromacy evolved from ancestral dichromacy through the division of a single long-wavelength-sensitive pigment into distinct L and M pigments (Bowmaker, 1998).

The Combination of Receptor Signals in the M, P, and K Channels

Three anatomically distinct cell types in the retina combine cone signals in distinct ways (Dacey, 2000). In all cases, the response has a “center-surround” organization. A set of cones from one part...
of the visual field influences the cell in one way, while a set of
cones from the surrounding area influences it in a different way.
Parasol cells receive input from L and M, but not S, cones. Inputs
from L and M cones are summed in both the center and surround
fields of parasol cells (Figure 2A). Parasol cells cannot convey in-
formation about wavelength independent of intensity. They project
to the magnocellular layer of the LGN, which in turn projects to
layers 4C\text{\textalpha} and 4B of primary visual cortex (V1). This pathway,
and its onward projections, is known as the M-channel. The M-
channel contributes to the perception of luminance and motion but
does not convey wavelength-coded signals.

Midget ganglion cells have color-opponent receptive fields. This
center-surround organization sharpens the effective wavelength se-
lectivity of the ganglion cell, helping to unconfound wavelength
and intensity variation. Consider first a nonopponent cell, sensitive
to medium wavelength light. This cell will produce the same re-
sponse to a given intensity of medium wavelength light, or a
stronger intensity of longer wavelength light. Although its peak
sensitivity is to medium rather than longer wavelength light, be-
cause sensitivity only reduces gradually as wavelength deviates
from the peak, the longer wavelength light still produces a re-
sponse. Now consider the responses of an opponent cell excited by
medium wavelength light in the center of its field and inhibited by
long wavelength light in the surround to different intensities and
wavelengths of light falling on its entire receptive field. Medium
wavelength light produces excitation in the center and no inhibition
in the surround; there is a net increase in the cell’s firing rate.
Higher intensities of medium wavelength light elicit stronger net
responses. A slightly longer wavelength produces some excita-
in the center field of the ganglion cell but also a small inhibitory
response in the surround. These roughly balance, and so the firing
rate of the cell is largely unaffected by the stimulus. The same
situation applies to a high-intensity stimulus; again, central exci-
tation is balanced by surround inhibition. This ganglion cell is
therefore capable of conveying information solely about the intens-
ity of medium wavelength light.

The vast majority of foveal midget ganglion cells are driven by
L or by M cones in the center of their receptive field; these centers
can be either excitatory or inhibitory. Away from the fovea, midget
ganglion cells lose their spectral opponency, as more than one cone
type drives both the center and surround. There appears to be little
input from S cones to midget ganglion cells, just as there are very
few S cones in the retina. About 2\%–3\% of parafoveal midget
ganglion cells have S-OFF central receptive fields with an ON sur-
round driven by both L and M inputs (Figure 2B). There are no S-
ON center midget ganglion cells.

Small bistratified ganglion cells receive inputs from all three
cone types; however, their central field always appears to be driven
by an excitatory input from S cones, while their surround combines
inhibitory L and M inputs. The bipolar cells that convey signals
from cones to the central field receive inputs only from S cones
and are driven by multiple cells, unlike the bipolar cells that drive
the central fields of midget ganglion cells, which receive inputs
from single cones. The result is that, although these cells do show
clear spatial and spectral opponency, the size of the central field
(100 \, \mu m standard deviation) is much larger than that found in
midget ganglion cells (25 \, \mu m) (Figure 2C). The surround fields of
small bistratified cells are smaller than those of midget ganglion
cells (140 \, \mu m and 205 \, \mu m, respectively), so these cells show rela-
tively weak spatial opponency. One additional consequence of the
S-cone specificity of the small bistratified cells is that the S-ON
center, LM-OFF surround organization extends into the peripheral
visual field, whereas midget ganglion cells lose spectral opponency
beyond the parafovea. There are no S cones in the central 0.3 de-
grees of the visual field, so foveal vision is effectively color-blind
to color variation mediated by S cones.

Midget ganglion cells project to the parvocellular layer of the
LGN, and thence to layer 4C\text{\textbeta} of V1. This pathway, and its onward
projections, is known as the P-channel. The P-channel conveys
information about long and medium wavelengths and fine detail.
It has been suggested that small bistratified ganglion cells convey-
ing short wavelength information also contribute to the P-channel.
However, it is now widely believed that small bistratified cells
drive a distinct class of geniculate cells. The P-channel does contribute to motion perception; however, its contribution is weaker than that of the M-channel and nonveridical—the speed of perceived motion depends on the chromatic contrast of the stimulus.

Small bistratified ganglion cells form the start of the K-channel (Hendry and Reid, 2000). They project to koniocellular neurons in the LGN, distinguished from magno- and parvocells on the basis of their cell membrane chemistry. These cells mainly form layers intercalated between the parvo- and magnocellular layers, but some K-cells are also found in the parvocellular layer, with a smaller number being found in the magnocellular layer. K-cells project not only to layer 1 of V1, but also directly to V2. There is a particularly rich innervation of V2 by K-cells with foveal receptive fields. K-cells’ receptive fields are large (at least as large as those of cells in the magnocellular layer) and often have irregular shapes. K-cells convey information contributing to color sensations, depending on contrasts of the output of S cones to combinations of M and L cone outputs; they may also contribute to motion perception.

The position summarized above remains controversial and has been challenged on a number of counts. In particular, it has been argued that the K-channel alone conveys chromatic signals (including L versus M information), while the P-channel is dedicated to fine spatial vision (Calkins and Sterling, 1999).

**Primary Visual Cortex**

The M, P, and K pathways project to groups of cells within V1 that can be distinguished on the basis of cytochrome oxidase reactivity (Livingstone and Hubel, 1984). K and P, but not M, pathways innervate cytochrome oxidase–stained regions known as blobs. P and M, but not K, pathways innervate the remaining regions, known as interblobs. There is recent evidence that cells show different specificities for wavelength processing in V1 (Conway, 2001; Johnson, Hawken, and Shapley, 2001). The cells discussed earlier in this article had a “single-opponent” organization. They can convey information about the intensities of light of particular wavelengths while being relatively uninfluenced by other wavelengths. They cannot, however, convey information about wavelength contrast. This requires “double-opponent” cells in which a central receptive field excited by one wavelength and inhibited by another is surrounded by a field in which the same two wavelengths have the opposite actions (Figure 1D). Double-opponent organization allows a cell to convey a consistent response to the boundary between two surfaces, regardless of the light illuminating them. If the illuminant changes, for example lengthening in wavelength, then longer wavelength light will be reflected from both sides of the boundary. Consider a double-opponent cell whose central receptive field is excited by long wavelengths and inhibited by medium wavelengths and whose surrounding field is inhibited by long wavelengths and excited by medium wavelengths. Imagine that the cell’s receptive fields fall on a boundary between a pair of surfaces, one of which is good and one poor at reflecting long wavelength light, so that the good reflector falls in the cell’s central field. The net result will be excitation—that ratio of long to medium wavelength light is high in the central field and low in the surround.

When the light illuminating both sides of the boundary lengthens in wavelength, the L/M ratios in both the excitatory center and the inhibitory surround will increase. The response of the cell is therefore largely unaffected by a change in illuminant. Obviously, such cells perform the preliminary computation necessary for color constancy. Of course, their responses only indicate spatially local changes in surface reflectance. To recover absolute reflectances throughout a scene, then, one also needs to estimate the response likely to be elicited by some fixed “anchoring” color in that scene and then to integrate local border contrasts from that anchoring point (see, e.g., Gilchrist et al., 1999, for similar arguments with respect to lightness perception). Until recently, evidence for the existence of double-opponent cells was controversial; however, recent findings indicate that such cells occur in V1 and, moreover, are sensitive to the orientation of chromatic (wavelength-dependent) borders as well as to the contrast of cone ratios across them.
Extrastriate Cortex

The clinical condition of cerebral achromatopsia, in which patients lose the ability to perceive color not as a result of retinal abnormalities but rather as a consequence of brain damage, provides strong evidence that brain areas specialized for color perception exist beyond striate cortex. The identification of these areas is, however, wreathed in controversy. The damaged areas include extrastriate cortex in the vicinity of the fusiform and lingual gyri. Neuroimaging studies have also shown increases in cerebral blood flow (implying increased brain activity) in these areas when normal subjects observed colored scenes. Zeki et al. (1991) therefore suggested that there was a specific color center in human extrastriate cortex. Early studies in which the responses from single neurons in monkeys were recorded in response to visual stimuli suggested that the color center might correspond to cortical area V4. A number of problems arose with this interpretation. The selectivity of the response of neurons to particular characteristics of stimuli differs only in degree between brain areas. Some neurons in nearly all visual areas respond selectively to wavelength; the proportion in V4 is not comparatively large. In addition, damage to area V4 in monkeys did not cause deficits in discriminations based on wavelength, although deficits were induced by damage to areas anterior to V4 (Heywood and Cowey, 1998). These findings appeared consistent with neuroimaging studies in humans identifying a color-selective area anterior to V4, christened V8 (Hadjikhani et al., 1998). Whether V8 really corresponds to the anterior areas that, when damaged, caused deficits for wavelength discrimination in monkeys remains controversial.

Wavelength Information Contributes to More Than Color Perception

The fact that our visual system can disambiguate wavelength and intensity makes it possible to ignore variations or sharp changes in intensity caused by shadows. One role of a wavelength-selective visual system is therefore segmentation of the visual scene on the basis of chromatic boundaries. Often chromatic boundaries will provide better cues for segmenting objects from their backgrounds than brightness boundaries—for example, in the dappled sunlight of a forest floor.

The residual abilities found in cerebral achromatopsia indicate that wavelength is exploited in more than one way. Although cerebral achromatopsics deny a phenomenal experience of color and cannot discriminate between stimuli differing only in wavelength, they can effortlessly perceive boundaries between areas differing only in wavelength (Heywood, Kentridge, and Cowey 1998). Their ability to use wavelength information to perceive form or motion, but not to perceive color suggests, that these functions may have distinct anatomical bases. Destruction of the putative color center, be it V4 or V8, disrupts the perception and experience of color, but not other functional uses of wavelength.

Discussion

Some of the earliest insights into the coding of color derived from work on color mixing. Following his discovery of the composition of white light, Newton developed the concept of the color circle, an arrangement of light sources around the periphery of a circle in which the mixture of any pair of diametrically opposite lights would produce white. Despite the color circle showing a continuum of light sources, Newton identified five primary colors (red, yellow, green, blue, and a violet-purple). However, attempts were soon made to discover how few colors were required in order to produce all other colors by mixing. Although there was some disagreement about which colors were primary, it was apparent to most investigators that three were sufficient. This culminated in the Young-Helmholtz trichromatic theory of color vision. Young believed that the primaries were red, green, and violet.

The fact that we require three primary colors in order to produce the full range of colored sensations reflects the fact that we have photoreceptors sensitive to three distinct wavelength distributions.
The consequence is that any combination of lights that produces
the same amount of activation in the three receptor types will pro-
duce the same response in the visual system and the same percep-
tion of color. There are, therefore, a large number of colors that are
potential primaries.

Other features of color perception suggest an alternative to the
trichromatic theory. In particular, there are limits to our abilities to
see pairs of colors tinting one another. People perceive bluish reds
and yellowish reds, but never greenish reds; they perceive reddish
yellows and greenish yellows, but never bluish yellows. These op-
ponent color pairings, red-green and blue-yellow, are also apparent
in afterimages, color shadows, and color contrast. Observations
such as these led Hering in 1905 to suggest a four-color opponent-
process theory of color vision.

Both these theories assumed that the similarities between color
sensations are completely determined by the outputs of the wave-
length-dependent neurons in the visual system. For example, it is
tempting to believe that opponent processes operating in V1 are
the direct precursors of our space of colors. They have been taken
as the sources of four primary colors (red, green, yellow, and blue)
that are irreducible to other colors, and each contains one sensation
that is pure (unique) in that it contains no trace of any other pri-
mary. However, the outputs of the cells in V1 would not produce
these unique colors even if there were agreement as to what they
might be (Saunders and van Brakel, 1997; Webster et al., 2000).
Nor would the categories of color arise from variation in discrim-
ination across the visible spectrum. The wavelengths at which there
are minima in threshold do not correspond to the boundaries be-
tween primary colors. Controversially, it has been argued from
cross-linguual evidence that color categories are determined by the
speaker’s color terms. The neurophysiology produces a given per-
cpt, but the assignment of that percept to a color category is a
matter of agreement among observers.

Roadmap: Vision
Related Reading: Contour and Surface Perception; Retina

References


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Figure 1. The relative absorption efficiencies of short-, medium-, and long-wavelength cone types, labeled s, m and l, are shown as dotted, short-dashed, and long-dashed lines, respectively. The solid line shows sensitivity to increments in luminance for lights of different wavelengths. The sensitivity decreases falling between the peaks of the cone absorption spectra are known as Sloan-Crawford notches.
Figure 2. Schematic representations of receptive field organization of cells in (A) the M-channel, (B) the P-channel, and (C) the K-channel; (D) an example of receptive field organization of a cortical double-opponent cell.