

A different point of hue

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A distinguished line-up of scholars recently got together to stir up discussion about the physiological basis for color and have, with a simple manipulation of decades-old data, challenged one of the fundamental tenets of our current understanding of the neurobiology of color (1).

Understanding color is not easy. Newton made some headway, but his demonstration of color's physical basis provided only limited insight because, as Young (2) pointed out, there simply is not enough space for a receptor for each of the seven million or so perceivable colors at each retinal location. Young argued for a triplet color code, and we now know that such a code exists in the form of the three cone types (Fig. 1).

Young's idea made color a construction of the brain, not a physical attribute, and paved the way for opponent color theory (3) in which color is determined not by trichromacy but by three opponent processes: red-green, blue-yellow, and black-white. This theory gained ground because it accounted for the fact that we are unable to see a continuous mixture of "reddish-greens" and "bluish-yellows," which should be perceivable if color were simply trichromatic.

In the 1960s, De Valois *et al.* (4) discovered that many cells in the lateral geniculate nucleus (LGN) (the thalamic relay from the retina to primary visual cortex) show chromatic opponency. LGN cells inherit this property from retinal ganglion cells. Some are excited by red and inhibited by green (R^+/G^-); others are excited by blue and inhibited by yellow (B^+/Y^-); others are excited by white and inhibited by black (W^+/Blk^-). R^-/G^+ , Y^+/B^- , and Blk^+/W^- cells also exist. It was natural to suggest that these cells are the basis for opponent colors, and most neuroscientists today accept some version of this view: the three cone types embody trichromatic theory, and the chromatically opponent LGN cells, each receiving specific cone inputs, represent opponent theory, although the purity of the cone inputs is disputed (5–7).

In a recent issue of PNAS, Romney *et al.* (1) have done two straightforward things to shake up this interpretation. First, they plotted the spectral reflectance from the 1269 Munsell color chips[§] in "cone space." Cone space is often used to show the relative input of the three cone types to neurons, but Romney *et al.* used

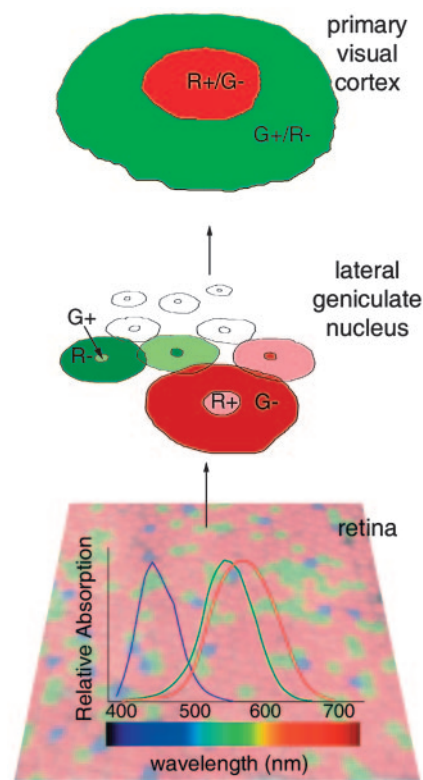


Fig. 1. Neural basis of color. The three types of cones (Bottom) are sampled by neurons in the lateral geniculate nucleus (Middle). R^+ indicates excitation by red cones; G^- indicates suppression by green cones. Spatially and chromatically opponent neurons arise in primary visual cortex (Top).

it to show how each Munsell color chip would activate the three cone types under standard illumination (Fig. 2A). Cells in the parvocellular layers of the LGN are clustered in cone space: they receive on average balanced opponent input from L versus M cones (8). As Romney *et al.* point out, the Munsell chips are not randomly distributed when plotted in cone space, but they cluster like LGN cells.

The second thing Romney *et al.* (1) did was to plot in color space the spectral sensitivity of the 147 LGN cells measured by De Valois *et al.* (4) (Fig. 2B). Color space uses perceptual coordinates of hue and saturation. Romney *et al.* treated the spectral sensitivities of the LGN cells as reflectance spectra, enabling a direct comparison with Munsell reflectance spectra. According to Munsell's original aim, the color chips populate the entire color space. Curiously, the LGN data seem to do so, too, despite being clustered in cone space (Fig. 2).

The clustering of LGN cells in cone space has been taken as proof that LGN cells represent the physiological implementation of opponent color theory. Romney *et al.* (1) ask how we can keep this conclusion if (i) the Munsell color chips also cluster in cone space and (ii) the LGN cells do not cluster when their spectral sensitivities are plotted in perceptual space. Well, they say, we cannot: "The LGN cells are more or less evenly distributed in perceptual space by ganglion cells that aggregate cone receptor responses in a large variety of combinations that represent all areas of the [color] space."

This punchy conclusion is going to stir some hearts because it threatens to undermine the idea that parvocellular cells embody opponent-color axes and, more generally, aims once again to make color a physical attribute tied to reflectance spectra.

But should we be surprised that the Munsell color chip data cluster in the same pattern as the LGN cells in plots of cone space? Well, maybe not. Munsell's color scheme has successfully standardized color and is used in almost all jobs that require color identification. Munsell used his own visual system in developing his system, so it might not be a coincidence that the reflectance spectra of Munsell's color chips match the sensitivity of the LGN cells if LGN cells serve as the building blocks for color discrimination. But Romney *et al.* (1) assert that reflectance spectra of natural objects, not just the Munsell spectra, also cluster in cone space just like the Munsell data (A. K. Romney, personal communication). Does this mean that the nonrandom distribution of LGN responses in cone space is an adaptation to the same nonrandom distribution of reflectance spectra in the world and not the brain's implementation of opponent color theory?

We don't think so. For starters, the clustering of Munsell chips in cone space is not nearly as tight as that of LGN cells.

See companion article on page 9720 in issue 27 of volume 102.

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[§]The Munsell color chips are small pieces of colored paper, like paint samples at the hardware store, that define a 3-dimensional color space, in terms of hue, saturation, and brightness, that describes all reflected colors.

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