Color Vision Cells Found in Visual Cortex

A discrete region of the visual cortex contains cells necessary for the perception of color contrast

Although neurophysiologists have learned in some detail how the visual system works, at least in the early stages of the pathway, and how it is that we see light intensities and contours, far less is known about the physiological basis of color perception. There were theories about what sort of cells would be necessary to explain the neurological basis of color perception, but those cells have been hard to find.

David Hubel and Margaret Livingstone at Harvard Medical School now have found those cells in an anatomically distinct region of the visual cortex. Hubel gave an invited lecture on this work at a meeting at Washington University School of Medicine in St. Louis.* Their findings are a major step toward explaining color perception in cellular terms. "At any rate," say Hubel and Livingstone, "the apparent tendency of the visual cortex to process form and color separately would seem to vindicate those who in recent years have argued for a processing of different kinds of perceptual information along separate parallel channels."

Among other things, we would like to find a physiological basis for Land's work," says Hubel, explaining that Edwin Land, inventor of the Polaroid Land camera, has formulated precise rules for color perception. Naïvely, it might be assumed that those objects that reflect red light, for example, would always be those that appear red. Land showed, however, that this assumption is false. The color that an object appears depends on the wavelengths reflected by everything else in the scene, including objects at the very borders of the visual field. When a scene is illuminated by long wavelength light only, the objects reflecting the most light look more white or washed-out pink than red. You never get good red unless you have other objects in the scene that reflect middle and short wavelengths (greens and blues). The relationship of perceived color to the wavelength composition of a scene is so precise, Land found, that if he is provided with the wavelength compositions of all the objects in a scene, he can predict what color each object will appear.

Hubel and his associate Torsten Wiesel have been studying the visual system for more than 20 years, and as a result they and others have come closer to understanding how nerve cell firings translate into vision of a black-and-white world. The cells in the lateral geniculate body, for example, mostly are concerned with contrasts of light and are fed by nerves projecting directly from the eye. A particular cell fires when a corresponding area of the visual field is stimulated by a small spot of light of a specific size. Spots that are larger than an optimum size suppress the lateral geniculate cell from firing.

Nerves project from the lateral geniculate body to the primary visual cortex. In the visual cortex are cells that fire when the animal sees line contours. Each of these cells has a particular orientation of line to which it responds. As you move tangentially across the cortex, the line orientations rotate. Information passes from these orientation-responsive cells to other areas of the cortex where it is analyzed further in ways that are still poorly understood.

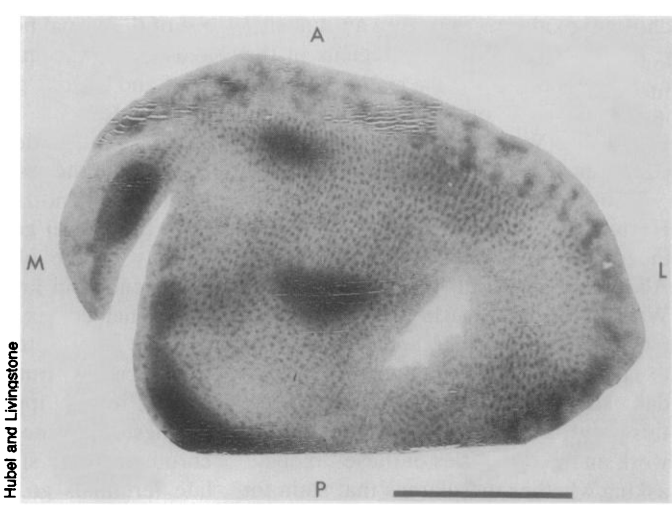
When it came to color contrast, investigators had an idea of what sort of cell to look for. It would be a so-called double opponent cell—one that would fire optimally in response to, say, a red spot on a green background, would fire less well in response to a red spot on a black or white background, would not respond at all to red on red or green on green or to white on white, and whose firing would be suppressed by a green spot on a red background. (The terms "red" and "green" refer to long and short wavelength light and not to perceived colors.) Thus such a red-green double opponent cell would make red appear much redder against a green background than against a red one.

The lateral geniculate body, which links the eyes to the visual cortex, obviously must carry some color information, physiologists reasoned. So they started there in the search for double-opponent cells. The results, however, were not what they had expected. The geniculate cells seemed to be just the reverse of what was required for color contrast. The cells, Hubel explained in his lecture, "give opponent color responses but the opponent mechanisms are spatially segregated." They are turned on, for example, by long wavelength light in the receptive field center and are turned off by short wavelengths in the area surrounding the receptive field. Such a cell will fire when stimulated by a red spot of light but will not fire if the red spot is ringed by a green band. "The problem is that although these cells certainly are color coded, they do not do anything for color contrast," Hubel remarks.

In the 1960's Nigel Daw, who is now at

Blobs in the visual cortex

This macaque visual cortex was stained for cytochrome oxidase after it was sliced tangentially. The section passes through layers 2 and 3.



Hubel and Livingstone

*The First McDonnell Conference on Higher Brain Function was held on 23 and 24 September.

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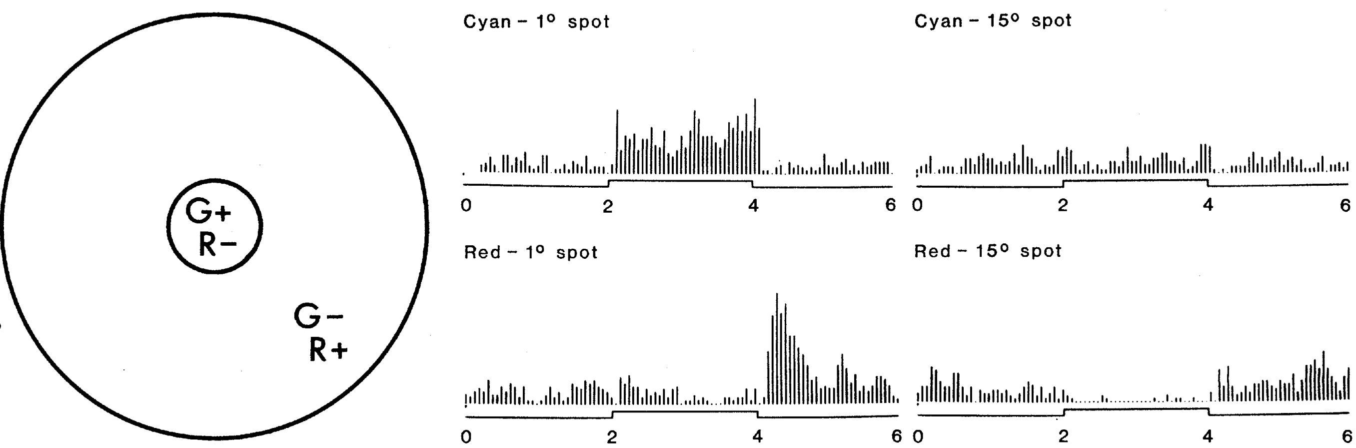

Hubel and Livingstone

A green-red double opponent cell

(Left) The drawing is of the receptive field of the cell. G means green, R means red, + means the stimulus increases the firing rate of the cell, and − means the stimulus suppresses the firing of the cell. (Right) The responses of the cell to red and green spots of light demonstrate the pattern indicated in the drawing. The cell showed no response to white light.

Washington University in St. Louis, found double opponent cells in the goldfish retina. He and Alan Perlman, who is also at Washington University, then looked diligently for double opponent cells in cats and monkeys. They found none in the monkey geniculate but oddly enough found a few in the cat geniculate. Cats are known to have color vision, but it is poor compared to that of most primates.

Then, in 1968, Hubel and Wiesel found two or three double opponent cells in the monkey visual cortex. "We couldn't understand why there were so few," says Hubel. Two years ago, Charles Michael of Yale Medical School reported finding these cells in layer IVc of the visual cortex, which is a band of tiny close-packed cells that get most of their input from the geniculate.

The key to finding an anatomical structure containing double opponent cells came in 1978 when Margaret Wong-Riley, now at the Medical College of Wisconsin, sent Hubel and Wiesel a letter saying that when she stained cells of the monkey visual cortex for cytochrome oxidase, she saw an unusual pattern—a set of orderly regions in the cortex was taking up the stain. Although interested in Wong-Riley's discovery, Hubel and Wiesel did not immediately pursue it.

Two years later, Hubel and Jonathan Horton at Harvard Medical School and, independently, Anita Hendrickson and Alan Humphrey at the University of Washington in Seattle cut the cortex parallel to the surface and learned that the tissue taking up the cytochrome oxidase stain forms a polka dot array. At this point, Livingstone and Hubel got to work on the properties of these "blobs," asking whether these areas that stain for cytochrome oxidase have different physiological characteristics than the rest of the cortex.

"We found to our amazement that the cells in the blobs are not orientation-specific," says Hubel, noting that all the other cortical cells he had looked at other than those in layer IVc, respond to straight lines of particular orientations. "Upon looking more carefully at the properties of the blob cells, we found they were center-surround, rather like geniculate cells." But they were not exactly like those in the geniculate. A large proportion of them were double opponent cells or were cells with a color opponent center but no surround. For example, they were cells that respond to a red light and are suppressed by a green light independently of the surrounding area. "The cells in the blob region are loaded with color interest. Half or more, probably the majority, are double opponent cells. We saw hundreds of double opponent cells in the past few months."

The blob cells, then, do exactly what is needed for the sort of color perception that Land described, but over small areas of the visual field. "They are not the answer to your prayers as far as explaining Land's work goes, but they may be an intermediate," Hubel says.

The next question is, How do the blob cells fit into the rest of the visual system? Livingstone and Hubel believe that cells from the lateral geniculate body project directly to the blobs, which are most conspicuous in layers two and three of the visual cortex. It is already known that the geniculate projects to layer IVc of the cortex, but it was not known to project to the upper layers. Hubel and Livingstone suspect, however, that cytochrome oxidase stains where the geniculate terminals go. Cytochrome oxidase stains layer IV of the cortex densely and uniformly. And when Hubel and Livingstone took horseradish peroxidase and injected it into the geniculate, they found, says Hubel, "Much to our surprise the tracer went not only to layer IV but also to the blobs."

Livingstone and Hubel also looked in the visual cortex at cells between the blobs. They found no nonoriented color cells there, although Wiesel and Hubel had found, in 1968, that a few of the orientation-specific cells there respond to colored lines. These cells, Hubel speculates, may be getting inputs from blob cells.

Livingstone and Hubel's hypothesis is that color perception is to some extent separate from but related to the already studied form system. After nerve impulses reach the blobs, these investigators believe, they go to other areas that take in a larger part of the visual field—sort of an integrator region.

Recently, Semir Zeki of University College in London described an area just in front of the visual cortex and several stages beyond it in processing that might be the integrator region. Cells in this area, Zeki reported, respond to color but the way they respond to small spots of color is affected by colors in a wide visual field.

Not all animals, of course, have color vision. Do they all have blobs? Horton and Hubel report that in cats, at least, blobs seem not to exist. They did, however, find blobs in every primate they looked at, including humans.

For now, the study of color perception is just opening up. The next step is to determine whether the terminals where the blob cells project provide the broader picture of color perception that Land described.—GINA KOLATA