Color in the cortex revisited

Karl Gegenfurtner

Johnson, Hawken and Shapley investigate color information in primary visual cortex (V1). Contrary to current opinion, they find that many neurons in V1 are highly sensitive to color and that color information is prominently used in the analysis of visual form.

For more than a century, the study of color vision has been very successful. The absorption properties of the cone photoreceptors in the retina have been determined up to many decimal places, the spatial arrangement of the different types of cones has been measured in the living human eye, and the retinal circuitry that transforms these signals and passes them on to visual cortex has been laid out in great detail (see ref. 1). However, we still do not have a good idea of what is happening to all these signals in the cortex[2]. In this issue, Johnson and colleagues[3] describe how information about color and form gets integrated in the neural responses in primary visual cortex.

Most current theories of the visual system are based on the so-called coloring-book idea. First, the image is processed by a purely black-and-white system that extracts edges and object boundaries. In a subsequent step, a color-based system kicks in and fills in the regions between the edges. This scheme with two separate systems for edge detection and filling in[4] is supported by findings from anatomy and physiology[5], suggesting independent pathways in the visual cortex for color and form information.

This idea also agrees with observations made when an image is decomposed into its luminance and chromatic components (Fig. 1). In the black-and-white luminance image, all the fine spatial detail is seen, whereas in the chromatic or 'isoluminant' image, which has the same luminance at all pixels, fine detail is lost. However, this type of comparison between a high-contrast, black-and-white image (Fig. 1c) and an isoluminant image (Fig. 1b) is not exactly fair. Whereas the black-and-white image leads to a very high contrast in the cone photoreceptors, the cone contrasts for the isoluminant image are much smaller, by about a factor of 30. When this factor is controlled, visual performance for isoluminant stimuli can match or even exceed performance for black-and-white stimuli[6].

A similar argument holds for characterizing the properties of cells in the visual system. Very few cells in the cortex respond well to isoluminant stimuli but not to black-and-white stimuli. These 'color' cells have properties similar to some of the cells in the parvocellular layers of the lateral geniculate nucleus. They respond best to uniformly colored patches and less to spatially structured stimuli[3,5,7]. In previous studies, it was simply assumed that all other cells would be concerned only with the analysis of luminance information.

Johnson and colleagues[3] recorded extracellularly from individual neurons in area V1 of anesthetized macaque monkeys and measured the spatial frequency tuning of the neurons both with luminance-defined sinewave gratings and with isoluminant gratings. Importantly, luminance and isoluminant gratings were matched in terms of cone contrast. In addition to the small proportion of 'color cells' described above, they observed that about a third of all neurons responded equally strongly to color and luminance. Johnson and colleagues called these cells 'color+luminance'. This finding agrees remarkably well with the functional magnetic resonance imaging results of Engel and colleagues[8], who found approximately equal sensitivity to luminance and chromatic contrast in human V1.

But what is the function of these cells? If color and form are processed independently, then we would expect these neurons not to be concerned with spatial vision. The spatial structure of a real-world scene is best described as a combination of edges, which occur at different levels of resolution and at different orientations. Figure 2 illustrates the scene shown in Fig. 1 at three different resolution levels. According to Fourier's theorem, every image can be decomposed into a weighted sum of sinusoidal gratings of different orientations and spatial frequencies. The images in Fig. 2 were created by such a decomposition followed by using only low, medium or high spatial frequency gratings in the synthesis. Depending on the size and organization of their receptive fields, cells will respond differently to the three images. Extracting the spatial structure of the scene requires neurons selectively tuned to all different levels of spatial frequency, and all different orientations[4].

Johnson and colleagues found that the spatial properties of the cells responding to both luminance and color were quite different from those of the color-only cells, which respond best to stimuli without any spatial structure. The color+luminance cells showed tuning to spatial frequency that was identical for luminance and chromatic stimuli. Because these neurons were also tuned for stimulus orientation, they are indeed suitable for extracting spatial features. It is important to note that the authors carefully checked that these responses were not simply due to residual luminance artifacts in their stimuli. Nearly all of the color+luminance neurons

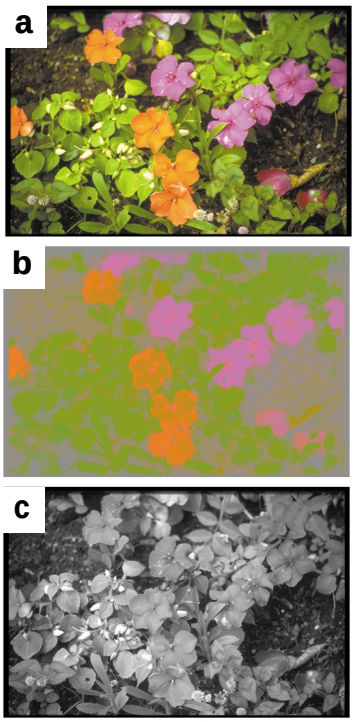

Fig. 1. Image decomposition. The image in (**a**) is the sum of its chromatic (**b**) and luminance (**c**) components. The chromatic image has a smaller stimulating effect on cone photoreceptors (1% average rms cone contrast versus 30% for the luminance image).

The author is in the Department of Psychology, Magdeburg University, PO Box 4120, 39016 Magdeburg, Germany.
e-mail: karl.gegenfurtner@nat.uni-magdeburg.de

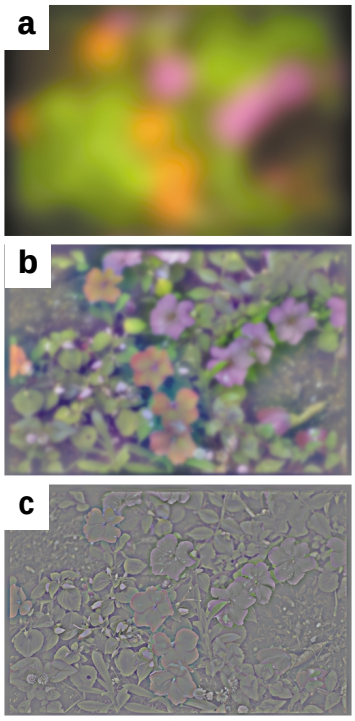

Fig. 2. The same image as in Fig. 1 decomposed into different frequency bands. The images contain only low (**a**), medium (**b**) or high (**c**) spatial frequencies.

received cone inputs of opposite sign, which means that these neurons were truly color opponent.

In additional experiments, gratings were used that selectively stimulate the red (L) or green (M) cones. For most color+luminance neurons, the same spatial selectivity was observed for L- and M-cone isolating gratings; only the response phase was different. This means that both the receptive field center and the surround are color opponent. A cell with such an organization of its receptive field is usually called 'double-opponent,' a property that is extremely important for color constancy. After their initial discovery in the retina of the goldfish[9], evidence for the existence of double-opponent cells in primary visual cortex of primates has been scarce and controversial[7,10,11].

Color constancy denotes the ability of our visual system to attach constant colors to objects in a scene, even though varying illumination can lead to dramatic changes in the spectral composition of the light entering the eye. However, changes in illumination typically influence the whole scene. Because double-opponent cells have an antagonistic surround with the same chromatic properties as the center, they will give a constant response regardless of a constant color bias and thus can make a big contribution to solving the problem of color constancy[12].

Until now, most investigators assumed that double-opponent cells are non-oriented and not responsive to luminance. The neurons described by Johnson and colleagues are of a slightly different breed. They respond both to color and to luminance, and they are orientation selective. Nevertheless, these cells will be able to extract the color of objects in a scene, irrespective of changes in illumination conditions.

There is currently a heated debate about the location of the color center in the visual cortex[13–15]. Although it is very likely that different parts of the brain have differential sensitivities to color and luminance, I would argue that there is no such 'center' that is only concerned with color. Rather, information about color and luminance is intermingled to extract visual form and to achieve a unitary and stable representation of the visual world.

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Cdk5 at the junction

Ming-Sum Lee and Li-Huei Tsai

Acetylcholine receptor gene expression is induced locally at the developing neuromuscular junction. A new paper shows that this process requires cyclin-dependent kinase 5.

Motor neurons communicate with skeletal muscle through the neuromuscular junction (NMJ); its most striking feature is the high concentration of acetylcholine receptors (AChRs) on the postsynaptic muscle membrane. Indeed, AChRs are more than a thousand times more concentrated at the NMJ than in membranes outside this structure. This high density of AChRs is set up through three distinct processes[1]. First, AChRs distributed diffusely along the muscle membrane are clustered at the nerve–muscle contact site. After receptor clustering, transcription of genes encoding AChR subunits is activated in nuclei under the synaptic site. In contrast, transcription of AChR subunit genes is repressed in nuclei far from the synaptic site. The activation of AChR gene transcription is particularly interesting. Of the thousands of nuclei in the muscle fiber, transcription is only activated in the few nuclei sitting right underneath the synaptic site. Such precise regulation seems to be achieved by a signal that comes from the nerve terminal, which strong evidence suggests is a secreted factor called neuregulin.

Neuregulin is an epidermal growth factor-like trophic factor. It exerts its effect through the ErbB family of receptor tyrosine kinases. To date, there are four isoforms of ErbB (ErbB1 to ErbB4). The ErbB receptors homo- or heterodimerize to transduce signals. On binding to neuregulin, they become tyrosine phosphorylated and initiate a signal

The authors are in the Department of Pathology, Harvard Medical School and Howard Hughes Medical Institute, 200 Longwood Avenue, Boston, Massachusetts 02115, USA.
e-mail: li-huei_tsai@hms.harvard.edu