

# Coding Mechanisms and Contextual Influences in Color Vision

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Coding of color in the retina and lateral geniculate nucleus is dominated by cone opponency, and selectivities cluster around the corresponding color space axes. In the visual cortex, a more distributed representation for color stimuli is found. Comparison of this population code for color with the coding of other visual features such as orientation indicates similar coding mechanisms for both features. Further similarities can be observed with respect to contextual interactions. The visual context affects processing and perception of both color and orientation, and results of psychophysical measurements indicate that the properties of these interactions in both domains are similar. These findings suggest that the visual cortex makes use of the same neural mechanisms for the processing of color as for other visual features.

## 1. Introduction

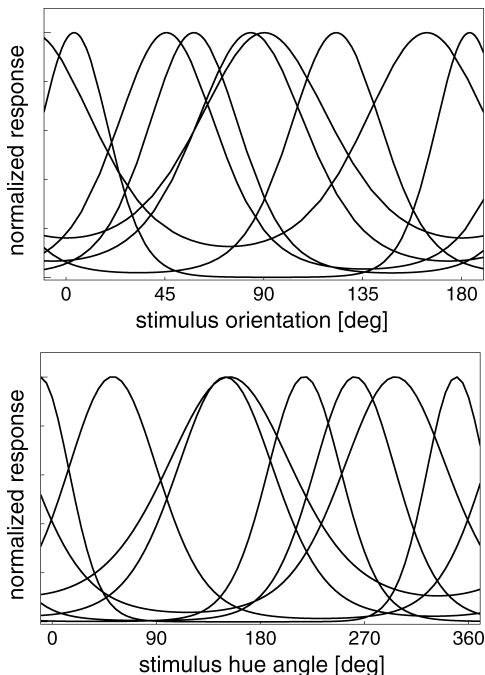
Neural signals for color vision in trichromatic primate species are mediated by two parallel retinal pathways. Both pathways carry opponent signals, corresponding to the difference of responses of the short-wavelength sensitive cones and the cones sensitive at longer wavelengths, and to the difference between medium- and long-wavelength sensitive cone responses, respectively. This dichotomy is reflected in the chromatic preferences of neurons in the retina and the lateral geniculate nucleus (LGN). At these stages of the visual system, neurons respond selectively to chromaticities that correspond to the color space axes of the two classes of cone opponency (Derrington et al., 1984)<sup>1)</sup>.

Cone opponency has been shown to reduce redundancy in the cone signals and thus achieve an efficient representation of color signals (Buchsbaum and Gottschalk, 1983)<sup>2)</sup>. Therefore, it may be surprising that opponency seems to play a less prominent role in the visual cortex.

As many studies have shown, color preferences in striate cortex (Thorell et al., 1984; Lennie et al., 1990; Hanazawa et al., 2000; Wachtler et al., 2003; Kuriki et al., 2007)<sup>3–7)</sup> and also in the extrastriate cortex (Zeki, 1980; Komatsu et al., 1992; Yoshioka et al., 1996; Kiper et al., 1997)<sup>8–11)</sup> are not restricted to the color space axes of cone opponency (for review see Komatsu, 1998)<sup>12)</sup>. If cone opponency is an efficient way of coding (Buchsbaum and Gottschalk, 1983; Lee et al., 2002)<sup>2,13)</sup>, why is this coding scheme abandoned as signals reach the visual cortex? I will review findings from physiological, psychophysical, and computational studies supporting the hypothesis that in the visual cortex color is represented using the same neural mechanisms as for other visual features. The cortical representation of sensory information may be particularly suited to support important processing mechanisms such as lateral modulatory interactions. Specifically, I will compare the coding of hue and the coding of orientation, two visual features that can be represented by angular variables.

## 2. Population coding in the visual cortex

One way to illustrate the color selectivity of neurons is to plot tuning curves as a function of stimulus hue, corresponding to the azimuth angle of cone-opponent color space. This reveals that color is represented in primary visual cortex by a population code: Color preferences are distributed more or less continuously, and tuning curves of neurons tuned to different hue angles show substantial overlap (Wachtler et al., 2003)<sup>6)</sup>. Thus, a given stimulus color is encoded by the responses of a large number of neurons,



**Fig. 1.** Population coding in primary visual cortex. Top: V1 tuning curves for orientation (data from Teichert et al., 2007)<sup>14)</sup>. Bottom: V1 tuning curves for color (data from Wachtler et al., 2003)<sup>6)</sup>. For illustration, data points are omitted, only Gaussian functions fitted to the data are shown. Note that orientation has a periodicity of  $180^\circ$ , hue of  $360^\circ$ . In both cases, tuning curves are broad and show high overlap.

and in order to precisely represent the color of a stimulus it is not necessary that individual neurons have narrow tuning curves. Such a distributed representation can be found for many visual features. In particular, orientation-selective neurons show similar tuning properties in the orientation domain (**Fig. 1**).

## 3. Adaptation to the visual environment

Color preferences in visual cortex are continuously distributed, but the distribution is not uniform. For orientation-selective neurons, non-uniform distribution of selectivities has been found in kittens that were raised in an environment with non-uniform distribution of orientations (Blakemore and Cooper, 1970)<sup>15)</sup>. This indicates that the coding of orientation is adapted to the properties of the visual environment. In monkey primary visual cortex, color selectivities show a predominance of preferences corresponding to an oblique orientation in cone-opponent color space (Wachtler et al., 2003)<sup>6)</sup>. Interestingly, the distribution of chromaticities in natural scenes shows a bias along the same direction (Webster and Mollon, 1997; Wachtler et al., 2001; Webster et al., 2007)<sup>16–18)</sup>, indicating that the coding of color, like orientation, is adapted to the statistical properties of the visual environment.

## 4. Contextual Interactions

Contextual influences are a hallmark of color perception. The appearance of a chromatic stimulus depends on the color of the background on which it is presented. Zeki (1980)<sup>8)</sup> showed that the responses of neurons in cortical area V4 were affected by the chromatic context in a way that was in accordance with the appearance changes. However, even in primary visual cortex, contextual interactions have been

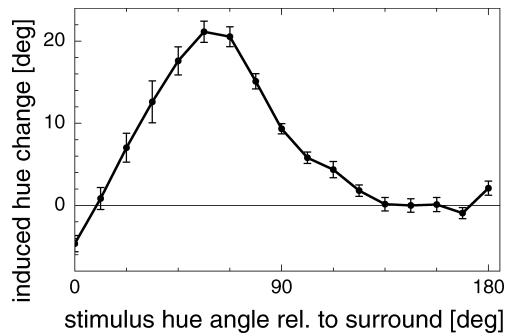
demonstrated, both for achromatic stimuli (Kinoshita and Komatsu, 2001)<sup>19)</sup> and for chromatic stimuli (Wachtler et al., 2003)<sup>6)</sup>. It has been found that the color of the background affects the color tuning of the neurons in a way that is compatible with a shift of the encoded color similar to the appearance shift induced by a colored background.

Contextual interactions are not only found in color processing, but are also known for other features. Blakemore and Tobin (1972)<sup>20)</sup> showed that the responses of neurons in cat primary visual cortex to an oriented stimulus were modulated by the orientation of the pattern surrounding the stimulus. These influences might underlie the perceptual effects of geometrical illusions such as the tilt effect.

The perceived orientation of a stimulus is influenced by the orientation of the surround, a phenomenon known as the tilt effect (Gibson, 1937)<sup>21)</sup>. The strength of this illusion depends in a characteristic way on the difference between the stimulus orientation and the surround orientation (O’Toole and Wenderoth, 1977)<sup>22)</sup>. A qualitatively similar pattern is found in color perception (Wachtler and Klauke, 2006)<sup>23)</sup>. The influence of background hue on the perceived hue of a chromatic test stimulus depends on the difference between the stimulus hue and the surround hue (**Fig. 2**). The similarities between the perceptual effects in color and in orientation suggest that the same neural mechanisms underlie these contextual influences.

## 5. Summary and Conclusions

The signals carrying chromatic information in the visual system undergo a transformation from cone-opponency in retina and LGN to a distributed representation in the visual cortex. Evidence from psychophysics and neurophysiology indicates that the cortical



**Fig. 2.** Change of perceived hue of a chromatic test stimulus as a function of difference between stimulus and background hue. Background hue angle was 0° (+L-M). Data points are averages for three subjects. The shape of the curve is similar to the corresponding curve for the tilt illusion obtained with oriented stimuli.

representation of color shares essential properties with the representation of orientation. This suggests that the visual cortex uses the same neural mechanisms for the processing of different visual features. The transformation of color signals might be a way to achieve a representation that supports the implementation of modulatory contextual interactions, which are found in the processing of most visual features (Gilbert and Wiesel, 1990)<sup>24)</sup>. Thus, specific phenomena in color vision, such as color induction and color constancy, may be achieved with neural mechanisms that are also operative in the processing of other features.

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