The chromatic tilt effect: Analogous coding principles for orientation and color in primary visual cortex

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Coding of chromatic information in the retina and lateral geniculate nucleus is dominated by cone-opponency. Chromatic preferences of color-selective neurons cluster around the specific color-space axes defined by opponent processing of cone signals. In the visual cortex, however, a different kind of representation is realized. This representation, as evidence from previous studies and new results suggest, has several properties in common with the cortical coding of orientation.

First, color is represented by a distributed code in visual cortex. Along the azimuth of cone-opponent color space, corresponding to hue, chromatic preferences in primary visual cortex are not restricted to the cone-opponency axes as in the lateral geniculate nucleus, but are distributed continuously [1]. The chromatic tuning curves show strong overlap, indicating a population code for color in visual cortex. This is similar to the coding by orientation-selective cells, where likewise tuning preferences are distributed continuously, tuning curves are highly overlapping, and a given orientation is represented by the differential activation of a population of neurons.

Second, the coding properties are adapted to the visual input. Orientation-selective neurons achieve an efficient representation that is adapted to the (achromatic) visual environment [2-4]. Likewise, comparison of the distribution of chromatic preferences in primary visual cortex with efficient codes for chromatic natural scenes [5] reveals corresponding properties, suggesting that the cortical representation of color is adapted for efficient processing of natural color stimuli.

Finally, processing of both orientation and color stimuli is influenced by the visual context. Responses of orientation-selective neurons in visual cortex to oriented stimuli are modulated by orientation in areas of the visual field that lie beyond the classical receptive fields of the neurons [6]. These well-documented effects have been proposed to underlie geometrical illusions like the tilt illusion [7], where the perceived orientation of a stimulus is influenced by oriented stimuli in the surround. In color vision, analogous perceptual effects exist and contribute to color induction and color constancy. So far, the neural mechanisms underlying these effects have received surprisingly little consideration. We measured the influence of color in the surround beyond the classical receptive field on the chromatic tuning of cortical color-selective neurons [1]. Surround color modulated the response of the neurons, leading to changes in the tuning curves. Population-coding analysis of the data revealed that these changes in the neural representation corresponded to color shifts qualitatively similar to the perceptual effects of color induction. For comparison at the perceptual level, we measured the changes in perceived color induced by a chromatic field surrounding the stimulus. When colors are expressed in terms of hue (azimuth) angle of cone-opponent color space, the results show the same qualitative dependence on the difference between stimulus and context as is obtained for the tilt illusion.

In conclusion, the results indicate that the cortical representation of color is achieved by neural mechanisms similar to those for the coding of orientation. The transformation from the strictly cone-opponent coding at precortical stages to a distributed code in the cortex may have the advantage that a more efficient representation can be achieved, and furthermore that common processing principles can be used across feature domains. This may be particularly important for tasks such as context integration, which may be easier to realize with a specific type of coding. Together, the findings provide strong evidence that the visual cortex employs analogous mechanisms for the coding of different features.

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