

Mechanisms of central color vision

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In monkey cerebral cortex, color information is processed along the ventral visual pathway. This pathway starts in the primary visual cortex and ends in area TE of the inferior temporal cortex. Recent studies indicate that the transformation of cone signals occurs early in the pathway to form neurons selective to a narrow range of hues. In addition, it has become apparent that area TE plays a vital role in color discrimination.

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Abbreviations

B	blue
CO	cytochrome oxidase
G	green
IT	inferior temporal cortex
K	koniocellular
L	long
LGN	lateral geniculate nucleus
M	middle
pLGN	parvocellular layer of the LGN
R	red
S	short
TE	anterior part of IT
V1	primary visual cortex
Y	yellow

Introduction

Color perception arises from the comparison of signals from photoreceptors with different spectral sensitivity functions. Macaque monkeys have three types of cone photoreceptors that are maximally sensitive to long (L), middle (M), and short (S) wavelengths (Figure 1, stage 1). Comparison of signals from different types of cones occurs in the retinal circuit, and after a relay at the lateral geniculate nucleus (LGN), color information is transmitted to the cerebral cortex. This review focuses on color processing in the cerebral cortex; however, I begin with a description of color-related signals in the LGN, which is important for understanding the input signals to the cerebral cortex.

Precortical stage of color processing

Color-opponent cells

In the LGN, there are two classes of neurons with chromatic opponency [1,2]. One class of neurons is excited by red light but inhibited by green light, or vice versa; these neurons are referred to as red/green or R/G color opponent cells. Another class of neurons

differentially responds to blue and yellow light; these neurons are known as yellow/blue or Y/B color-opponent cells (Figure 1, stage 2). R/G color-opponent cells receive signals from L and M cones in opposite polarities (i.e. +L –M or –L +M). Y/B color-opponent cells receive signals from S cones and the sum of L and M cones in opposite polarities (i.e. S–{L+M}) [2–4]. Responses of these neurons to color stimuli are well represented by the linear sum of cone signals. The existence of two classes of color-opponent cells in the LGN indicates that there are only two chromatic channels at this stage of color processing. Krauskopf *et al.* [5] identified three cardinal directions in color space in which adaptation in one direction did not affect the detection threshold in the other directions. One of these is luminance modulation, whereas the other two correspond precisely to the directions in color space to which color-opponent LGN neurons are tuned [3]. Although the two classes of color-opponent LGN neurons might be associated with the two color-opponent mechanisms proposed initially by Hering [6], they do not correspond to each other because Hering's unique hues do not coincide with the directions of the cardinal axes.

S cone inputs to primary visual cortex

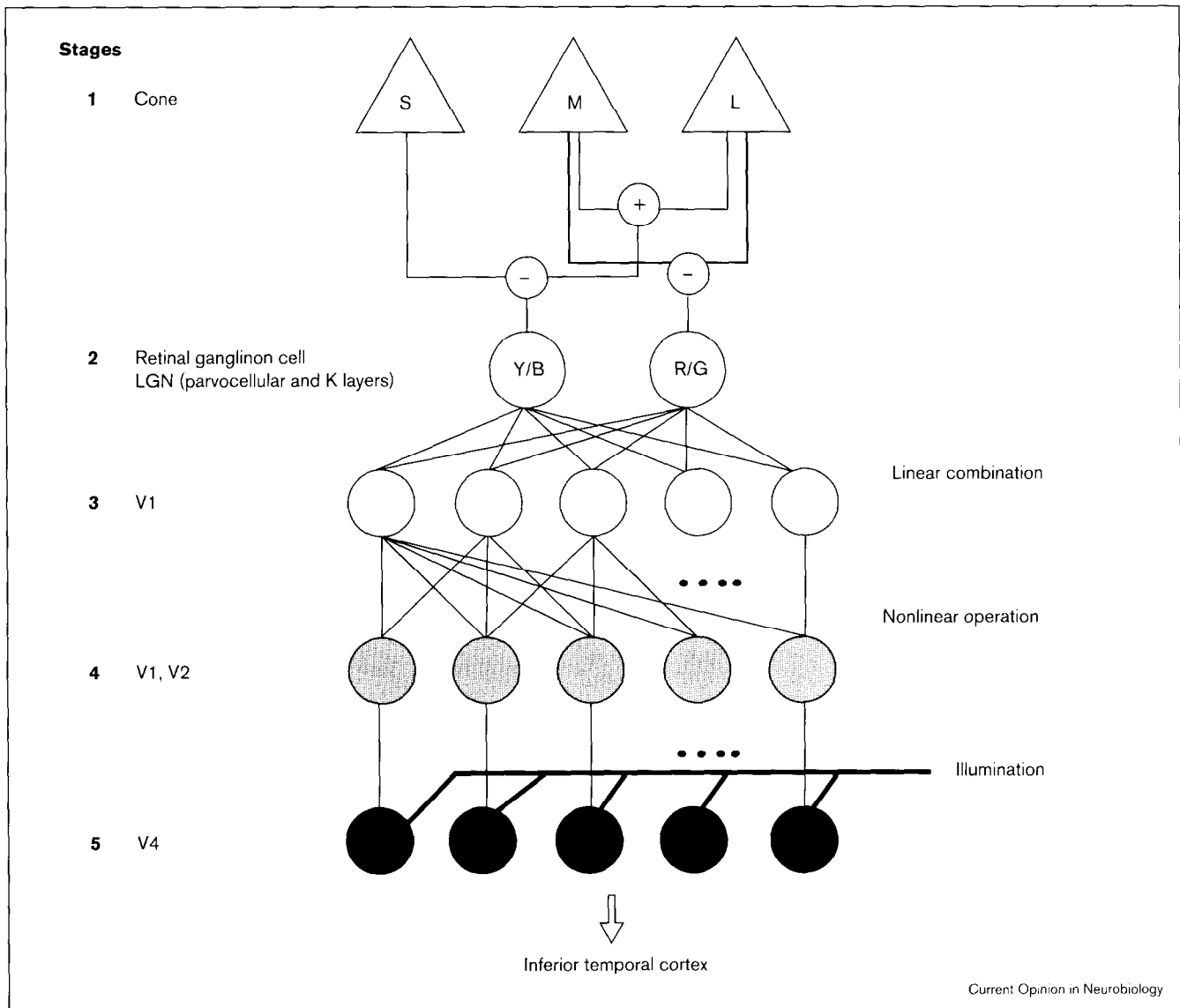
In the past, it was generally thought that there exists a single subcortical pathway for color that involves midget retinal ganglion cells, and after a relay in the parvocellular layer of the LGN (pLGN), terminates in layer 4C β or 4A of the primary visual cortex (V1). Recent studies indicate that there exists another pathway for color that involves interlaminar (koniocellular, or K) layers of the LGN located ventral to each principal layer. A distinct retinal ganglion cell type, the small bistratified cell [7], receives excitatory inputs from S cones [8] and projects to the K layers of the LGN (RC Reid, JM Alonso, SHC Hendry, *Soc Neurosci Abstr* 1997, 23:13). Neurons in K layers, in turn, project to cytochrome oxidase (CO) blobs in layers 2 and 3 of V1 ([9,10]; see also [11]). Neurons that are activated by modulation of S cone signals are found in and around K layers of the LGN ([12,13*]; RC Reid, JM Alonso, SHC Hendry, *Soc Neurosci Abstr* 1997, 23:13). Thus, these experiments provide converging lines of evidence that color-opponent signals sensitive to S cone excitation are transmitted to the cortex, at least in part, through direct input to the CO blobs in V1 *via* the K layers of the LGN.

Early cortical mechanisms

Color selectivity of V1 neurons

It has been shown that color-selective V1 neurons have receptive field structures that are not found in the LGN: some V1 neurons exhibit orientation selectivity as well as color selectivity [14,15], whereas others exhibit

Figure 1



Hypothetical scheme of color processing at different stages along the visual pathway. Five different stages are shown. The first stage consists of three types of cone photoreceptors (S, M and L). In the second stage, there are two classes of color-opponent cells (Y/B and R/G). The outputs of color-opponent cells are linearly combined in the primary visual cortex (V1) to form neurons tuned to various directions in color space at the third stage. Nonlinear interactions of the signals from these neurons occur at the fourth stage, which involves V1 and V2, and cells tuned to a narrow range of hue or saturation are formed. The effect of illumination is discounted at the fifth stage, which involves V4, to form neurons whose responses parallel the perceived surface color as a result of color constancy. Different color processing stages in the cortex are indicated by different shadings.

double opponency [16,17] or broadband suppression from the receptive field surround [18]. With regard to the specificity to color, however, a clear distinction between the LGN and V1 is not indicated by experiments testing spectral sensitivity or wavelength-response relation using monochromatic lights. Though spectral bandwidth differs from cell to cell, most neurons seem to have a peak sensitivity to red, yellow, green, or blue colors [18–20]. More recently, experiments using color stimuli based on color space revealed a clear difference in color specificity between V1 and LGN.

Lennie *et al.* [21] studied the responses of V1 neurons to modulation of color along various directions in color space. They found that the direction in color space in which maximum activation occurs differed from cell to cell. This is clearly different from the LGN, in which the preferred direction coincides with the cardinal axes of the color space. Other recent studies have also shown that preferred color is variable across different V1 neurons ([22]; A Hanazawa, I Murakami, H Kondo, H Komatsu, *Soc Neurosci Abstr* 1997, 23:1026). Many psychophysical studies suggest the presence of higher-order chromatic

mechanisms tuned to more than two directions in color space [23–25], and the variety of color preferences observed in V1 is consistent with this suggestion.

Linear summation of cone signals

Both perceptual color space (e.g. Krauskopf's color space; see [5]) and cone space, which represents the activation of three types of cones, are three dimensional and are related by a linear transformation. Thus, the responses mapped in color space provide useful information for estimating the input cone signals to a given neuron. Lennie *et al.* [21] examined the color selectivity of V1 neurons by modulating stimulus color along various directions in color space and found that the activities of most neurons change in a regular way, indicating that these neurons receive inputs that are the linear sum of the cone signals. Color-selective LGN neurons behave in the same manner [3].

When the responses of such neurons to various iso-luminant colors are plotted on a chromaticity diagram (e.g. Commission Internationale de l'Eclairage [CIE] xy chromaticity diagram), the contour line connecting positions with the same response magnitude was logically expected to be aligned on a straight line [26]. We found this to be the case for nearly all color-selective neurons examined in the LGN, and also for many color-selective V1 neurons (A Hanazawa, I Murakami, H Kondo, H Komatsu, *Soc Neurosci Abstr* 1997, 23:1026).

In these studies, however, a clear difference was found between LGN and V1 with regard to the relative weights with which different types of cone signals fed into each neuron. In contrast with the LGN, where only a limited number of combinations of cone signals are observed, relative weights of cone signals differ from cell to cell in V1. These results suggest that the outputs of the two classes of color-opponent cells (i.e. R/G and Y/B cells) in the LGN are linearly combined in V1 with various weights to form color-selective neurons tuned to various directions in color space (Figure 1, stage 3). De Valois and colleagues [27,28•] have proposed a model that assumes that signals from Y/B cells in the LGN are linearly combined with the signals from R/G cells at some cortical stage to form neurons tuned to unique hues. Their model is consistent with the observation that the outputs from LGN neurons are linearly combined in V1, though combinations of LGN signals are not limited, as their model would predict.

Similarly, when color selectivity of neurons in areas V2 and V3 were examined using a method very similar to those used by Derrington *et al.* [3] and Lennie *et al.* [21], it was observed that neurons in these areas, which are driven by linear combinations of cone signals, are tuned to various directions in color space [29,30•,31•].

Nonlinear interaction of cone signals

In the study mentioned above, Lennie *et al.* [21] found that a few V1 neurons had sharp color selectivity, which

cannot be explained as a linear combination of cone signals. They noted that they may have underestimated the proportion of such neurons in their work. Recent studies have confirmed the existence of such neurons (A Hanazawa, I Murakami, H Komatsu, *Soc Neurosci Abstr* 1996, 22:640; NP Cottaris, SD Elfar, LE Mahon, RL De Valois, *Soc Neurosci Abstr* 1997, 23:13). In our experiment, a significant proportion of neurons had responses that clearly produced curved contour lines in chromaticity diagrams, suggesting a nonlinear interaction of cone signals (Figure 1, stage 4). Some of these neurons exhibited selectivity to a particular hue or saturation. Nonlinear interactions of cone signals should have a key role in forming selectivity to specific hues or saturation. These experiments suggest that such a process starts to take place in V1.

Sato *et al.* [32] found that wavelength tuning of neurons in CO blobs was considerably broadened following iontophoretic administration of bicuculline. This finding suggests that these V1 neurons receive excitatory input signals from various types of cones, and that sharp wavelength tuning occurs as a result of intracortical inhibitory mechanisms.

In V2, the proportion of nonlinear neurons increases compared to V1 [29,30•]. These neurons are tuned to a narrower range of hues than are linear neurons. In V3, in contrast with V2, responses of neurons are consistent with the linear model [31•].

Higher cortical mechanisms

V4 and color constancy

In humans, it is thought that there is a cortical site that plays a central role in color perception, because damage to the ventromedial extrastriate cortex causes a severe deficit in color perception (known as cerebral achromatopsia). In monkey cortex, area V4 has many color-selective neurons [33,34], and several studies have examined the effect of V4 lesions on color discrimination behavior [35–37]. It was found that lesions of V4 induce only a very mild deficit in color discrimination; however, they severely disrupt color constancy [37,38]. In addition, it has been reported that responses of V4 neurons correlate with the color perceived as a result of color constancy rather than the color reflected from the stimulus surface [39].

For color constancy to occur, the effect of illumination must be discounted from the light reflected off the object surface. It is not yet known how the information about illumination is represented in the visual system. V4 neurons have a large suppressive surround, which functions most effectively when the receptive field center and surrounds are stimulated by the same spectral light [34]. It is proposed that such a receptive field structure might have an important role in discounting the effect of illumination [40]. On the basis of such an assumption

Figure 1 illustrates that information about illumination is fed into V4 (Figure 1, stage 5); however, this does not imply that such information is represented explicitly.

Inferior temporal cortex and color discrimination

The inferior temporal (IT) cortex, the final stage of the ventral cortical visual pathway, also possesses many color-selective neurons [41]. These neurons are selective to both hue and saturation, and they have clearly curved response contours on chromaticity diagrams, suggesting that inputs to these neurons are a nonlinear combination of cone signals [26]. In monkey, some IT neurons exhibit sustained activity while a particular color is kept in memory during a delayed matching to sample task [42]. Recently, functional imaging of the monkey brain with positron emission tomography revealed that a color discrimination task activates IT cortex [43*].

Although it has been sporadically reported that damage in IT causes severe deficits in color discrimination [44,45], these results have been largely neglected. Several recent studies have confirmed these earlier reports. Horel [46] found that cooling area TE severely disrupts even a very easy color discrimination task, though the deficit was temporary. Heywood *et al.* [47] made bilateral lesions of IT to study the effects on a hue discrimination task in which an odd color stimulus must be detected out of eight other simultaneously presented colors, a similar gray discrimination task, and a hue detection task in which one chromatic stimulus must be detected out of eight gray stimuli varying in luminance. Preoperatively, the gray discrimination task was slightly more difficult than the hue discrimination task. Postoperatively, however, performance on both the hue discrimination and hue detection tasks was severely disrupted, but only a mild deficit was observed in the gray discrimination task. More recently, Buckley *et al.* [48**] compared the effects of bilateral ablation of area TE of the IT cortex and perirhinal cortex using a task in which the same green stimulus must be discriminated from eight other stimuli differing in hue or saturation. The monkey with the TE lesion could not relearn the task, suggesting that area TE plays a vital role in color discrimination.

A possible role for the inferior temporal cortex in color categorization

Although color changes continuously in color space, it is recognized categorically. The range of colors designated by eleven basic color names (red, orange, yellow, green, blue, purple, pink, brown, white, black and gray) are similar across different races [49,50], and between humans and chimpanzees [51]. It is likely that there is a biological foundation for this phenomenon. Dean [44] proposed that IT cortex might be responsible for categorical perception of color. Heywood *et al.* [45] suggested that this may explain the difference in the effect of IT lesions on color discrimination and gray discrimination, because color, but not gray, is perceived categorically.

In IT cortex, there are neurons that selectively respond to a range of colors similar to those designated by basic color names [52*]. As mentioned above, nonlinear processing of cone signals required to form such color selectivity starts in early cortical areas; thus, it is not clear whether IT is important for the formation of color selectivity itself. One possibility is that IT cortex has templates corresponding to color categories and that IT cortex is involved in processes that match a stimulus color to one of these templates and that determine the color category to which a given stimulus belongs. Such an idea is consistent with the notion that IT cortex has an important role in the formation of prototypes of visual stimuli [53,54].

Conclusions

Although we can perceive an almost infinite variety of colors, they can be basically described using only three parameters. This provides a great advantage over other visual attributes, such as shape, for systemic study of neural representation. Through the efforts of many researchers, only a few of which are summarized in this review, we are now able to trace color processing from the retina to higher cortical areas. Further studies are necessary, however, to understand the details of the processing at each stage and the interactions between different stages. The process of interactions between signals from different types of cones within the retinal circuit has recently been studied in detail [55–57], but future studies are needed to understand how nonlinear interactions of cone signals occur in the early cortical areas. In the higher cortical areas, the mechanisms of color constancy and color categorization are important areas for future research.

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