Neural mechanisms for color perception in the primary visual cortex

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New neurophysiological results show the existence of multiple transformations of color signals in the primary visual cortex (V1) in macaque monkey. These different color mechanisms may contribute separately to the perception of color boundaries and colored regions. Many cells in V1 respond to color and to black–white (luminance) patterns. These neurons are spatially selective and could provide signals about boundaries between differently colored regions. Other V1 neurons that prefer color over luminance respond without much spatial selectivity to colored stimuli, and could be the neural basis for the response to local color modulation within a region. How these different types of color cells combine inputs from cone photoreceptors is what gives them their different spatial selectivities for color.

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Abbreviations

fMRI	functional magnetic resonance imaging
LGN	lateral geniculate nucleus
V1	primary visual cortex
V2	secondary visual cortex

Introduction

Until recently, it was unclear how the primary visual cortex (V1) contributed to color vision. It was known that neural signals carrying information about color arrived at the cortex from the retina, relayed through the lateral geniculate nucleus (LGN), the specific visual nucleus of the thalamus. However, it was impossible to draw firm conclusions from previous studies about how V1 acts on the chromatic signals received from the LGN. In this review, we consider new neurophysiological results that reveal the existence of multiple transformations of color signals in V1 cortex, and we propose that these different color mechanisms may contribute separately to perception of color boundaries and colored regions.

Macaques and humans

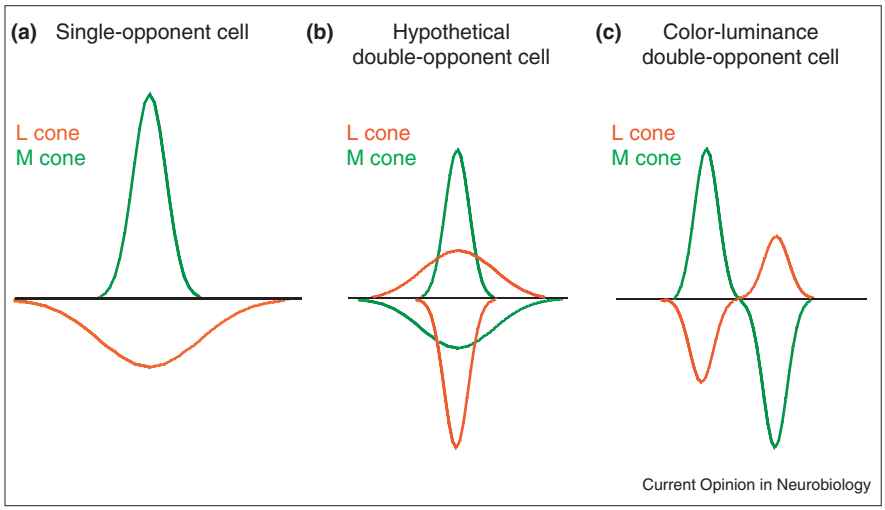
The visual system of the macaque monkey resembles the human's in its structure and function, from the retina through to V1. Old World primates, including macaques, and humans have trichromatic vision. Both macaques and humans possess cone photoreceptors with wavelength maxima near 440 nm (S cones), 535 nm (M cones) and 562 nm (L cones) [1,2]. Both humans and macaques have multilayered LGNs. In these species, the LGN is usually divided into six layers: four more dorsal layers — the parvocellular layers — and two more ventral layers — the magnocellular layers [3]. Opponent color signals travel from retina to cortex through the parvocellular neurons [4,5]. Color-opponent neurons in the parvocellular layers compute the difference between two opponent cone signals — for instance those coming from M cones and L cones, illustrated for the L+M– single-opponent neuron in Figure 1a — and therefore respond in opposite directions to different wavelengths [6–8]. The LGN parvocellular neurons are called single-opponent because there are two (opponent) receptive field mechanisms of opposite sign, but each cone input is of one sign [6] (Figure 1a). Such single-opponent neurons can compute the color modulation of a local region compared to its local adaptation level, and as such could be useful in signaling the color of a small region.

LGN color signals are relayed to V1 in the parvocellular-recipient layer 4cβ, and thence to upper and lower cortical layers [9–11]. Some neurons are also intercalated between the main cell layers of the LGN. These intercalated cells mainly appear to carry signals derived from S+L–M– color-opponent ganglion cells [12,13]. These 'blue–yellow' intercalated (or koniocellular) neurons have direct input to cortical cells in the zone of layer 3b or 4a. In contrast to the parvocellular and intercalated neurons, cells in the magnocellular layers are to a first approximation 'color blind'. Their receptive field centers sum signals from the L cones and M cones. Thus, when cone inputs in the receptive field center are balanced and opposite in sign, as happens when either color modulation of a region or a color boundary is the stimulus, the magnocellular cells are insensitive [14,15].

Color regions and boundaries

When humans perceive the color of a region, their perception is influenced not only by the local distribution of wavelengths from within the region, but also by longer distance color and brightness contrast effects at the boundaries of the region. An example of this is given in Figure 2, in which the three green circles have identical wavelength distributions, but the adjacent surrounding regions are different. Therefore, the brightness contrast at the boundary between each colored circle and its adjacent region is different in each case. The circles appear different in color, demonstrating that a region's color appearance is influenced by the boundary. For instance, the circle in the middle is more closely matched in brightness to its immediate surround than are the other two colored circles; its color therefore appears most saturated [16]. The perception of the hue that is common to all three circles could be derived from color-opponent mechanisms like those observed in the LGN that respond to local color modulation; however, the boundary effects must require further cortical spatial processing. Other color boundary effects, for example the

Figure 1



Receptive field models for color responsive neurons. **(a)** Single-opponent red–green sensitive neurons receive inputs from L and M cones that are opposite in sign, but signals from each cone type are all the same sign. As an example an M+ L– neuron is depicted. Such neurons are found in the parvocellular layers of the LGN and in V1. **(b)** Hypothetical double-opponent neurons that receive both excitation and inhibition from each single cone input. It was originally thought that these would be exactly balanced and arranged in a center-surround geometry as shown here. **(c)** Proposed sensitivity profile for a color-luminance neuron that is double-opponent. Here, each cone sends signals that are opposite in sign, but are not precisely balanced in strength. In addition, the spatial symmetry is no longer the same as for a center-surround neuron but resembles the spatial receptive fields of other cortical cells for black–white stimuli.

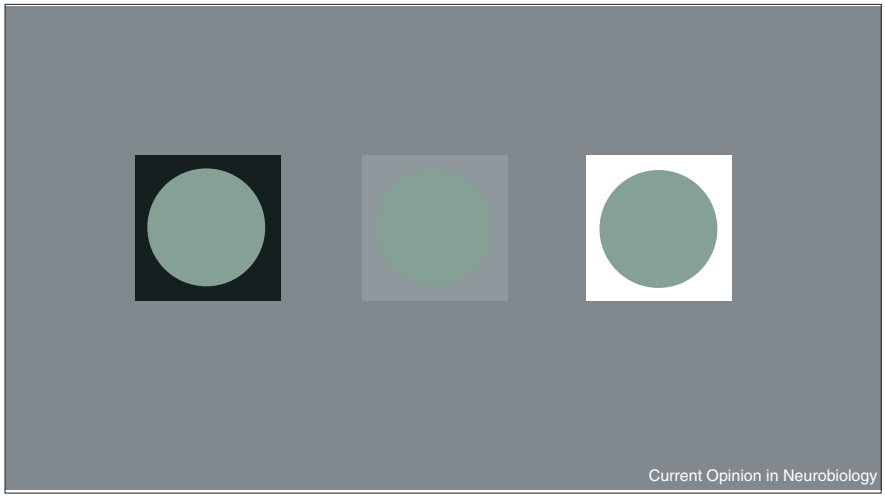
induction of color into a gray region by surrounding color, also require additional neuronal elements that respond preferentially to color boundaries and that send this signal around the cortex to propagate the boundary's effect into perceived regions.

Color boundary effects have been thought previously to depend upon double-opponent color-sensitive neurons in V1 [17,18]. Such neurons were thought to be circularly symmetric, with center and surround mechanisms each color-opponent but opposite in sign one to another. For instance, the center might be M+L–, but the surround would be L+M–, as illustrated for a hypothetical double-opponent cell in Figure 1b. Such neurons were hypothesized and then reported in a number of earlier studies of macaque V1 [18,19], but more recent studies with large samples of V1 cells have found very few neurons that have a receptive field organization like that shown in Figure 1b [20•,21•].

V1: luminance, color-luminance and color-preferring cells

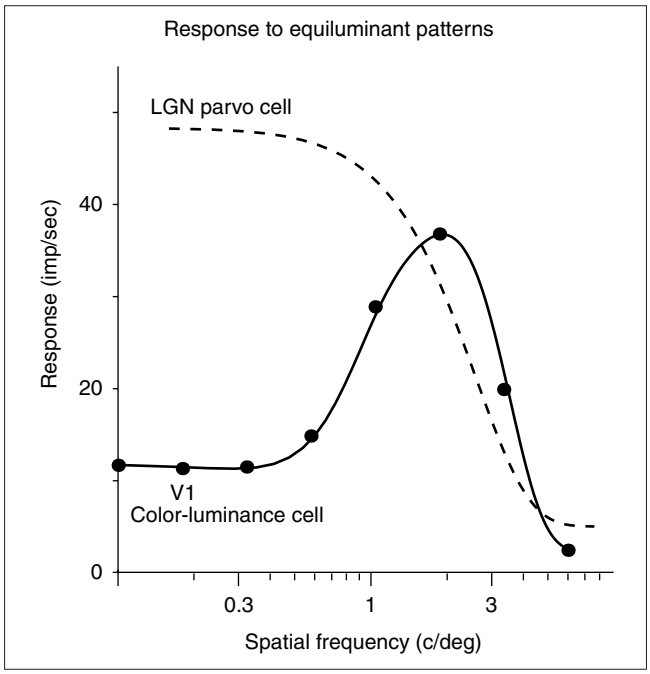
In a recent study of a population of 167 macaque V1 neurons, done in collaboration with our graduate student Elizabeth Johnson, we looked for double-opponent neurons in V1 [22••]. We used sine grating patterns as stimuli, in part because they were effective in exciting most V1 neurons. We compared the responses to achromatic, black–white patterns with responses to red–green equiluminant gratings, as a function of spatial frequency. The measurement of the spatial frequency response function allows one to test for single-opponency versus

Figure 2



Demonstration of the effect of boundaries on color perception. Three identical green circular regions are immediately surrounded by small square-shaped regions of low, medium and high brightness, that appear black, gray, and white, respectively. The appearance of the green changes substantially because of the brightness of the region around the boundary. Far from the boundary, the surrounding region is the same for all three, another mid-gray. To most observers, the green circle on the gray background appears a more saturated green than the green circles on black or white backgrounds. This effect is best seen on a CRT screen from the .pdf file of this article.

Figure 3



Red–green equiluminant spatial frequency tuning for a red–green parvocellular LGN neuron and a color-luminance V1 neuron. The stimuli consisted of drifting red–green equiluminant gratings on a white background. Response was measured as modulation of the spike rate. The response of the color-luminance cell is typical for this group of neurons in V1. Such a spatially tuned response means that color-luminance cells respond better to an optimal color pattern than to spatially uniform modulation of color. This makes them sensitive to color contrast. Reproduced with permission from [22••].

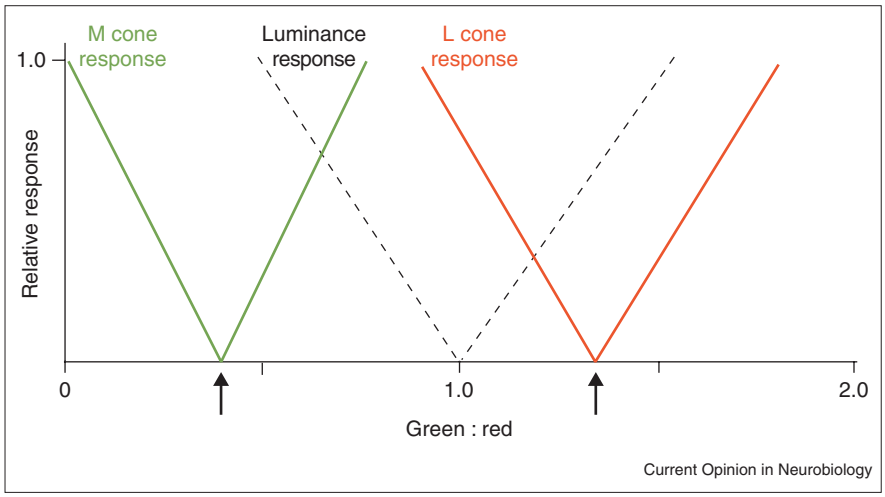
double-opponency. This is because a single-opponent neuron, for example an LGN parvocellular cell, will respond optimally to an equiluminant colored grating pattern at the lowest spatial frequencies (Figure 3). On the other hand, a double-opponent neuron should have an optimum spatial frequency that is higher than zero. It should be tuned for spatial frequency of a colored pattern for the same reason that it is especially responsive at color boundaries — because the double-opponent spatial organization produces cancellation of opposite-signed cone inputs in response to large regions of color, but yields strong responses to steep changes in color that preferentially excite only the receptive field center.

In the Johnson *et al.* study [22••], we attempted to equate the colored and black–white stimuli for average cone contrast, so that their effectiveness in driving V1 neurons could be compared quantitatively. In order to compare relative color sensitivity across the population of neurons, we assigned to each neuron a single number, its sensitivity index, which was defined as I=max{equilum response}/max{lum response}. The index I was distributed broadly, ranging in value from zero to 64. High values indicated preference for colored stimuli compared to achromatic stimuli. We divided the population somewhat arbitrarily into three groups: luminance-preferring cells (I<0.5); color-luminance cells (0.5<I<2); and color-preferring cells (I>2). A majority (100 out of 167; equivalent to 60%) of V1 cells were luminance preferring, but for the purposes of this review we will not discuss these. The color-luminance cells were interesting because almost all of them (40 out of 48; 83%) were spatially tuned for equiluminant grating patterns, meaning that they passed one major test for double-opponency. In fact, the spatial frequency preference and bandwidth for such cells was approximately the same for black–white or red–green equiluminant patterns. These color-luminance neurons had been observed and reported before [20•], but for various reasons, their spatial and chromatic properties have not been studied systematically until now [20•,21•].

Furthermore, the color-luminance neurons were stimulated with color gratings that isolated a single cone through the use of silent substitution [23,24•,25]. Silent substitution is illustrated in Figure 4 with the simplified case of a neuron that receives input only from two cones, the M and L cones, and red–green modulation only. In this example, a color stimulus is created that is the sum of a modulation by a red light and a green light in antiphase, so the green light becomes bright when the red light becomes dim and vice versa. The red modulation can then be fixed at its maximal value. Then, as the ratio of the green modulation compared to the red increases over the range from 0–2, the response of M cones and L cones will vary. At a particular value of the ratio of green modulation to red, say green:red = 0.4, the M cones will not respond at all; this is because when the red light becomes brighter, the green light becomes darker by just the right amount so that the net effect on the M cones is zero. Such nulling of the cone's response is called silent substitution, because the red substitutes for the green; however, this produces zero effect on the cone's response, so the cone is 'silent' [23,24•,25]. At this ratio, the M cone null ratio, only the L cones will be responding, so the stimulus isolates the contribution to the neuron's response from L cones — an M-cone-nulling stimulus is an L-cone-isolating stimulus. At a different ratio, say green:red=1.25, the L cones will receive no net modulation, so the contribution from the M cones will be the only contributor to the neuron's response.

Cone isolation is a powerful technique for studying the spatial mapping of cone inputs onto central neurons [6,24•,25]. By this direct measurement, we observed that individual cone inputs to color-luminance neurons in V1 were usually tuned for spatial frequency, implying that each cone receptive field was spatially opponent, that is, it had spatially segregated excitatory and inhibitory zones. In addition, because some color-luminance cells (the simple cells) had spike rates that were modulated at the grating's drift rate, it was possible to measure their temporal phase of response to an optimal spatial stimulus. The phase of response to L cones was determined to be separated by

Figure 4



Silent substitution for a red–green neuron in a color exchange experiment. This figure represents a simplified case of a neuron that receives input from only two cones, the M and L cones, and red–green modulation only. The color exchange stimulus is the sum of a modulation by a red light and a green light, where the green light becomes bright when the red light becomes dim and vice versa. The red modulation is set at its maximal value. At a ratio of green:red modulation of 0.4, the M cones will not respond because the net effect on the M cones is zero. This is silent substitution because at this ratio the red substitutes for the green producing zero effect on the M cone's response. Then the M cone's effect on the red–green neuron is 'silent' [23,24•,25]. This is indicated in the figure by the arrow at green:red = 0.4 where the M cone response goes to zero. At a different ratio, say green:red = 1.25, the L cones will produce no modulation, as indicated by the arrow at 1.25 on the green:red axis. The dashed curve is the response of a hypothetical luminance mechanism that will be silenced at a green:red ratio of 1.0 (equiluminant color exchange).

approximately one half a cycle from the phase of response to M cones. This means that such color-luminance neurons received approximately opposite signed inputs from L and M cones in response to optimal stimuli. This is consistent with the idea that color-luminance neurons are sensitive to color because of cone-opponent signals.

Therefore, we believe that the receptive field organization of color-luminance cells more closely resembles the model in Figure 1c than that in 1b. It is worth noting that a receptive field organization similar to the one in Figure 1c was suggested by the prior experimental results of Thorell *et al.* [20•]. Each subregion of the two-dimensional receptive field of a color-luminance neuron seems to be elongated rather than circularly symmetric because, as reported in [22••], many color-luminance cells are orientation selective. The net result is that the color-luminance population of V1 performs a spatial transformation on the color signals transmitted from the LGN, as illustrated in Figure 3. Here, the spatial frequency tuning curve of an LGN cell, a single-opponent cell, is compared to that of a cortical color-luminance cell. Both tuning curves were obtained with equiluminant red–green gratings. The color-luminance double-opponent cells are spatially selective for color patterns.

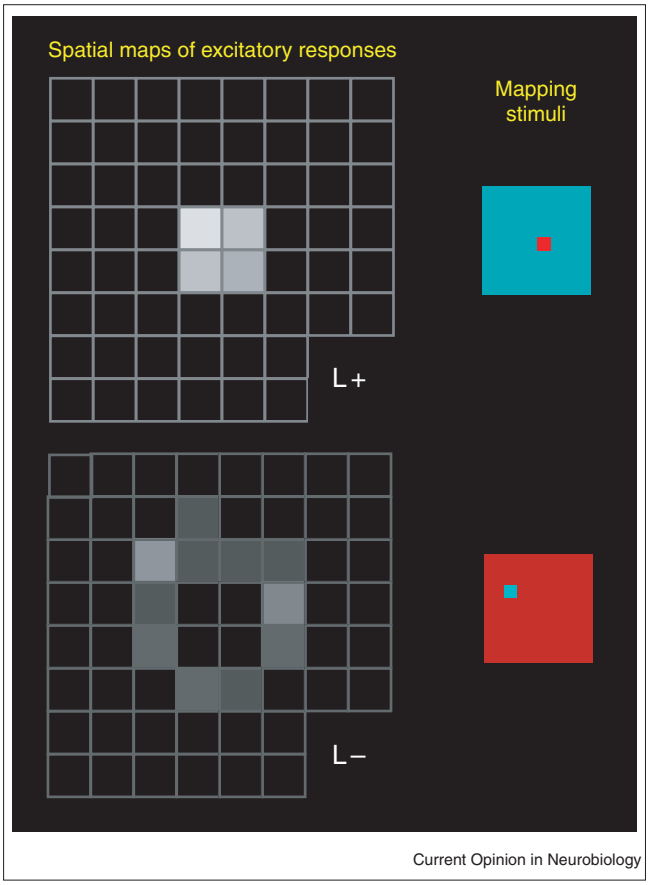
The color-luminance cells are not the only V1 cells that are sensitive to color. A small group of color-preferring cells are also present. These were relatively rare (19 out of 167; 11%) in our sample. Almost all of them (14 out of 19) were single-opponent cells, meaning that their spatial frequency responses to equiluminant patterns, and to cone-isolating patterns, resembled the spatial low-pass parvocellular LGN tuning curve depicted in Figure 3. Therefore, a single-opponent receptive field model, as shown in Figure 1a, may account for the spatial organization of color-preferring neurons. Color-preferring neurons are excited by large regions of color and therefore could be important for perception of color in extended regions. In studies of human color vision with functional magnetic resonance imaging (fMRI) [26,27,28•], color-preferring neurons probably contribute disproportionately to the signals thought to be evoked by color stimuli. This is because a differencing paradigm is often used in fMRI studies, in which a subject's response to an achromatic pattern is subtracted from their response to a colored pattern, to obtain a pure color signal. Thus, the responses of color-luminance cells are cancelled and the only signal left will be from color-preferring neurons. Also, if natural images (which are strong in amplitude at lower spatial frequencies) are used as stimuli, the total neural activity from color-preferring cells may be large relative to the spatially selective color-luminance population. Nevertheless, color-luminance cells should give the strongest responses at color boundaries.

Thus, there are at least two different kinds of color-responding neurons in V1 — the color-preferring and the color-luminance varieties — that send different kinds of signals about color to other visual processing areas of the cerebral cortex.

'High contrast' color stimuli and double-opponent cells

Another recent paper adopts different methods and comes to different conclusions from ours about the properties of

Figure 5



Reverse correlation mapping experiments with high color contrast. The stimuli used are represented to the right – small squares of colored light flashed at random locations on a highly colored background. The colors were chosen to isolate the L cone signals. The upper map is for L+ signals, whereas the lower map depicts L– signals. In this sketch, response magnitude is indicated by a gray scale – the larger the response, the brighter the mapped location. Similar maps were constructed for M+ and M– signals with two different colored squares on two other different colored surrounds (see text). The figure illustrates typical results from [29••]: L+ signals were spatially complementary to L– signals (and M+ signals were spatially complementary to M– signals); the spatial arrangement was a circularly symmetric center-surround organization; the surround signals were usually somewhat weaker than the center signals (hence the higher values of the L+ signals compared to the L– signals in this figure).

color-responsive neurons in macaque V1 [29••]. Working with awake behaving monkeys, Conway [29••] used reverse correlation with sparse noise to map receptive fields, in the manner of Jones and Palmer [30]. He selected a small population of cells from a large population of recorded neurons, using a screening technique that led him to study what we believe are what we called color-preferring cells. However, Conway used what he termed 'high-contrast' color stimuli for cone-isolation, because of his concern that the conventional technique of creating cone-isolating stimuli by color modulation around a white point would not drive the cortical color cells strongly enough [29••]. As illustrated in Figure 5, different signed inputs from each cone were measured using highly saturated backgrounds of different colors. L+ was determined with a bright red square flashed briefly at all locations on a deep blue-green background, whereas L– input was determined from mapping blue-green squares on a large reddish background. Similarly M+ input was measured with bright green squares on a bright red background whereas M– input was measured with bright red squares on a bright green background. The results reveal response maps for both L and M cones that are similar to our sketch of the L cone data in Figure 5: circularly symmetric receptive fields with center-surround structure. Conway concluded that many of the color-preferring neurons studied in this manner revealed center-surround organization, indicating that they were in fact double-opponent cells.

Our opinion is that these results are interesting in that they provide evidence regarding the effects of color adaptation on V1 neurons. However, we believe that they do not tell us which neurons are acting as double-opponent cells in normal color vision. What is important is the adapting point. All our experiments were done adapted to a white point (compare [6,21•]). This approximates color stimuli in natural scenes — the modulation of color around a given fixed adapting point. In nature, the adapting color is the reflectance of natural surfaces in sunlight, such as an unsaturated green (trees or grass), the unsaturated brown of earth, or the unsaturated gray or blue of the sky. In Conway's experiments, each cortical cell is studied at multiple adaptation points. This does not correspond to any natural situation — in nature, there is only one adaptation point at a time at a given location. Therefore, in our opinion, the procedure of summing the center and surround mechanisms [29••], for example for L+ and L– mapped in Figure 5, does not correspond to a receptive field for the L cone that ever exists. This is because such a sum combines maps measured on different backgrounds. In our own experiments, which studied color modulation around a white point, a large majority of color-preferring neurons were single-opponent, preferring the lowest spatial frequencies of colored patterns, like the LGN cell graphed in Figure 3. We believe that this is how most of the cells in Conway's sample would act — as single-opponent neurons on any given background.

Conway's experiments [29••] raise the interesting question: do color–spatial interactions measured with strong chromatic adaptation originate in the cortex? The spatial organizations of subcortical color-sensitive neurons have not been explored with such 'high-contrast' color stimuli. It would be worth investigating whether or not the strong surround effects observed in these experiments on V1 cells might be a reflection of strong chromatic adaptation in the retina, measured downstream.

Modified type II cells in V1

Others have suggested that macaque V1 neurons that had previously been thought to be double-opponent [18,19] were

actually modified type II cells [31]. Type II cells are a subclass of single-opponent cells in the LGN in which the opponent cone mechanisms are so well balanced in strength and spatial extent that the responses to all achromatic stimuli are almost completely cancelled out [5]. Modified type II cells in V1 have been described as having a central region that is single-opponent, and a strong suppressive surround that is not color-selective [31]. Such modified type II cells produce weak responses to any spatially extended stimulus, achromatic or chromatic, because of their strong suppressive surrounds. Thus, we would not be able to study them with our set of stimuli (patterns on a large background), and they are not included in our database of V1 neurons. The perceptual function of modified type II cells is unclear, because these neurons only respond robustly to small spots of colored light on a dark background.

Relation to color properties of extrastriate cortical neurons

Some visual neurons in extrastriate visual areas are sensitive to color. For instance, it has been shown that a substantial fraction of neurons in macaque secondary visual cortex (V2) and visual area V3 respond to equiluminant patterns, and that this response comes from cone-opponent mechanisms [32•]. Also, macaque visual area V4 has long been known to contain color-sensitive neurons although the functional role of V4 in color vision is not yet clear [33–35]. One clear result from the experiments of Kiper *et al.* in V2 [32•] is the prevalence of neurons that are sensitive both to color and luminance. This is completely understandable if these V2 neurons are receiving feedforward inputs from color-luminance cells in V1.

Zeki [36] compared V1 and V4 neurons and concluded that V1 neurons respond to wavelength rather than to color. By this he meant that changes in illumination that altered the spectral distribution of reflected light from a surface caused greater changes in response selectivity of V1 color-sensitive neurons than of V4 color-sensitive cells. However, because we now believe that color-sensitive neurons in V1 are not all the same, it is worth reconsidering these conclusions. Zeki selected V1 neurons on the basis that their response to color was stronger than their response to luminance. These were probably what we now term color-preferring neurons. However, we now know that such a neuron will most likely have a single-opponent receptive field similar to that shown in Figure 1a. Therefore, it would likely not be affected by color contrast. However, if Zeki had also examined the responses of color-luminance cells in V1, which are double-opponent, he probably would have found that the responses of some of them were linked to the color of the illuminated targets, as were the responses of the V4 cells he investigated. In other words, it is now conceivable that color contrast perception (including color constancy) begins in V1 and not in extrastriate cortex.

Conclusions

New neurophysiological investigations of color signals have found many neurons in V1 that respond robustly to pure color stimuli, and that are spatially selective for colored patterns. A smaller number of color-preferring cells in V1, which respond to local regions of color contrast but are not sensitive to color boundaries, also exist. The perception of color in the world likely depends on both of these types of neurons, and on further cortical processing of their signals. The existence of different types of color transformation in V1 may help to explain the richness and apparent complexity of color perception.

Acknowledgements

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- • of special interest
- •• of outstanding interest

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The experiments in this paper were conducted with cone-isolating stimuli of high color contrast, created by flashing highly saturated colored lights onto highly saturated color backgrounds. Cells were recorded in the V1 of awake monkeys. Spatial maps of cone inputs revealed opposite signed inputs from a single cone when the responses were measured with differently colored stimuli on different highly colored backgrounds. However, whether this means the neurons that showed this behavior were really double-opponent or not is still debatable.

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