Single and double-opponent neurons in primate visual cortex

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ABSTRACT

The primary visual cortex, V1, contributes to colour vision but until recently it was unclear what V1 did to colour signals relayed by the Lateral Geniculate Nucleus from the retina.. However one could not draw firm conclusions from conflicting previous studies about how V1 acts on the chromatic signals from the LGN. In this paper I present our neurophysiological results that show that there are multiple transformations of colour signals in V1 cortex, and propose that these different colour mechanisms may contribute separately to perception of colour boundaries and coloured regions. There are single-opponent neurons that are the colour-preferring cells. There are double opponent neurons. These are the colour-luminance cells. Finally there are colour-blind neurons, the luminance-preferring variety that simply sum the cone inputs. Each of these types of visual neuron plays a role in colour vision.

1. INTRODUCTION

The visual system of the macaque monkey resembles the human's in structure and function from the retina through to V1. As Old-World primates, macaques and humans both have trichromatic vision based on cone photoreceptors with wavelength maxima near 440 nm (S cone), 535 nm (M cone) and 562 nm (L cone) [1, 2]. Both humans and macaques have a multi-layered LGNs. In these species, the LGN is divided usually into six layers: four more dorsal, Parvocellular layers, and two more ventral Magnocellular layers [3]. Opponent colour signals travel from retina to cortex through the Parvocellular neurons [4, 5]. Colour opponent neurons in the Parvocellular layers take the difference between two opponent cone signals, for instance M-L, as illustrated for the +L-M single-opponent neuron in Figure 1a, and therefore respond with opposite signs to different wavelengths [6, 7, 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] as in Fig. 1. Such single opponent neurons will compute the colour modulation of a local region compared to its local adaptation level, and as such could be useful in signalling the colour of a small region. LGN colour signals are relayed to V1 in the Parvocellular-recipient layer 4cβ, and thence to upper and lower cortical layers [9, 10, 11]. There are also neurons within the LGN intercalated between the main cell layers. These intercalated cells appear to carry mainly signals derived from S+L- colour 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. Cells in the Magnocellular layers are to a first approximation “colour blind”. Their receptive field centers sum signals from the L and M-cones. Thus, when cone inputs in the receptive field center are balanced and opposite in sign, as happens when either colour modulation of a region or a colour boundary is the stimulus, the Magnocellular cells are insensitive [14, 15].

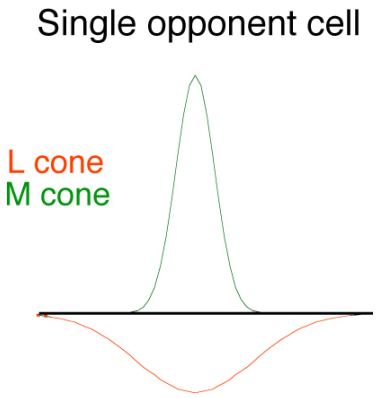

Figure 1. Single opponent red-green sensitive neurons receive inputs from L and M cones that are opposite in sign, but signals from each cone are all the same sign. For example what is depicted is an M+ L- neuron. Such neurons are found in the Parvocellular layers of the LGN and in V1.

Colour regions and boundaries. When humans perceive the colour of a region, the perception is influenced not only by the local distribution of wavelengths from within the region, but also longer-distance effects from colour and brightness contrast at the boundaries of the region. An example is given in Figure 2 in which the three red circles have identical wavelength distributions, but the adjacent surrounding regions are different. Therefore, the brightness contrast at the boundary between each coloured circle and its

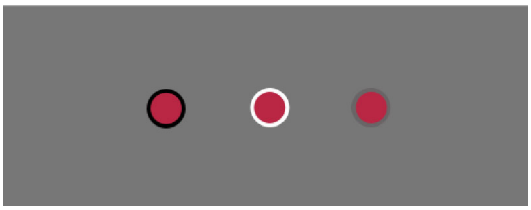

Figure 2. Demonstration of the effect of boundaries on colour perception. Three identical red circular regions are immediately surrounded by small square-shaped regions of low, high and medium brightness, that appear black, white, and gray, respectively. The appearance of the red circles changes substantially 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 red circle on the gray background appears a more saturated than the coloured circles on black or white backgrounds.

adjacent region is different in each case. The circles appear different in colour, demonstrating that a region's colour appearance is influenced by the boundary. For instance, the rightmost circle is more closely matched in brightness to its immediate surround than are the other two coloured circles, and its colour appears most saturated [16]. The hue that is common to all three circles could be derived from colour-opponent mechanisms like those observed in the LGN that respond to local colour modulation, but the boundary effects must require further cortical spatial processing.

Colour boundary effects have been thought previously to depend upon double-opponent colour-sensitive neurons in V1 [17, 18]. Such neurons were thought to be circularly symmetric with center and surround mechanisms that are each colour-opponent but opposite in sign one to another. 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 the concentric double-opponent cells reported by Michael and Livingstone [20-22].

2. RESULTS

V1: luminance, colour-luminance, and colour-preferring cells. In a recent study of a population of 167 macaque V1 neurons, done in collaboration with Mike Hawken and Elizabeth N. Johnson, I 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 vs double opponency. This is because a single opponent neuron, for example an LGN Parvocellular cell, will respond optimally to an equiluminant coloured grating pattern at the lowest spatial frequencies (see Fig. 3). On the contrary, a double opponent neuron should have an optimum spatial frequency that is higher than zero. It should be tuned for spatial frequency of a coloured pattern for the same reason that it is especially responsive at colour boundaries---because the double-opponent spatial organization produces cancellation of opposite-signed cone inputs in response to large regions of colour.

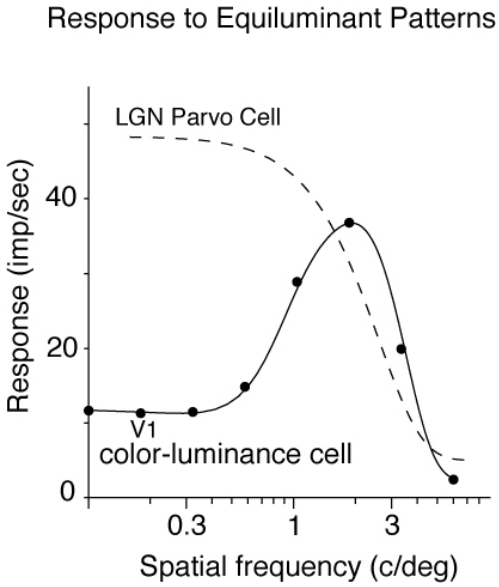

Figure 3. Red-green equiluminant spatial frequency tuning for a Parvocellular LGN neuron and a colour-luminance neuron. The stimuli were drifting red-green equiluminant gratings on a white background. Response was measured as modulation of the spike rate. The colour-luminance cell's response is typical for this group of neurons in V1. Such a spatially tuned response means that colour-luminance cells respond better to an optimal colour pattern than to spatially uniform modulation of colour. This makes them sensitive to colour contrast. Redrawn from ref. 22.

In the Johnson et al. study we approximately equated the coloured and black-white stimuli for average cone contrast. In order to compare relative colour 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 from 0-64. High values indicate preference for coloured stimuli compared to achromatic. We divided the population somewhat arbitrarily into three groups: luminance-preferring (I <0.5); colour-luminance cells (0.5< I < 2); and colour-preferring (I > 2). A majority (60%=100/167) of V1 cells were luminance-preferring.. The colour-luminance cells were almost all of them (83%=40/48) were spatially tuned for equiluminant grating patterns, meaning they passed one major test for double opponency. These colour-luminance neurons had been observed and reported before [20], but for various reasons the spatial and chromatic properties of this population have not been studied systematically before [20, 21].

Furthermore, the colour-luminance neurons were stimulated also with colour gratings that isolated a single cone through the use of silent substitution [23, 24, 25]. 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 colour-luminance neurons in V1 were usually tuned for spatial frequency, implying that each cone input was spatially-opponent, that is it had spatially-segregated excitatory and inhibitory zones. Also, for colour-luminance cells the spike rates of which were modulated at the drifting grating's drift rate (the simple cells), and therefore for which temporal phase of response to an optimal spatial stimulus could be measured, the phase of response to L cones was determined to be separated by approximately one half a cycle from the phase of responses to M cones. This means that such neurons received approximately opposite signed inputs from L and M cones in response to optimal stimuli. This is consistent with the idea that colour-luminance neurons are sensitive to colour because of cone opponent signals.

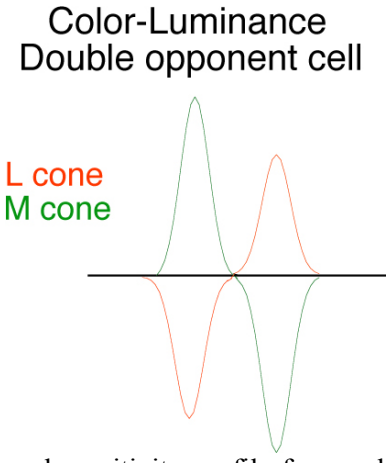

Figure 4. Proposed sensitivity profile for a colour-luminance neuron that is double opponent. Here each cone sends signals that are opposite in sign, but they are not precisely balanced in strength. Also the spatial symmetry is no longer the same as for a center-surround neuron but resembles the odd symmetry of the spatial receptive fields of V1 cells for black-white stimuli.

Therefore, we believe that the receptive field organization of colour-luminance cells resembles the model in Figure 4. It is worth noting that a receptive field organization like the one in Figure 4 was suggested by the prior experimental results of Thorell et al. [20]. The two-dimensional receptive field of a colour-luminance neuron seems to be elongated rather than circularly symmetric since, as reported in ref. 22, many colour-luminance cells are orientation selective. The net result is that the colour-luminance population of V1 performs a spatial transformation on the colour 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 a cortical colour-luminance cell's. Both tuning curves were obtained with equiluminant red-green gratings. The colour-luminance double opponent cells are spatially selective for colour patterns.

The colour-luminance cells are not the only V1 cells that are sensitive to colour. There is a small group of colour-preferring cells. These are relatively rare (11%=19/167) in our sample. Almost all of them (14/19) were single-opponent cells, meaning their spatial frequency responses to equiluminant patterns, and to cone-isolating patterns, resembled the spatial low-pass Parvocellular LGN tuning curve in Figure 3. Therefore, the spatial organization of a colour-preferring neuron may be accounted for by a single-opponent receptive field model like Figure 1. These colour-preferring neurons will be excited by large regions of colour and therefore could be important for perception of colour in extended regions. In studies of human colour vision with fMRI [26, 27, 28], colour-preferring neurons are likely to contribute disproportionately to the signals thought to be evoked by colour stimuli. This is because a differencing paradigm is often used in fMRI studies to obtain a pure colour signal. Then the responses of colour-luminance cells will be cancelled. Also, if natural images (that are strong in amplitude at lower spatial frequencies) are used as stimuli, the total neural activity from

colour-preferring cells may be large relative to the spatially selective colour-luminance population. Nevertheless, colour-luminance cells should give the strongest responses at colour boundaries.

3. CONCLUSIONS

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

Acknowledgments. Thanks to Mike Hawken and Elizabeth N. Johnson for all the work that went into this project. Our research was supported by grants from the U.S. National Eye Institute, EY001472 and EY008300 and an U.S. NRSA grant to Elizabeth Johnson.

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