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Latency of chromatic information in area V4

Mindy Chang [a], Sherry Xian [b], Jonathan Rubin [c], Tirin Moore [b,*]

[a] Department of Bioengineering, Stanford University, Stanford, CA, USA
[b] Department of Neurobiology, Stanford University, Stanford, CA, USA
[c] Interdisciplinary Center for Neural Computation, Hebrew University, Jerusalem, Israel

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ABSTRACT

In the primate visual system, information about color is known to be carried in separate divisions of the retino-geniculo-cortical pathway. From the retina, responses of photoreceptors to short (S), medium (M), and long (L) wavelengths of light are processed in two different opponent pathways. Signals in the S-opponent pathway, or blue/yellow channel, have been found to lag behind signals in the L/M-opponent pathway, or red/green channel in primary visual area V1, and psychophysical studies have suggested similar perceptual delays. However, more recent psychophysical studies have found that perceptual differences are negligible with the proper controls, suggesting that information between the two channels is integrated at some stage of processing beyond V1. To study the timing of color signals further downstream in visual cortex, we examined the responses of neurons in area V4 to colored stimuli varying along the two cardinal axes of the equiluminant opponent color space. We used information theory to measure the mutual information between the stimuli presented and the neural responses in short time windows in order to estimate the latency of color information in area V4. We found that on average, despite the latency difference in V1, information about S-opponent signals arrives in V4 at the same time as information about L/M-opponent signals. This work indicates a convergence of signal timing among chromatic channels within extrastriate cortex.

1. Introduction

Color vision is a fundamental aspect of visual processing that is closely related to the perception of form, as colors help to define borders and facilitate object recognition. In the primate visual system, anatomical and physiological evidence suggests that information about color and form are carried in separate divisions of the retino-geniculo-cortical pathway (Wiesel and Hubel, 1966; Derrington et al., 1984; De Valois et al., 2000; Chatterjee and Callaway, 2003). However, the degree to which the pathways are parallel in each area remains controversial.

The retina contains three classes of photoreceptors, called S, M, and L cones, that respond to overlapping wavelengths of light, with peaks at short (S, blue), medium (M, green), and long (L, red) wavelengths respectively. Each cone is color-blind, responding only to the level of activation, and unable to distinguish between changes in intensity and changes in wavelength. As the cone activation signals are passed to the lateral geniculate nucleus (LGN) in the thalamus, they are processed in opponent pathways: two chromatic pathways, and an achromatic pathway. The two chromatic pathways are $S-(L+M)$ (the difference between S-cone activation and the sum of L- and M-cone activation, also known as the blue/yellow channel or S-opponent pathway) and $L-M$ (the difference between L- and M-cone activation, also known as the red/green channel or L/M opponent pathway). S-opponent signals are carried predominantly in the koniocellular layers of LGN, while the L/M-opponent signals are carried in the parvocellular layers of the LGN. The third achromatic channel, which contains luminance signals ($L+M$), is carried in the magnocellular layers of the LGN. In the cortex, color signals are passed along the ventral pathway from primary visual area V1–V2, V4, and TE. Within each of these areas, studies have shown clustering of color-selective regions. Color selective regions are concentrated in blobs in V1 (Livingstone and Hubel, 1984) and thin stripes in V2 (Hubel and Livingstone, 1987), as revealed through cytochrome oxidase staining for metabolic activity. There is also evidence that processing of different features is integrated early on in the visual system (Sincich and Horton, 2005). Recent fMRI, optical imaging, and electrophysiological work have found color-selective regions, or 'globs', within area V4 (Conway et al., 2007; Tanigawa et al., 2010; Kotake et al., 2009).

In order to create a percept of color and form, the information from separate channels must be integrated at some stage of processing. Several studies have suggested that the S-opponent pathway is slow compared to the L/M-opponent and luminance pathways. In particular, a study by Cottaris and Devalois found that

* Corresponding author. Address: 299 Campus Drive West, Room D200, Stanford, CA 94305-5125, USA. Tel.: +1 (650) 725 8712; fax: +1 (650) 725 3958.
E-mail address: tirin@stanford.edu (T. Moore).

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in primary visual area V1, the S-opponent pathway is slow compared to the L/M opponent pathway, with a delay of about 30 ms (Cottaris and De Valois, 1998). Although morphological and functional differences have been observed between the S-opponent and L/M-opponent pathway earlier in the visual pathway, no concrete evidence has been found for differences in latency at the level of the receptors in the retina (Schnapf et al., 1990), ganglion cells (Yeh et al., 1995), or LGN (Tailby et al., 2008). Psychophysical studies have also suggested that the perception of S-cone signals is sluggish compared to other channels, but evidence for this is weak once controls for behavioral readout and adaptation are taken into account (see Section 4).

An examination of brain regions beyond V1 could provide insight into the temporal properties and degree of integration between the two chromatic pathways. In this study, we used information theory to measure the mutual information between short segments of the neural responses and the color of the stimulus presented in order to estimate the latency of color information in area V4. We presented a series of short bar flashes within the RF of single neurons recorded in area V4, varying color along the two cardinal axes of the equiluminant opponent color space. Despite the latency difference in V1, we found that on average, information about S-opponent signals arrives in V4 at the same time as information about L/M-opponent signals.

2. Materials and methods

2.1. Subjects

We recorded the responses of single V4 neurons in two adult male rhesus monkeys (Macaca mulatta, 5–10 kg) using standard neurophysiological methods. General experimental and surgical procedures have been described previously (Graziano et al., 1997). Each animal was surgically implanted with a head post, a scleral eye coil, and recording chambers. Surgery was conducted using aseptic techniques under general anesthesia (isoflurane) and analgesics were provided during post-surgical recovery. All experimental procedures were in accordance with National Institutes of Health Guide for the Care and Use of Laboratory Animals, the Society for Neuroscience Guidelines and Policies, and Stanford University Animal Care and Use Committee.

2.2. Visual stimuli

All stimuli were presented on a colorimetrically calibrated CRT display (Mitsubishi 2070SB-BK, 29 cm vertical and 39 cm horizontal, 60 Hz) controlled by a Pentium-based computer with an NVIDIA FX5200 video card (8 bits per gun). Judd chromaticities of the phosphors were measured with a Photo Research PR-650 SpectraColorimeter and the output of each phosphor was linearized using an International Light IL1700 Radiometer (Judd, 1951). The values were Red (0.628, 0.342), Green (0.294, 0.612), and Blue (0.152, 0.081). Stimuli were chromatic, oriented bars ($1 \times 0.25°$ of visual angle) presented on the neutral gray background and centered in the RF of individual V4 neurons (Fig. 1A). Orientation of the bar was 0°, 45°, 90°, or 135°, pre-determined during the RF mapping.

The luminance of all bar colors was held constant at 25 cd/m^2, an increment to the background luminance which was fixed at 15 cd/m^2. In natural scenes, differences in color are usually associated with differences in luminance, and increases in luminance have been found to facilitate detection of chromatic stimuli (Eskew Jr et al., 1994; Cole et al., 1990). Luminance was corrected for individual monkeys using methods described below. The chromaticities of the stimuli were specified in a color space based on opponent representation of cone responses (MacLeod and Boynton, 1979). Cone excitations were calculated using Smith–Pokorny cone fundamentals based on human observers (Smith and Pokorny, 1975). This color space is similar to the one proposed by MacLeod

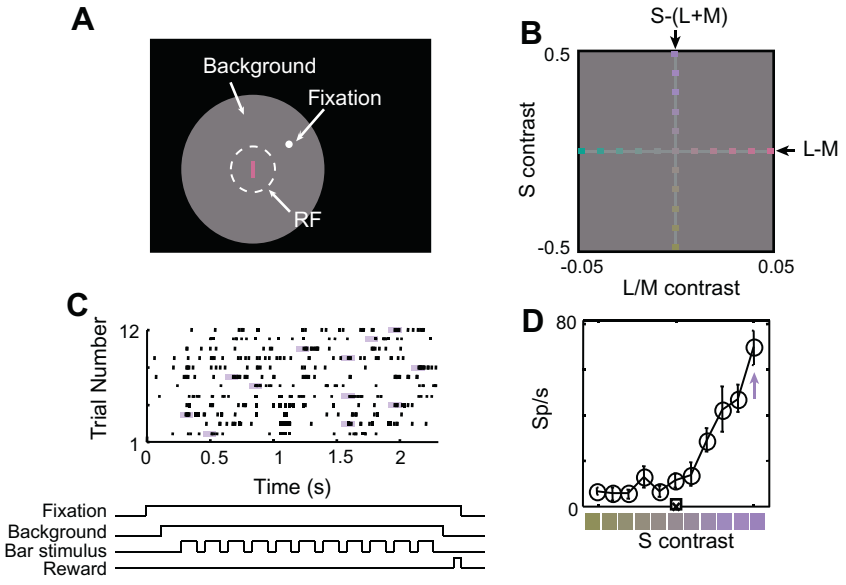

Fig. 1. Experimental setup: color stimuli and example recording. (A) Layout of visual stimulation. In this passive viewing task, the monkey maintained fixation on a white dot while a gray EES (Equal Energy Spectrum, L − M = 0.665, S − (L + M) = 1.02, 25 cd/m^2) background and colored, oriented bar stimuli were flashed in the center of the mapped response field (RF) of a single V4 neuron. (B) Contrast stimulus space. The tested contrasts were distributed along orthogonal axes, based on the normalized Macleod–Boynton equiluminant chromaticity space. S contrasts ranged from −0.5 to 0.5, while L/M contrasts ranged from −0.05 to 0.05 relative to EES. (C) Timing of stimulus presentation. Once fixation was acquired, a gray EES background appeared followed by a pseudorandom sequence of 11 colors along one of the two contrast axes. Each stimulus lasted 100 ms followed by a 83 ms of the EES background. Within a trial, each contrast was presented only once. The example raster shown shows tick marks for each spike within each trial across time, with highlighted boxes indicating the time windows in which the 0.5 S contrast stimulus was presented. (D) Example tuning curve, based on part C. Average spike rate responses are plotted as open circles for each contrast level with error bars indicating SEM. The open square denotes the mean response to the EES background and the cross denotes the spontaneous activity.