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Hue maps in primate striate cortex

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The macaque striate cortex (V1) contains neurons that respond preferentially to various hues. The properties of these hue-selective neurons have been studied extensively at the single-unit level, but it is unclear how stimulus hue is represented by the distribution of activity across neuronal populations in V1. Here we use the intrinsic optical signal to image V1 responses to spatially uniform stimuli of various hues. We found that (1) each of these stimuli activates an array of patches in the supragranular layers of the parafoveal V1; (2) the patches activated by different hues overlapped partially; 3) the peak locations of these patches were determined by stimulus hue. The peaks associated with various hues form well-separated clusters, in which nearby peaks represent perceptually similar hues. Each cluster represents a full gamut of hue in a small cortical area (~160 μm long). The hue order is preserved within each peak cluster, but the clusters have various geometrical shapes. These clusters were co-localized with regions that responded preferentially to chromatic gratings compared with achromatic ones. Our results suggest that V1 contains an array of hue maps, in which the hue of a stimulus is represented by the location of the peak response to the stimulus. The orderly, organized hue maps in V1, together with the recently discovered hue maps in the extrastriate cortical area V2, are likely to play an important role in hue perception in primates.

Keywords: Striate cortex; Primate; Color; Map; Perception; Optical imaging

Introduction

The macaque striate cortex (V1) may play an important role in transforming the cone-specific inputs from the lateral geniculate nucleus into signals that are more specific for color perception (Hanazawa et al., 2000; Conway, 2001; Johnson et al., 2001; Wachtler et al., 2003). Numerous studies have focused on the receptive field properties and spatial organization of individual color-selective cells in V1, and have generated important hypotheses regarding cortical processing of color information (for reviews, see Shapley and Hawken, 2002; Lennie and Movshon, 2005). However, the responses of a neuron to repeated presentations of a given stimulus are variable (Schiller et al., 1976; Dean, 1981; Snowden et al., 1992; Croner et al., 1993; Gur and Snodderly, 1997; Kara et al., 2000; Gur and Snodderly, 2006). In addition, many neurons in V1 are selective for more than one attributes of a stimulus (Leventhal et al., 1995; Johnson et al., 2001; Friedman et al., 2003). In order to reliably extract information about a particular attribute of a stimulus from a single trial, a subject may rely on information coded in the spatiotemporal pattern of activity across neuronal populations. So far, it is unclear how information about color is coded in this pattern of activity in V1.

A previous study has found that extrastriate cortical area V2 encodes information about stimulus color in the *spatial* distribution of activity across neuronal populations (Xiao et al., 2003). This finding raised the possibility that stimulus color might be coded by the spatial distribution of activity across V1 as well. To explore this possibility, imaging techniques and stimuli consisting of individual colors, rather than pairs of opponent colors, are required. One such study using the ^{14}C-2-deoxy-D-glucose (2DG) technique found that stimuli of diffuse color activated an array of patches in both supragranular and infragranular layers (Tootell et al., 1988b). Regardless of the stimulus color, the peak region of these activated patches all overlapped with the cytochrome oxidase (CO) blobs, a compartment that has been hypothesized to play a particularly important role in color processing (Livingstone and Hubel, 1984; Ts'o and Gilbert, 1988). However, because the 2DG technique at that time could not be used to visualize the response of a cortical region to more than one stimulus, that study did not examine fine-scale spatial relationships among the activation patches associated with several colors.

An earlier study from our lab used intrinsic optical imaging, and found that color gratings also activated an array of patches in V1 (Orbach et al., 1996). The patches associated with different colors partially overlapped, but were centered at different locations. However, the spatial resolution of images in that study was relatively low (>50 μm/pixel). In addition, that study used colored gratings as stimuli. Since the orientation of gratings affects the spatial distribution of activity in V1 (Blasdel and Salama, 1986), it was difficult to interpret the results of that study regarding the coding of stimulus color by this spatial distribution.

In the current study, we used spatially uniform colored stimuli, and imaged the intrinsic optical signal at a very high spatial

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resolution. Our results suggest a possible mechanism by which the spatial distribution of V1 activity represents stimulus color.

Materials and methods

Physiological preparation

Experiments were carried out on four anesthetized monkeys (*Macaca fascicularis*). All procedures were approved by the local institutional Animal Welfare Committee, and were in full compliance with the NIH guidelines for the use of laboratory animals. Anesthesia was induced by ketamine (10 mg/kg), and continued with a mixture of propofol (4 mg/kg/h) and sufentanil citrate (0.05 μg/kg/h). Paralysis was maintained with pancuronium bromide (0.25 mg/kg/h) to prevent eye movements. End tidal CO_2 was maintained at 32 mm Hg (~4.5%) and the body temperature was kept at 37.3 °C. Blood pressure and EKG were continuously monitored to assure adequate anesthesia. A craniotomy and durotomy exposed the dorsal portion of V1 that represents retinal eccentricities of 1.5–5°. A recording chamber was installed over the exposed cortex, filled with silicon oil and sealed with glass during imaging.

Visual stimulation

Visual stimuli were presented on a Sony GDM-400PS color monitor (refresh rate: 100 or 60 Hz, resolution: 640×480 or 1024×768), placed at a distance of 57 cm, which covered a 36°×27° of the visual field, and centered on the fovea of the tested eye with a modified fundus camera. Phosphor emission spectra of the monitor were measured at 4 nm intervals using a spectrar-adiometer (PR-650, Photoresearch, CA). The monitor was driven by a VSG graphics card (Cambridge Research Systems, United Kingdom). Gamma correction was performed using the VSG software and the OptiCAL photometer (Cambridge Research Systems). Spatially uniform colors or gray was presented on the entire screen, and were all photometrically isoluminant (9.5 cd/m^2). The CIE 1931-*xy* coordinates of the tested stimuli were: red(R) (0.55, 0.33), orange(O) (0.54, 0.40), yellow(Y) (0.45, 0.47), lime (L) (0.35, 0.54), green lime (GL) (0.28,0.61), green(G) (0.27, 0.49), aqua(A) (0.23, 0.36), blue(B) (0.16, 0.08), purple(P) (0.23, 0.12), reddish purple(RP) (0.31,0.17), pink(K) (0.38, 0.27) or (0.43, 0.24), and gray(W) (0.32, 0.32) or (0.35, 0.32). The letters in parentheses are abbreviations of the color names that are shown in Fig. 1A, which illustrates the location of all our stimuli on a CIE 1931-*xy* diagram. The CIE-*xy* coordinates of the three phosphors (red, green, blue) of the CRT were (0.62, 0.35), (0.28, 0.61), and (0.15, 0.07), respectively. The hue angel of each stimulus color, or h_{uv} as defined in the CIE 1976 ($L^*u^*v^*$)-space, was calculated according to Wyszecki and Stiles (1982). The CIE illuminant C was used as the white object-color stimulus in that calculation.

To visualize the previously reported color patches that respond preferentially to chromatic grating compared with achromatic ones, responses to photometrically isoluminant red/green gratings were compared with those to black/white gratings (Roe and Ts'o, 1999; Landisman and Ts'o, 2002a). Both types of gratings had the same spatial and temporal frequencies (0.5 cycle/degree, 2 cycle/second, square wave), and were presented at two alternating orientations (horizontal and vertical). The two colors in the red/green gratings are those of the red and green phosphors of the CRT, respectively.

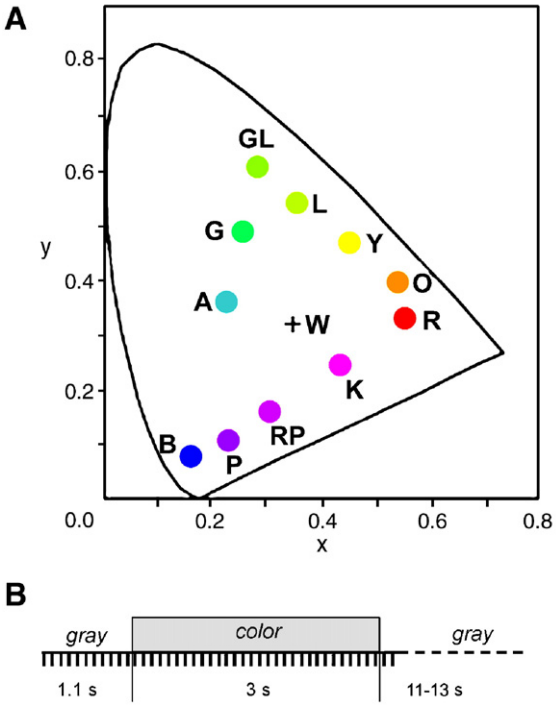

Fig. 1. (A) CIE 1931-*xy* coordinates of the stimulus colors. R, red; O, Orange; Y, Yellow; L, Lime; GL, green-lime; G, green; A, aqua; B, blue; P, purple; RP, reddish purple; K, pink; W, gray. (B) A schematic depiction of the experimental protocol, showing the temporal sequence of stimulus presentation and data acquisition. Each tick mark indicates the time at which a cortical image was acquired.

The stimuli were presented either to the contra-lateral eye or to both eyes. In one animal that had a glaucomatous eye, the stimuli were presented to the normal eye.

Optical imaging and data analysis

The intrinsic optical signal was recorded using a CCD camera with 652×492 pixels (PlutoCCD, PixelVision, OR, which has a 2X2 set of CCD detectors). The camera was focused 0–400 μm below the cortical surface by a tandem lens macroscope (Ratzlaff and Grinvald, 1991). The camera took 10 frames/second at a resolution of 6.1 μm/pixel. The cortex was illuminated by 610 (±8) nm light from LEDs driven by a stabilized power supply.

During each imaging trial, 11 frames were taken before, 30 during, and 2 after the 3-s presentation of a stimulus, followed by a rest period of 11–13 s, during which the display was uniformly gray (Fig. 1B). In two earlier experiments (Cases 1 and 2) that generated panels M–N and O–P of Fig. 6, respectively, 18 frames were taken during the 1.8-s presentation of a stimulus. An imaging block consisted of one imaging trial for each stimulus, including a control trial without stimulation, presented in a pseudo-random order. Functional maps were derived from an experiment consisting of 50–51 imaging blocks. To test the reproducibility of the functional images, the red stimulus was presented twice in each imaging block.

For each imaging trial, we calculated the average of 11 pre-stimulation frames and the average of the last 7 frames (5 during-stimulation frames and 2 after-stimulation ones). They are called pre-stimulation frames and response frames, respectively. To calculate a