Cortical representation of color is binocular

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It is widely believed that the cortical mechanisms of color vision are monocular because stereopsis is poor for isoluminant patterns. By measuring and comparing the chromatic tuning of binocular and monocular neurons in cortical areas V1 and V2 of macaque, we show that this is not the case. Not only are many color-preferring cells in early visual cortex well-driven binocularly, but their color preferences are unusually well-matched in the two eyes. The receptive fields of these neurons are well equipped to convey information about binocular surface color, but because they are insensitive to local spatial contrast they are ill-suited to convey information about stereoscopic depth. Our observations suggest that in early cortical processing, binocular depth and binocular surface color are represented by two different groups of neurons: one that encodes binocular spatial detail at the expense of binocular chromatic detail and another that does the reverse.

Keywords: V1, V2, binocular vision, color vision, electrophysiology, stereopsis

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Introduction

Disparity acuity reaches less than 5 arcsec under optimal conditions (Andersen & Weymouth, 1923; Berry, 1948; Westheimer & McKee, 1978)—less than the width of a single cone (Curcio, 1987). In constructing a neuron's receptive field, the visual system cannot control both the positions of the cone photoreceptors from which the neuron draws signals and the types of cones (L, M, or S) from which it draws signals: High-precision spatial sampling is purchased at the expense of high-precision chromatic sampling and vice versa. This problem is compounded by the random arrangement of cone photoreceptors of different types in the retinal mosaic (Roorda, Metha, Lennie, & Williams, 2001), which gives rise to clusters of cones of a single type. Clusters in the two eyes will be aligned only by chance, so it might be especially difficult to provide a binocularly driven neuron with both the high-precision spatial sampling required for computing stereoscopic depth and the high-precision chromatic sampling required for encoding chromaticity. Frequent findings of poor chromatic stereopsis (e.g. de Weert, 1979; Kingdom & Simmons, 1996; Krauskopf & Forte, 2002) suggest that the brain might have resolved this problem by confining chromatic analysis to monocular pathways (Hubel & Livingstone, 1987), although some studies suggest that isoluminant stereopsis remains possible under ideal conditions (Grinberg & Williams, 1985; Kingdom & Simmons, 1996).

We test this directly by characterizing the tuning of V1 and V2 neurons in the macaque for chromatic stimulation in both eyes. We show that color-preferring cells are often driven well through both eyes, and further that in these cells the chromatic properties of the receptive fields are well matched, so they are equipped to provide a binocular representation of color. The receptive fields of color-preferring cells generally show little selectivity for spatial form (Hubel & Wiesel, 1968; Johnson, Hawken, & Shapley, 2001; Lennie, Krauskopf, & Sclar, 1990; Solomon, Peirce, & Lennie, 2004), and as a result they are poorly suited for coding binocular depth, which must involve precise comparisons of spatial signals from the eyes (Anzai, Ohzawa, &

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Freeman, 1999; Ohzawa, DeAngelis, & Freeman, 1990). The receptive fields of binocular neurons that responded well to both color and luminance usually show greater spatial selectivity, but the chromatic properties of their receptive fields are less well matched, and they are therefore poorly suited for coding binocular color.

Materials and methods

As part of a larger series of experiments, recordings were made from 613 neurons in V1 and V2 of 37 macaque monkeys. All procedures conformed to the guidelines approved by the New York University Animal Welfare Committee. Each animal was anesthetized initially with ketamine hydrochloride (Vetalar; 10 mg/kg, i.m.). The saphenous veins were cannulated, and surgery was continued under thiopental sodium anesthesia. The monkey was intubated, the head was placed in a stereotaxic frame, and a craniotomy was made over the occipital cortex. Electrodes were attached to the skull to monitor the electroencephalogram (EEG) and to the forearms and legs to monitor the electrocardiogram (ECG).

Postsurgical anesthesia was maintained by continuous infusion of sufentanil citrate (4–12 μg/kg/h) in physiological solution (Normosol-R; Abbott Laboratories, Abbott Park, IL) with added dextrose (2.5%). Muscular paralysis was then induced and maintained by continuous infusion of vecuronium bromide (100 mg/kg/h). The monkey was ventilated artificially so as to keep end-tidal CO2 near 33 mmHg. The EEG and ECG were monitored continuously, and at any sign of the anesthesia becoming less effective the dose of sufentanil citrate was increased. Temperature was monitored with a rectal probe and kept near 37°C with a heating blanket.

The pupils were dilated with atropine sulfate (typically to 7 mm), and the corneas were protected with high-permeability contact lenses that remained in place for the duration of the experiment. No artificial pupils were used. Supplementary lenses (with power determined by ophthalmoscopy) were used to focus the eyes at a distance of 114 cm. At the beginning of the experiment, and at regular intervals afterward, the positions of the foveae were mapped by reverse ophthalmoscopy. A small incision was made in the dura, and a guide tube containing the electrode (Ainsworth tungsten-in-glass or paralyene-coated tungsten; 1–5 MΩ; FHC, Bowdoinham, ME) was positioned over this. The dura was covered with warm agar, and the craniotomy was sealed with dental acrylic. The analog signal from the electrode was amplified, filtered, and sampled at 11.025 or 22.05 kHz by a dual processor Power Macintosh computer. Putative spikes were displayed on a monitor, and templates for discriminating spikes were constructed by averaging multiple traces. The timing of waveforms that matched the template was recorded with an accuracy of 0.1 ms. Electrode tracks were reconstructed from the positions of the lesions made during the experiment as described previously (Solomon et al., 2004).

Visual stimuli

Stimuli were presented on a calibrated CRT monitor (Sony G500) refreshed at 90 Hz and viewed at a distance of 114 cm, where the screen subtended 19° × 14.25°. Two small gimbaled mirrors were placed in the optical axes to bring the receptive fields in each eye onto separate parts of the CRT. The display was white (CIE 1931 x, y ~0.3, 0.32) at a mean luminance of ~50 cd/m^2, and all stimuli were defined by spatiotemporal modulations of chromaticity and luminance around this point. These modulations can be represented in a three-dimensional color space defined by the following axes (Derrington, Krauskopf, & Lennie, 1984): an L–M axis along which only the signals from L- and M-cones vary, in opposition, without variation in luminance; an orthogonal S-cone axis along which only the signals from S cones are modulated; an achromatic axis along which the signals from all three cone classes vary in proportion. Within the plane defined by the L–M and S axes chromaticity varies without a change in luminance. The intersection of these axes defines the white point. Sinusoidal grating patterns, or spatially uniform fields modulated in time, were defined by modulation along some vector through the white point. A vector is specified by two angles: the elevation (θ, angle from the isoluminant plane) and azimuth (ϕ, where an angle of 0 degrees produces +L–M modulation and 270 degrees is +S modulation) (Figure 1A).

Data collection and analysis

When searching for the isolatable signals of single neurons, we presented to each eye a broad range of achromatic and chromatic drifting gratings, varying in chromaticity, orientation, spatial frequency, and size. For each isolated neuron, we measured the preferred orientation, spatial frequency, size, and temporal frequency using patches of drifting grating (when a neuron showed excitatory inputs from both eyes, we made these measurements on the receptive field in each). Measurements were usually made with achromatic stimuli, except in the rare cases that the neuron did not respond to them.

Using the optimally configured stimulus, we measured the chromatic preferences of each eyes receptive field by presenting drifting gratings or flickering uniform fields modulated along each of nine directions in the color space of Figure 1A. Four vectors were in the isoluminant plane, one was achromatic, and four were at intermediate elevations (Solomon et al., 2004). Each eye was stimulated

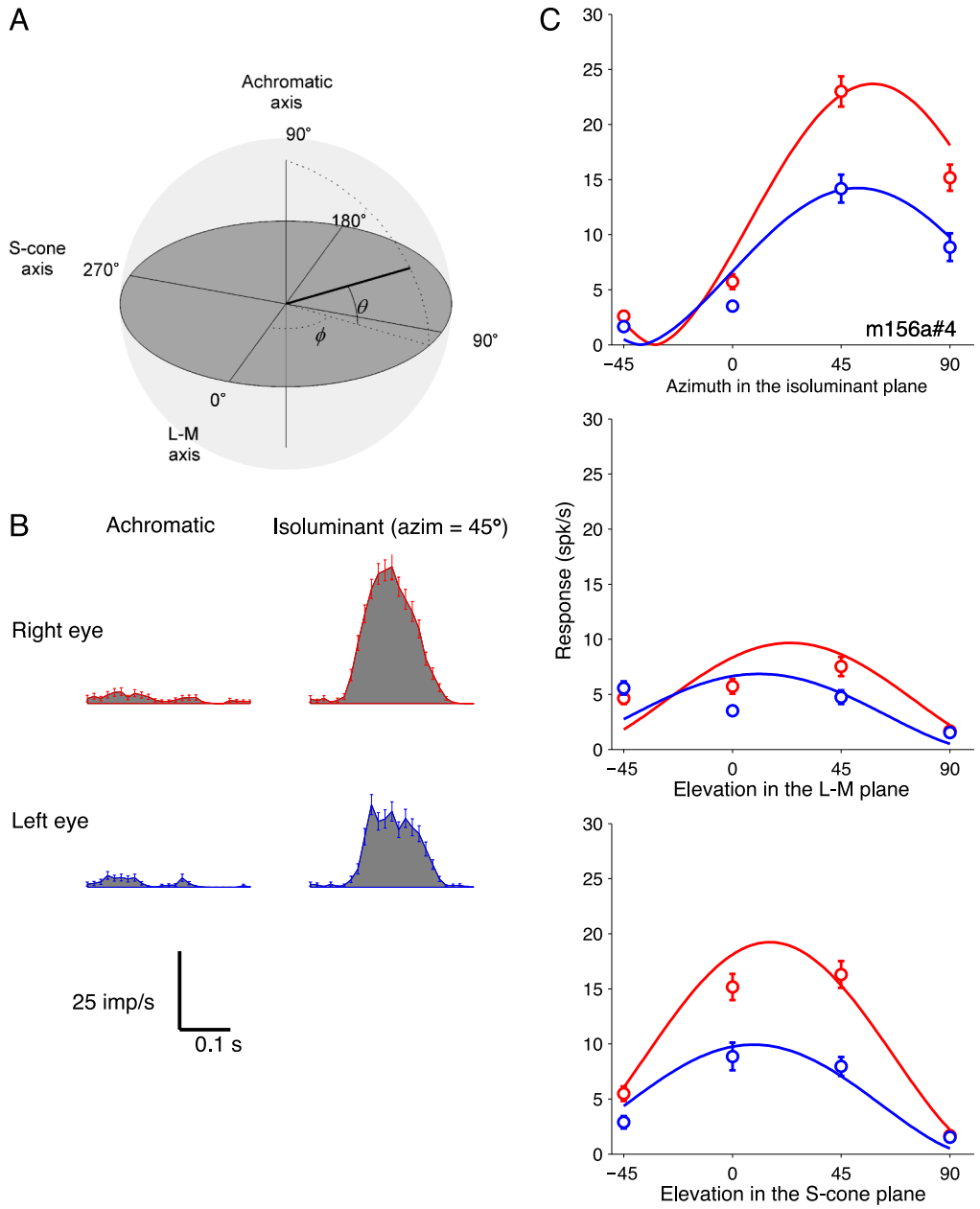

Figure 1. Mapping color preference in the stimulus space. (A) Three-dimensional color space in which a stimulus is represented by a vector passing through the white point at the intersection of its three axes (achromatic, L–M, S-cone). A neuron's chromatic signature is represented by the azimuth (ϕ) and the elevation (θ) of the vector of its preferred stimulus, derived using the model described in the text. (B) PSTH of responses from the dominant eye (upper panels) and non-dominant eye (lower) to achromatic and isoluminant chromatic stimulation (at azimuth 45 deg) for a color-preferring cell. (C) Response rate and fitted linear model for all color directions presented. In the top panel, stimuli are all in the isoluminant plane and vary only in azimuth. In the middle and lower panels, the stimuli vary only in elevation from the isoluminant plane and all fall in the L–M or S-cone planes, respectively.

independently, and the set of stimuli (which always included a blank screen to measure spontaneous activity) was presented in pseudorandom order, 10–20 times, in trials lasting 2 s. For most neurons, the trials for the two eyes were included in the randomization, although for a few the eyes were characterized serially. Between each trial, the screen was held at the mean luminance for 0.5 s.

We calculated for each neuron an Ocular Balance Index, OBI (Anzai, Bearse, Freeman, & Cai, 1995) that provides a measure of the binocularity of the cell. This ranges from 0 when input arises entirely from one eye) to 1 (when the two eyes' inputs are perfectly matched):

$$\mathrm{OBI} = 1 - 2 * |\mathrm{ipsi}/(\mathrm{ipsi} + \mathrm{contra})|, \quad (1)$$

where ipsi represents the response in the ipsilateral receptive field and contra represents the response in the contralateral receptive field, both to the optimal stimulus.

From the impulses discharged by each cell, we extracted the mean rate and the amplitude of the Fourier component at the frequency of stimulation. To these data, we fit a linear model (for cells where the amplitude of the modulated response exceeded the increase in mean rate) or a full-wave rectified variant of it to estimate the cell's chromatic signature (Lennie et al., 1990). The model gives us an estimate of each neurons preferred direction in the color space of Figure 1A, and this defines the relative sign and weight of the L, M, and S cones to the receptive field. We use the preferred color direction to summarize the chromatic tuning of the receptive field and to compare the chromatic tuning of each eye, but analysis of the cone inputs produced similar results (data not shown).

For a neuron to be accepted for subsequent analysis, the maximum response had to be greater than 5 impulses/s; if responses to stimulation in both eyes exceeded this criterion, the neuron was classified as binocular. For each neuron, standard errors of the means were calculated for the model fits using a bootstrap procedure. For each condition, 5000 bootstrap resamples were generated from the original data samples. From these, a new condition mean was calculated, as in the experiment. The condition means were used to fit the model repeatedly for the same neuron. The procedure gives an indication of how reliable the fitting procedure was and how well it was constrained by the data. Neurons whose azimuth had a standard error of the mean greater than 5 degrees were excluded from the analysis, as were neurons for which the model did not explain at least 70% of the variance in response rates. These criteria admitted 395 of the 613 neurons encountered, 236 of which were found in V1 and 134 in V2. The inclusion criteria did not introduce any bias in sampling; the analyses were also run on the complete set of neurons with similar results. The responses of an additional 25 neurons are included, where we were unable to confirm from the histology whether they were in V1 or V2 because V1 and V2 neurons did not differ in the analyses here. The neurons we studied here almost always had receptive fields within 5 degrees of the fovea, and most were within the central 2 degrees.

Results

For each neuron encountered, we characterized the chromatic preference of the receptive field by measuring the response to modulation along each of several vectors in the color space of Figure 1A. For cells with receptive fields in both eyes, we measured independently the responses from each eye's receptive field. Figures 1B and 1C show the responses of one binocular neuron in V1. Figure 1B shows histograms of the response to one cycle of modulation, for achromatic modulation (left panels; elevation 90 degrees) and isoluminant modulation along the red-green axis (right panels; azimuth 0 degrees). The neuron preferred isoluminant modulation over achromatic modulation in both its dominant eye (in this case the right eye) and in its non-dominant eye. We conclude that neurons preferring chromatic modulation can have binocular receptive fields. Figure 1C shows the amplitude of response along each color direction measured for the dominant eye (red) and the non-dominant eye (blue). The top panel in Figure 1C shows responses to modulation along color directions within the isoluminant plane; the middle panel shows responses to modulations in the plane formed by the achromatic axis and the red-green axis; the bottom panel shows response in the plane formed by the achromatic axis and the S-cone axis. The smooth lines show the best-fitting predictions of the model described in the methods: For the dominant eye, the preferred color direction was an elevation of 13.2° and an azimuth of 58.0°; for the sub-ordinate eye these were 6.8° and 51.9°.

Color-preferring neurons are binocular

Figures 2A and 2B show, for monocular and binocular neurons, respectively, how the chromatic signatures of neurons are distributed in the color space of Figure 1A. In this and subsequent figures, we do not identify cells by visual area (V1 or V2) because no analysis distinguished them. A neuron's preferred elevation is represented by its radial distance from the center of the plot and its preferred azimuth by the polar angle. For binocularly driven neurons, lines connect the signatures of the two receptive fields. A cell's preferred elevation provides a convenient measure of the extent to which it favors chromatic stimuli over achromatic ones. Figures 1C and 1D show respectively the distributions of preferred elevations for monocularly driven neurons and for the dominant eye of binocularly driven ones. We cannot distinguish these distributions.

It is useful to organize further analysis by grouping cells informally by the chromatic signatures of their dominant-eye receptive fields. In keeping with previous work (Solomon & Lennie, 2005), we distinguish three groups: group C cells that respond well to chromatic modulation (elevation <50°); group B cells that receive weakly opponent cone inputs, with no class of cone providing more than 80% of total input (elevation between 50° and 80°); group A cells that prefer achromatic modulation (elevation >80°). The dashed rings in Figures 2A and 2B and the dashed vertical lines in Figures 2C and 2D show the boundaries between the groups. The cell in Figure 1 was classified as group C. Binocularly driven neurons were at least as common among group C cells (22 of 37: 59%) as among cells of groups A (74 of 167: 44%) and B (106 of 191: 55%). The average Ocular Balance Index

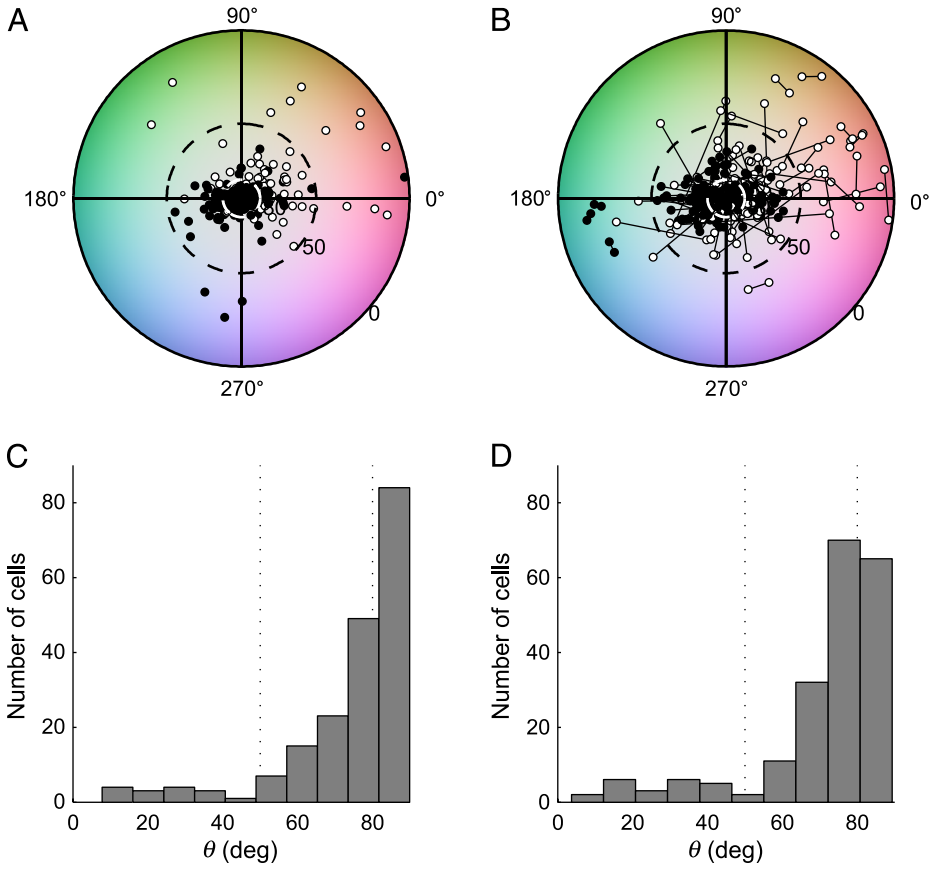

Figure 2. Distribution of preferred color vectors for cortical neurons. (A) The distribution of the chromatic signatures for monocularly driven neurons. Simple cells are represented by open circles, and complex cells by filled circles. In this view of the sphere in panel A, azimuth is represented by polar angle, and elevation by distance from the circumference. (B) Same as panel A, for binocularly driven neurons. Lines connect the pairs of points for each cell. (C and D) Distribution of preferred elevations of neurons represented in panels A and B, respectively. Dashed lines show elevations that separate cells falling in the informal groups discussed in the text.

was at least as balanced in Group C (0.53) as in A (0.33) and B (0.50).

Binocular matching of chromatic tuning

The match between the chromatic properties of a binocular neuron's receptive fields is of considerable interest. Preferred orientation and spatial frequency are generally well matched between the two eyes (Bridge & Cumming, 2001; Skottun & Freeman, 1984), and for reliable binocular representation of color, we might expect the same for the chromatic signature. To represent the difference between any two chromatic signatures, we calculate their angular separation in color space (on a great circle). We call this quantity $\Delta\lambda$. Figure 3A shows, for all binocularly driven cells, $\Delta\lambda$ between the dominant eye and the non-dominant one, plotted against the preferred elevation of the dominant eye.

Overall, differences between the two eyes' signatures span a substantial range, and we want to understand how small $\Delta\lambda$ should be for the signatures to be considered "well matched." A useful way to frame the issue is to ask whether the chromatic properties are more alike than would be expected by chance. We do not know what ought to be the distribution of chromatic preferences among neurons, but we can assume that in the course of characterizing the properties of a large pool of neurons we have established this empirically, and we can use the observed distribution as the foundation on which to estimate likelihoods. For the dominant eye of each binocularly driven neuron, we computed $\Delta\lambda$ between its receptive field and that of (a) its fellow eye and (b) the dominant eye of every other neuron (including monocular ones). From this, we determined the fraction of other neurons for which the $\Delta\lambda$ was less than $\Delta\lambda$ for the fellow eye. We call this quantity $P(\Delta\lambda)$. It provides a measure of the likelihood that differences between the two eyes' chromatic signatures arise by chance. The analysis compensates for the fact that neurons preferring achromatic modulation are much more common than those preferring isoluminant modulation and that, as a result, finding the two eye's preferred color vector to have a $\Delta\lambda$ of 5° is rather more surprising for a neuron that prefers

isoluminant stimulation than for one that prefers achromatic stimulation.

Figure 3B shows how $P(\Delta\lambda)$ varies with preferred elevation of the dominant eye. Among neurons of groups A and B, $P(\Delta\lambda)$ is broadly distributed, but among neurons of group C, it is heavily concentrated around low values. Figure 3C shows the distributions of $P(\Delta\lambda)$ separately for the three groups. Our null hypothesis is that the chromatic preference of the two receptive fields of a binocular neuron is unimportant: In this case, we expect that the chromatic preference of the dominant eye would be no more similar to that of its fellow eye than that of any other neuron. The distributions of $P(\Delta\lambda)$ for groups A and B are similar and show for many neurons a high likelihood that the two eyes' chromatic signatures may be related only by chance. The distribution for group C is unlike the others: For only four neurons (all of which fall close to the boundary with Group B neurons) is there a substantial likelihood that $\Delta\lambda$ arises by chance. This is not just because it was relatively rare to encounter a binocular neuron that prefers isoluminant modulation: Were the chromatic signature of the other eye's receptive field assigned by chance then we expect it to resemble that of most of other receptive fields, preferring achromatic modulation, and the $P(\Delta\lambda)$ would be as high as those of most neurons in groups A and B. If we take $P(\Delta\lambda) < 5\%$, to identify neurons with a better than chance match between their two eyes' chromatic signatures, we find proportionally far more of them among neurons in group C than among neurons in groups A and B (68.2% vs. 25.7% and 24.5%). Knowing that a neuron is in group C makes it likely that the fellow eye has similar tuning; knowing that a neuron is in group A or B conveys little about the tuning of the fellow eye.

We undertook an additional analysis to establish whether $\Delta\lambda$ between a neuron's receptive fields was associated more with differences in preferred elevation than differences in preferred azimuth (since a network designed to cope with different specular highlights seen by the two eyes might accommodate substantial differences in elevation while requiring well-matched azimuths). We found no indication that the two receptive fields differed more in elevation than they did in azimuth. Considering only differences in elevation or only differences in azimuth, small values of $P(\Delta\lambda)$ were more frequent in group C neurons than in neurons of groups A and B.

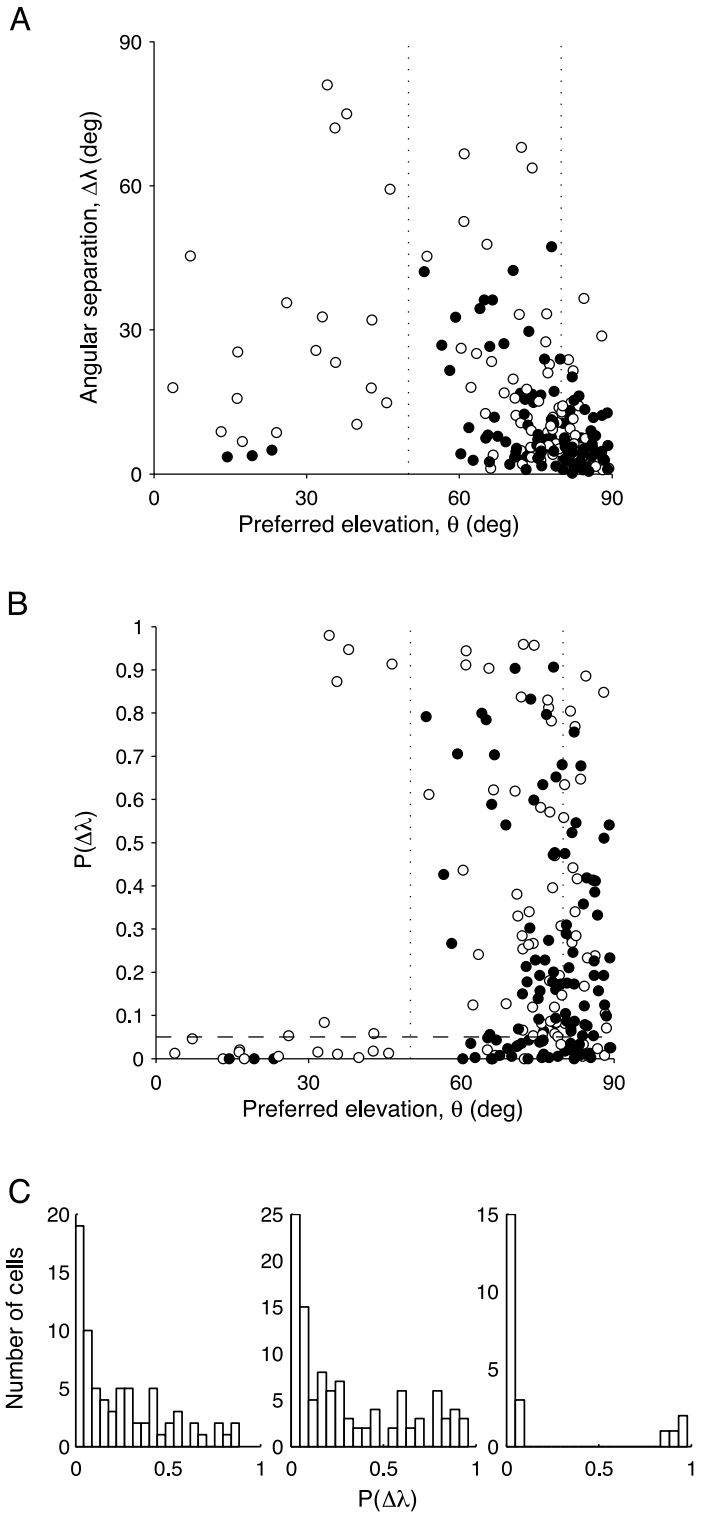

Figure 3. Relationship between the chromatic signatures of a binocular neuron's receptive fields. (A) How the great circle angle that separates the chromatic signatures ($\Delta\lambda$) varies with the neuron's preferred elevation. Each point represents one neuron. Simple cells are represented by open circles, and complex cells by filled circles. Dashed lines show elevations that separate cells falling in the informal groups discussed in the text. (B) How the likelihood that the separation arose by chance $P(\Delta\lambda)$ depends on the neuron's preferred elevation. Conventions as in panel A. (C) Distribution of $P(\Delta\lambda)$ among neurons in the three informal groups A, B, C. The horizontal dotted line indicates $P(\Delta\lambda) = 0.05$.

Spatial organization of receptive fields

Given the consistent observation that stereopsis is poor for chromatic stimuli, it is useful to understand the spatial

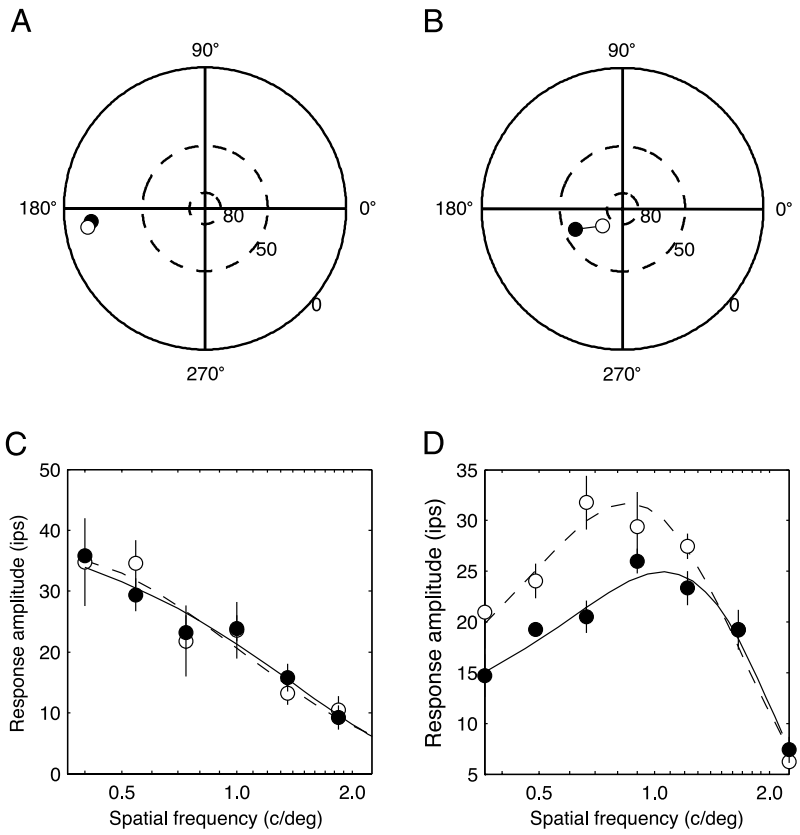

Figure 4. Spatial selectivity of two V2 binocular cells that responded to chromatic modulation; a group C cell most sensitive to chromatic modulation (A, C), and a group B cell sensitive to both chromatic and luminance modulation (B, D). (A, B) Chromatic signatures of receptive fields in the dominant eye (open symbols) and non-dominant eye (closed symbols). Conventions as in Figure 2. Spatial frequency was 1.3 cycles/degree in panel A and 0.9 in panel B. (C, D) Spatial frequency tuning for the dominant eye (open symbols) and non-dominant eye (closed symbols). The gratings were isoluminant (azimuth 0 degrees) in panel C and achromatic in panel D. The receptive fields of the color-preferring group C cell were not selective for spatial frequency, and the chromatic signatures were very similar ($\Delta\lambda$ = 3.5°, $P(\Delta\lambda) < 0.005$). The receptive fields of the group B cell showed well-matched selectivity for spatial frequency, but their chromatic signatures differed ($\Delta\lambda$ = 17.6°, $P(\Delta\lambda) = 0.26$).

organization and selectivity binocularly driven neurons that respond to chromatic modulation. Figures 4C and 4D show the spatial frequency tuning of two representative neurons, the chromatic signatures of which are shown in Figures 4A and 4B. The group C (color-preferring) neuron in Figure 4 was not selective for spatial frequency (Figure 4C) and responded as well to modulation of a spatially uniform field as it did to gratings; both chromatic and spatial properties were well matched in the two eyes. The group B neuron in Figure 4 was more selective for spatial frequency and responded less well to uniform fields. While the spatial frequency tuning was well matched in the two eyes, the chromatic signature was not.

In nine binocular group C neurons (6 in V1 and 3 in V2), we measured spatial frequency tuning using isoluminant gratings modulated along the preferred color direction. All showed low-pass spatial frequency tuning in both eyes, responding as well to uniform fields as they did to drifting gratings: The average response to uniform fields was 90% of the peak response. They were also unselective for orientation. We conclude that binocular color-preferring neurons are not usually selective for the spatial frequency of chromatic gratings. Among 65 group B neurons, which responded well to both chromatic and achromatic modulation, responses to achromatic gratings of low spatial frequency were on average 57% of peak response. Among 50 group A neurons, responses to achromatic gratings of low spatial frequency were on average 47% of peak. Among the cells of groups A and B, the loss of response at low spatial frequencies was significantly greater than the loss among cells of group C ($p < 0.05$ in both cases, Student's *t*-test with Bonferroni correction).

Discussion

Our findings make clear that even in early visual cortex neurons are color-preferring and binocularly driven. In fact, most color-preferring neurons that we encountered in

V1 and V2 were well driven by both eyes. Our analysis also makes clear that among color-preferring (group C) neurons the chromatic properties of the two receptive fields are well matched. For most group A and B neurons, the chromatic properties of the two receptive fields appear to be matched no better than would be expected by chance.

The good match between the chromatic properties of the two receptive fields of a group C neuron is presumably important for binocular vision. In humans, it is clear that lights of different colors presented to the two eyes can be fused to generate a novel percept, usually a mixture of the two (Erkelens & van Ee, 2002; Ikeda & Nakashima, 1980; Ikeda & Sagawa, 1979). This might be expected if color-preferring binocular neurons provided a chromatic signal that was an amalgam of the two monocular signals. We have verified in separate experiments (not described here) that group C cells do combine quite linearly the signals from the two eyes. Several psychophysical studies of binocular contrast summation suggest the existence of binocular color neurons (Simmons, 2005; Simmons & Kingdom, 1998), although Jimenez, Valero, Anera, Martinez, and Salas (2003), using similar stimuli, found no evidence of neural summation for binocular color signals. Nevertheless, color and luminance contrast combined might have a role in solving the correspondence problem, thereby indirectly facilitating stereopsis (de Haan, van Ee, & den Ouden, 2005; Jordan, Geisler, & Bovik, 1990).

Given the prevalence of binocularly driven color-preferring cells, why is stereopsis so poor for isoluminant stimuli? The answer probably lies in the spatial organization of the receptive fields. Coarse sensitivity to stereoscopic depth is conferred on binocular neurons by the position of the receptive field in each eye, but high stereoacuity seems also to require sensitivity to the position of stimuli within each receptive field (Anzai et al., 1999; Ohzawa et al., 1990). Most color-preferring neurons have spatially homogenous receptive fields that lack orientation and spatial selectivity and are therefore generally insensitive to the precise spatial form of stimulation (Hubel & Wiesel, 1968; Johnson et al., 2001; Lennie et al., 1990; Solomon et al., 2004). This receptive field organization—which perhaps reflects the difficulty of controlling both the spatial properties and the chromatic properties of receptive fields—makes the neurons well equipped to provide a binocular signal about regions of uniform color. Yet it will tend to make the same neurons much less sensitive to the small changes in relative stimulus position that are readily detected by the simple and complex cells that constitute the bulk of neurons in groups A and B.

Most binocular neurons in group B, and some in group A, responded well to isoluminant modulation, and many of these will be selective for the spatial frequency of isoluminant gratings (Johnson et al., 2001; Lennie et al., 1990; Solomon et al., 2004; Thorell, De Valois, & Albrecht, 1984). This selectivity is usually thought to indicate the presence of antagonistic subregions within the receptive field (Movshon, Thompson, & Tolhurst, 1978; Shapley & Hawken, 2002), so these neurons should be able to signal spatial phase, and hence stereoscopic depth, for isoluminant stimuli with an acuity that approaches that for achromatic stimuli. Nevertheless, the chromatic properties of the two receptive fields are often ill-matched, suggesting that the spatial organization and signs of cone inputs to the two receptive fields can be quite different: The depth signal provided by these neurons will then vary with the chromaticity of the stimulus and *vice versa*. This instability suggests that cells in groups A and B cannot reliably convey the joint information about color and depth. No cortical mechanism seems capable of both the precise spatial sampling and precise chromatic sampling necessary for high acuity chromatic stereopsis. The visual system appears instead to support binocular depth perception and binocular surface color perception through separate mechanisms. Our results provide evidence for the existence of binocular neurons that signal surface color (Kulikowski & Walsh, 1995; Livingstone, 1996; Simmons, 2005).

While the details of those systems are yet to be elaborated, one thing seems certain; cortical cells responding most strongly to isoluminant stimulation can very often be driven by either eye.

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