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Chromatic properties of neurons in macaque area V2

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Abstract

We recorded from single cells in area V2 of cynomolgus monkeys using standard acute recording techniques. After measuring each cell's spatial and temporal properties, we performed several tests of its chromatic properties using sine-wave gratings modulated around a mean gray background. Most cells behaved like neurons in area V1 and their responses were adequately described by a model that assumes a linear combination of cone signals. Unlike in V1, we found a subpopulation of cells whose activity was increased or inhibited by stimuli within a narrow range of color combinations. No particular color directions were preferentially represented. V2 cells showing color specificity, including cells showing narrow chromatic tuning, were present in any of the stripe compartments, as defined by cytochrome-oxidase (CO) staining. An addition of chromatic contrast facilitated the responses of most neurons to gratings with various luminance contrasts. Neurons in all three CO compartments gave significant responses to isoluminant gratings. Receptive-field properties of cells were generally similar for luminance and chromatically defined stimuli. We found only a small number of cells with a clearly identifiable double-opponent receptive-field organization.

Keywords: Visual cortex, Color, V2, Isoluminance, Macaque

Introduction

The early stages of color information processing in the visual system are quite well understood. In the normal human or macaque retina, there are three classes of cones, short-, middle-, and long-wavelength sensitive, that linearly sum light of different wavelengths. These early mechanisms have been studied in great detail at the psychophysical, physiological, and molecular levels (Smith & Pokorny, 1975; Nathans et al., 1986; Schnapf et al., 1987). At the subsequent stage, retinal ganglion cells combine the cone inputs linearly in different fashions, resulting in three classes of color-opponent cells. These early "cardinal direction" mechanisms (commonly called red–green, blue–yellow, and luminance) are preferentially represented in the lateral geniculate nucleus (LGN) as well (DeValois, 1965; Derrington et al., 1984). The activity of these mechanisms alone can explain a surprisingly large number of psychophysical results (Krauskopf et al., 1982; Lee et al., 1988).

The processing of color information at the later stages of the visual pathways is less well understood. Early studies of the primate visual cortex reported only a very small proportion of chromatically responsive cells (Hubel & Wiesel, 1968). Since then several studies showed that many cells that respond to luminance variations also respond to color variations, bringing the overall proportion of color selective cells to about 50% in the striate cortex of macaque monkeys (Dow & Gouras, 1973; Gouras, 1974; Yates, 1974; Thorell et al., 1984). More interesting than the percentage of cells being selective to color is the question of their functional role.

Yates (1974) and Gouras (1974) reported the presence in striate cortex of an unspecified number of cells sensitive to a narrow range of wavelengths, a specificity that is absent at earlier stages. In addition, several studies reported the existence of a large population of double-opponent cells in the primary visual cortex of primates (Michael, 1978*a*,*b*,*c*, 1979; Livingstone & Hubel, 1984). These cells have a spatially and chromatically antagonistic center-surround organization, and were hypothesized to play an important role in achieving color constancy (Zeki, 1980; Valberg & Seim, 1983; Rubin & Richards, 1982; Gershon et al., 1986). In a more recent and quantitative study Lennie et al. (1990) found less than 2% of cells narrowly tuned to wavelength in V1. Furthermore, they and others (Ts'o & Gilbert, 1988) failed to demonstrate the existence of double-opponent cells in this area. Their experiments show that, as in the LGN, cells in the primary visual cortex also tend to combine cone inputs linearly. But unlike in the LGN, cardinal directions are not preferentially represented at the V1 level.

Narrow wavelength selectivity and color constancy are the properties that some studies have found in V4 of macaques (Zeki, 1980) and which have led to the characterization of area V4 as the most important area for color processing. Although more recently the interpretation of these results has been questioned on methodological grounds (de Monasterio & Schein, 1982; Schein et al., 1982), it is generally accepted that a major proportion of neurons in area V4 selectively respond to color (Schein & Desimone, 1990).

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Little is known about the processing of color information between areas V1 and V4. The present study aims at understanding the function of area V2, which directly follows V1 in the cortical hierarchy, and which has prominent projections to area V4. Since a number of recent psychophysical results (Webster & Mollon, 1991; Gegenfurtner & Kiper, 1992; Krauskopf & Gegenfurtner, 1992; Zaidi & Halevy, 1993; Krauskopf et al., 1996) revealed the existence of mechanisms tuned to specific colors, often termed "higher-order color mechanisms", we particularly concentrated on the issue of the tuning characteristics of color-sensitive cells in V2.

Previously, we have reported general aspects of stimulus selectivities and their distributions across the functional compartments in V2 (Gegenfurtner et al., 1996). Here we concentrate on the processing of the chromatic signals alone.

Methods

Preparation and maintenance

These experiments were performed on eight young adult cynomolgus monkeys (*Macaca fascicularis*). As the quantitative data on chromatic properties reported here were obtained during the same experimental sessions as those described in an earlier report (Gegenfurtner et al., 1996), we would direct the reader to that report for the details of surgical preparation, physiological maintenance, and anatomical analysis of these animals. Briefly, following preparatory surgery under halothane anesthesia, the animals were anesthetized with a continuous infusion of Sufentanil citrate, with a dosage between 4 and 8 μg/kg/h, adjusted to each animal's tolerance of the drug. Paralysis to minimize eye movements was maintained with an infusion of vecuronium bromide (Norcuron: 0.1 mg/kg/h) in lactated Ringer's solution with dextrose. The animals were artificially ventilated with room air or with a 49:49:2 mixture of N_2O, O_2, and CO_2. Peak expired CO_2, rectal temperature, EEG, and EKG were all monitored continuously to ensure the adequacy of anesthesia and the soundness of the animal's condition. A small craniotomy was made over the lunate sulcus, and after making a small slit in the dura, a tungsten-in-glass microelectrode (Merrill & Ainsworth, 1972) was positioned approximately 1 mm behind the lip of the sulcus; the hole was then covered with warm agar.

Anatomical methods

At the conclusion of the recording session, all animals were overdosed with sodium pentobarbital (typically about 60 mg/kg injected intravenously, until complete flattening of the EEG was observed), and perfused through the heart with 4% paraformaldehyde. Frozen sections were cut at 40 μm in the coronal plane, and adjacent series of sections were stained for cytochrome oxidase (CO) (Wong-Riley, 1979), NADPH diaphorase, which we have found to coincide with CO in V2 as well as V1 (Sandell, 1986; method 1), with cresyl violet, and for Cat-301.

Track reconstruction

Sections containing electrode tracks were drawn at low power using an Olympus BHS microscope equipped with a camera lucida. Adjacent sections were aligned precisely using blood vessels and the section outlines as fiducial marks. The laminar locations of the recorded units were assigned on the basis of distance from recorded gray/white matter transitions and from electrolytic lesions made during the recording sessions.

The identification of thick and thin CO stripes can be quite difficult in macaques. To increase the certainty with which our assignments were made, we examined each dark stripe in two, or if possible, three adjacent CO-stained sections. In all cases where CO was robust and consistent across sections, the NADPH diaphorase reactivity exactly coincided with CO. In some animals, the CO reactivity was weak or variable, but NADPH diaphorase reactivity could still be used to locate and identify the dark stripes. The nearest sets of Cat-301 stained sections were used to assist in thick stripe identification. As described by DeYoe et al. (1990), Cat-301 immunoreactive neurons are more numerous and darkly stained in the thick stripes.

Characterization of receptive fields

Receptive fields were initially mapped by hand on a tangent screen using black and white or colored geometric targets. When a single neuron's activity was isolated, we established the neuron's dominant eye, and occluded the other for quantitative experiments. Generally there was little difference between left and right eye responses. Very few neurons responded to binocular stimulation only. We first mapped the location and size of the neuron's minimum response field (Barlow et al., 1967), and then determined selectivity for the orientation, direction of motion, and stimulus size (particularly endstopping). After this initial qualitative characterization, we positioned the receptive field on the face of a display CRT, and quantitative experiments proceeded under control of a personal computer.

Each experiment consisted of several (generally 4–10) blocks of trials. Within each block, all stimuli were presented for the same amount of time, generally 4 s. There were very few units that showed signs of adaptation; for these we chose shorter durations. To minimize effects of response variability, stimuli were presented in a random order within each experimental block, and the results of several repeated blocks (typically between 4 and 10) averaged. We also always measured responses to a uniform grey field of the same mean luminance as our other stimuli to measure the cell's spontaneous firing rate. Responses were compiled into average histograms synchronized to each temporal cycle of the stimulus. These histograms were then Fourier analyzed to calculate the average response (DC) and the response at the fundamental stimulus frequency (F1). For complex cells, which respond with an unmodulated elevation in discharge rate, we used the DC response (mean firing rate minus spontaneous activity) as the response measure; for simple cells we used the F1 response. The repeated trials were used to calculate standard errors of the responses. These are shown as error bars in all graphs.

Visual stimulation

Stimuli were displayed on a BARCO CCID 7351B color television monitor driven by an AT Truevision Vista Graphics board. At a viewing distance of 174 cm the screen subtended 12.5 deg × 9 deg of visual angle. Drifting sinusoidal grating stimuli were modulated around an average white point with C.I.E. xy coordinates of (0.31, 0.32) with an average luminance of 30 cd/m^2. Fig. 1 is a schematic diagram illustrating the color stimuli used in these experiments. The color space we used has been described in detail elsewhere (Krauskopf et al., 1982; Lennie et al., 1990; Gegenfurtner et al., 1996). At the origin is a neutral white point. Along the "L–M" axis, the excitation of the L- and M-cones covaries as to keep their sum constant. Along the "S–(L+M)" axis, only the excitation of the

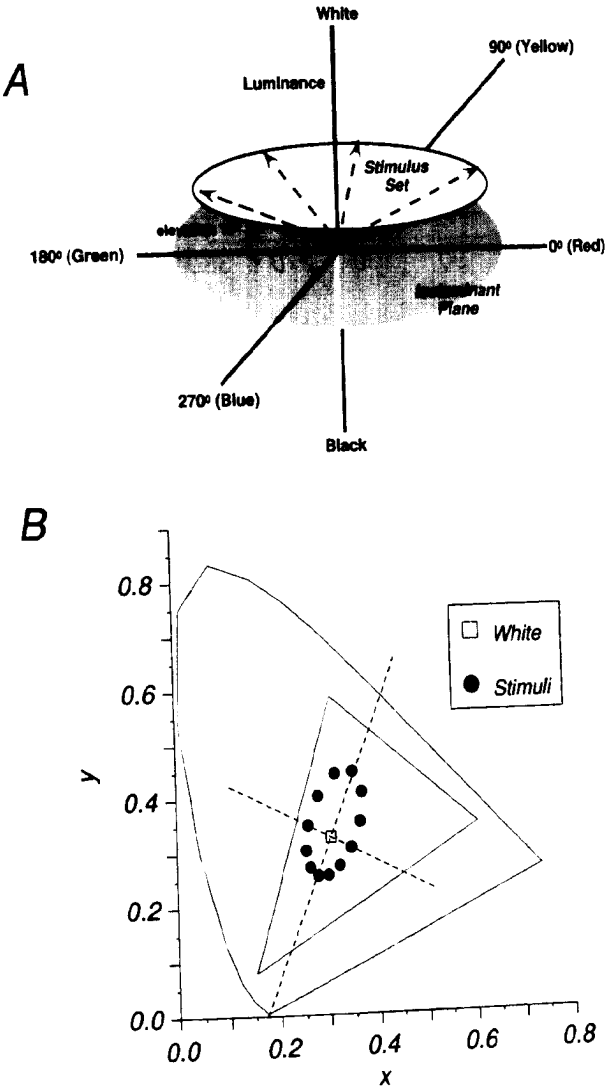

Fig. 1. (A) Schematic diagram illustrating the color stimuli used in the color experiments. The color space we used has been described in detail elsewhere (Krauskopf et al., 1982; Derrington et al., 1984). At the origin is a neutral white. Along the "L–M" axis, the excitation of the L- and M-cones axis covaries as to keep their sum constant. Along the "S–(L+M)" axis, only the excitation of the S-cones varies. Along the "Luminance" axis, the excitation of all three cones varies in proportion to their excitation at the white point. A stimulus in this space is defined by its azimuth, which is the angle made by its projection on the isoluminant plane with the L–M axis, and its angular elevation above the isoluminant plane. The inverted cone represents the set of stimuli with an elevation of 10 deg and an azimuth varying between 0 deg and 360 deg. The scaling of the three axes in this space is arbitrary; in our experiments the maximum modulation along the luminance axis was 100% luminance contrast, 85% S-cone contrast along the S–(L+M) axis, and 6% L–cone and 13% M-cone modulation along the L–M axis. (B) C.I.E. *xy* chromaticity diagram illustrating the same color stimuli. The dashed lines indicate the placement of the axis of the color space described above. The triangle indicates the C.I.E. coordinates of the phosphors, of our monitor. Since the mean luminance of our stimuli was higher than the maximum luminance of the red and the blue phosphors, the range of color was even more restricted than the triangle.

S-cones varies. Along the "Luminance" axis, the excitation of all three cones varies in proportion to their excitation at the white point. The scaling of the three axes in this space is arbitrary; in our case the maximum modulation along the luminance axis was 100% luminance contrast, 85% S-cone contrast along the S–(L+M) axis, and 13% M-cone and 6% L-cone modulation along the L–M axis. A stimulus in this space can be defined by its azimuth, which is the angle made by its projection on the isoluminant plane with the L–M axis, and its angular elevation above the isoluminant plane. All the stimuli we used were sine-wave gratings modulated in this space around the origin. The inverted cone in Fig. 1 represents a set of stimuli with an elevation of 10 deg and an azimuth varying between 0 deg and 360 deg; these were used to measure the bandwidth of chromatic tuning. The luminance contrast of these stimuli was 12%. Fig. 1B shows the distribution of these colors in the C.I.E. *xy* chromaticity diagram. The two isoluminant cardinal directions are indicated by the dashed lines in Fig. 1B.

Results

We recorded from 140 single neurons in area V2 of eight macaque monkeys. Of these cells, we were able to assign 119 unambiguously to one of the CO compartments. 90% of the units had receptive fields centered within 5 deg of the fovea. 72% of all neurons were complex cells, and 28% simple cells. For each neuron, we initially measured its preferred orientation, spatial frequency, temporal frequency, and preferred stimulus size using achromatic gratings (Gegenfurtner et al., 1996). With these optimal parameters established, we proceeded with the experiments described below, which we were able to run on 84 cells. The average peak spatial frequency of the neurons in our sample was 1.24 cycles/deg, and the average peak temporal frequency was 4.2 Hz.

Tuning in color space

To measure the selectivity with which V2 cells respond to chromatic stimuli, we used a set of stimuli with varying azimuth and a fixed elevation of 10 deg. At this elevation all stimuli had a luminance contrast of 12%. We used stimuli with a luminance contrast since most cells in area V2 respond only weakly to isoluminant stimuli, which are defined by pure chromatic contrast. All cells on which we ran this experiment gave good responses at least to some of these stimuli. A black-and-white luminance stimulus with the same contrast of 12% was included in the stimulus set as a control to differentiate luminance and chromatic contributions to the response. Fig. 2 shows the responses of four cells to these stimuli. On the abscissa is the stimulus' azimuth, and the cell's response is plotted on the ordinate. The horizontal dashed lines represent the cell's spontaneous firing rate to a uniform gray field. The solid horizontal line shows the cell's response to the achromatic control stimulus. The cell in Fig. 2A was located in the upper layers of V1, whereas the other cells were from V2. As was previously shown (Lennie et al., 1990), the responses of the V1 cell in Fig. 2A are well predicted by a model that assumes a linear combination of cone inputs. The predictions of this model are shown by the solid curve. The above model allows a characterization of the chromatic properties of each cell with only two parameters, namely the elevation and the azimuth of the color direction to which it responds best. Responses to all other colors can be derived from that vector because the shape of the tuning curve is assumed to be linear and identical for all cells. More precisely, the predicted response is given by the dot product of the color direction of the stimulus and the color direction of the cell's preferred direction:

$$R = b + A\,|\sin(\mathrm{elev})\sin(\Phi) + \cos(\mathrm{elev})\cos(\Phi)\cos(az - \Psi)|, \quad (1)$$

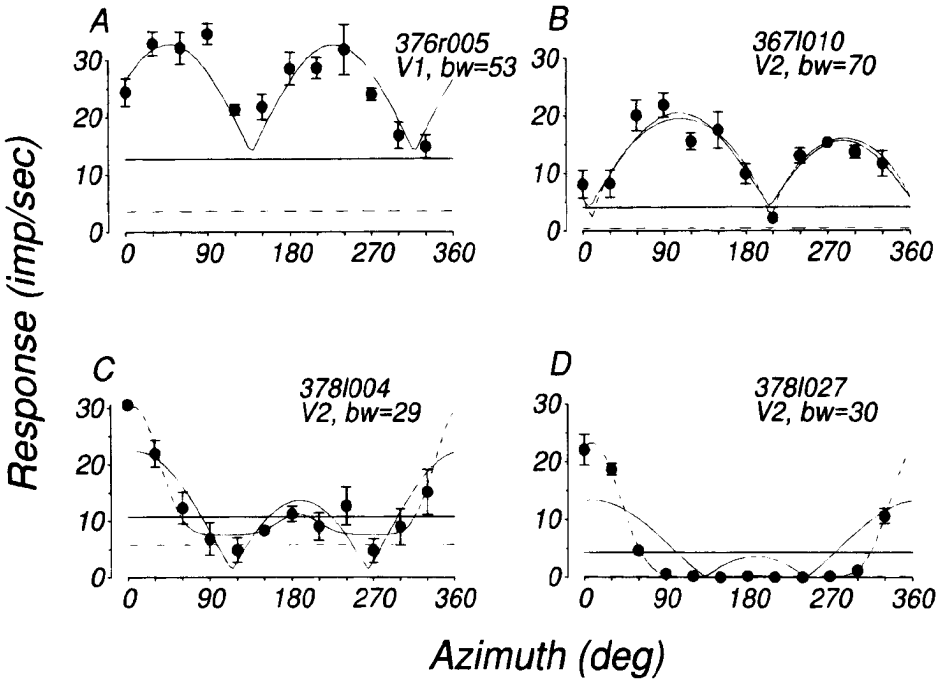

Fig. 2. Responses of a typical V1 cell (A) and of 3 V2 cells (B, C, and D) to stimuli of various azimuths and a constant elevation of 10 deg (as shown in Fig. 1). The solid curves fitted through the data represent the prediction of a model that assumes a linear summation of cone inputs (Derrington et al., 1984). The horizontal dashed line (baseline) represents the response to a blank screen of space-averaged luminance equal to that of the stimuli. The horizontal solid line represents the response to a grating modulated only in luminance, with a contrast equal to that of the chromatic stimuli. The dashed curves through the data represent the best fit of a nonlinear function.

where b is the response baseline, A the response amplitude, Φ is the cell's preferred elevation, and Ψ its preferred azimuth. The nonlinear function minimization program STEPIT (Chandler, 1969) was used to minimize the squared and normalized deviations of eqn. (1) and the observed firing rates. The dashed curves through the data represent the best fit of a nonlinear function: $\hat{R} = R^{\gamma}/(R^{\gamma} + R^{sat})$, where R is the response of the linear model described above, and R^{γ} and R^{sat} can be interpreted as parameters of a nonlinear contrast-response function.

As seen in Fig. 2A, the model fits quite well, and this is generally the case for cells in V1 (Lennie et al., 1990). In that respect V1 cells behave similarly to cells in the LGN (Derrington et al., 1984), but they often prefer color directions that do not fall on the cardinal directions of color space. The responses of the V2 cell illustrated in Fig. 2B also follow the linear model's predictions closely. Like complex cells in V1 (Fig. 2A), complex cells in V2 show a full-wave rectification along the direction opposite to their preferred azimuth. As the model predicts, a cell that prefers bright red and dark green gratings will also respond to dark red and bright green gratings. These cells can be characterized as linearly summing their cone inputs and full-wave rectifying their output. The majority of cells in V2 (55 of 84, 65%) behaved in this simple, quasilinear way.

A minority of neurons showed systematic deviations from this linear model. For the cells shown in Figs. 2C and 2D, the tuning in color space is much narrower than the linear prediction (solid curve). This narrow tuning was found in about a third of V2 cells (29 of 84, 35%). The cell in Fig. 2D, for example, responded only to stimuli consisting of bright red and dark green grating bars, gave no response to stimuli of the opposite polarity (bright green and dark red), and no response to a bright orange stimulus (azimuth = 60 deg), even though this stimulus had a relatively high contrast along the color direction preferred by the cell.

To determine each cell's bandwidth of tuning in color space we used a nonlinear function to interpolate between the data points (dashed curves in Figs. 2B–2D). At a constant elevation of 10 deg, bandwidth was defined as the angular difference between the color vector giving the peak response, and that vector where the response had fallen to 50% of the difference between peak vector and 90 deg away. This definition has the advantage that it predicts a constant bandwidth for linear cells, independently of their preferred azimuth and elevation. Because of the term $\sin(\text{elev})\sin(\Phi)$ in eqn. (1), an actual response null does not have to occur in the direction orthogonal to the preferred direction. A true null would occur only if the stimuli had an elevation of 0 deg, or for cells whose preferred elevation is 0 deg. But for all linear cells the bandwidth at *half-height* with respect to the orthogonal direction should be equal to 60 deg, the angle whose cosine is 0.5.

The resulting distribution of bandwidths for all 84 neurons is shown as a histogram in Fig. 3. The distribution is distinctly bimodal, showing subpopulations of narrowly tuned cells (like the ones in Figs. 2C and 2D), and of cells with an approximately linear tuning (like that of Fig. 2B), which are clustered around a bandwidth of 60 deg. The rightmost column represents cells for which we could not reliably determine any color specific tuning because they only responded to the luminance component of the stimuli. It is important to remember that earlier in the visual system the responses are well fitted by the linear model (Derrington et al., 1984). Thus, most color-selective LGN and V1 neurons have a bandwidth around 60 deg. Bandwidths were derived from the fits of the nonlinear function described above, but similar results were obtained using a smooth spline function to interpolate between

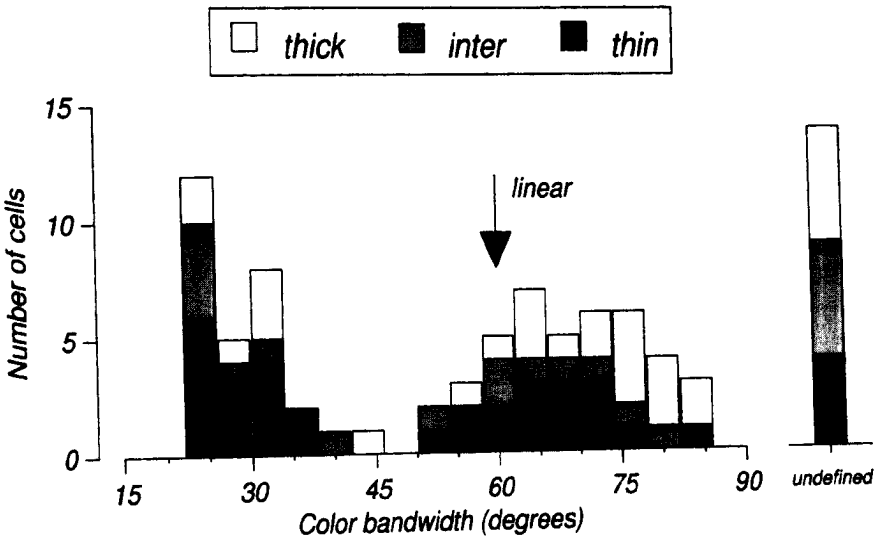

Fig. 3. Histogram of the bandwidth of tuning in color space. For each value of bandwidth, the proportions of cells located in thin, thick, or interstripe (as defined by CO staining) are shown. Bandwidths for the cells in Figs. 2A–2D were 53 deg, 70 deg, 29 deg, and 30 deg, respectively. At a constant elevation of 10 deg, bandwidth was defined as the angular difference between the color vector that gave the best response at that elevation, and the color vector where the response had decreased by 50% compared to the response 90 deg away from the maximum. This definition predicts a constant bandwidth of 60 deg, indicated by the arrow, for cells that linearly sum cone inputs. For the cells to the far right the responses to all chromatic stimuli were constant, and thus chromatic tuning bandwidth was not defined.

data points. Even though we found that the hyperbolic function gave good fits for all cells including the narrowly tuned ones, the estimated parameters for our model nonlinearity in general did not agree with estimates of nonlinearities that were independently estimated from contrast–response functions.

Area V2 is anatomically segregated into stripes that differ in their content of the mitochondrial enzyme cytochrome oxidase (CO) (Tootell et al., 1983). Thick-, thin-, and inter-stripe regions are thought to have distinct functions as well. In particular, the thin stripes are considered part of the parvo-cellular system responsible for color vision; cells responding selectively to color occur more frequently in the thin stripes (DeYoe & Van Essen, 1985; Hubel & Livingstone, 1987; Levitt et al., 1994*a*; Roe & Ts'o, 1995; Gegenfurtner et al., 1996). If narrowly tuned cells play a specific role in analyzing color information *per se*, one might expect them to be restricted to the thin stripes. Therefore, we histologically determined each cell's location with respect to CO compartments. The different shadings of the histogram bars in Fig. 3 indicate the three different CO compartments. Cells with narrow tuning were not restricted to thin stripes, nor were "luminance" cells restricted to the thick stripes. Narrowly tuned cells were slightly more frequently encountered in the thin stripes (15 out of 84, 18%) than predicted by chance (12 out of 84, 14%), but this tendency was not statistically significant. A two-way contingency test found no significant interaction between cell type (narrowly tuned, linear, and luminance) and CO compartment ($\chi^2 = 3.99$, $df = 4$, $P > 0.1$). Furthermore, both complex (24 of 63, 38%) and simple (5 of 21, 24%) cells showed narrow tuning.

One of the major unresolved questions in color vision is the mismatch between the early "cardinal directions" (Krauskopf et al., 1982; Derrington et al., 1984) and the perceptually defined "unique hues", red, green, blue, and yellow (Hering, 1878; Hurvich & Jameson, 1955). While neurons in the LGN show clear preferences for the cardinal directions, it is still debated whether neurons later in the pathway, particularly in extrastriate area V4, show such clustering around the unique hues (Zeki, 1978; de Monasterio & Schein, 1982; Schein & Desimone, 1990). Using the nonlinear function that we fitted to the data earlier, we could derive the preferred azimuth of all the cells in our sample. The resulting distribution of preferred azimuths is shown in Fig. 4. The labeled arrows in Fig. 4 indicate the "unique hues" for the type of stimuli we used, as determined by informal visual inspection. While there

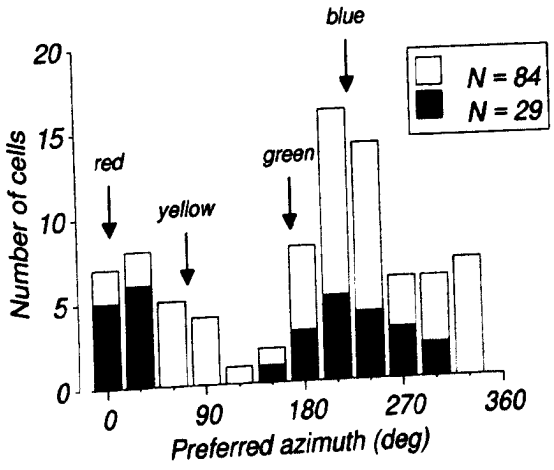

Fig. 4. Histogram of preferred azimuths for our V2 cells. Preferred azimuth was derived from the fits of the extended model, but was quite robust with respect to the method of fitting (the azimuths predicted by the linear model or by the smooth spline interpolation correlated highly, $r = 0.93$ and 0.91, respectively, with those shown here). Open bars show the azimuths for the whole sample, filled bars for the narrowly tuned cells only. We defined narrowly tuned cells as cells from the left mode of the histogram in Fig. 3, all of which had bandwidths smaller than 45 deg.

is a preference for the cardinal directions, the preferred azimuths are not restricted to them. There is no systematic clustering around these "unique hues" for either linear or narrowly tuned cells.

Responses at isoluminance

In the above experiment, we used stimuli with a fixed luminance component, since many of the cells give relatively weak responses when the stimuli do not have a luminance contrast. Stimuli without luminance contrast, isoluminant stimuli, have been used extensively during the past two decades to characterize primate color vision. Our goal was to determine the nature of the response to isoluminant stimuli, because previous research (Gegenfurtner et al., 1994; Dobkins & Albright, 1995) has shown that the isoluminant point can vary slightly from cell to cell. We tested cells with a range of stimuli at different elevations around zero (isoluminance). This way we could detect null points even in cells that do not strictly adhere to photometric isoluminance.

Two sets of stimuli were used: black-and-white achromatic gratings of increasing contrasts, and hetero-chromatic gratings, which consisted of an isoluminant colored grating to which we added a black-and-white achromatic grating. The azimuths of the hetero-chromatic gratings were chosen to be the ones where the cells gave the best response in the previous experiment. If a cell simply responds to the luminance component of the stimuli, its response will be the same to the achromatic and the hetero-chromatic grating of the same luminance contrast. Thus, when the hetero-chromatic grating is isoluminant, the response will be zero. This zero, or point of isoluminance, frequently does not correspond to the human photopic luminance sensitivity curve V_λ. For these cells a small amount of luminance contrast needs to be added or subtracted to obtain a zero response. The response curves for chromatic and achromatic stimuli will be parallel, but shifted horizontally. On the other hand, cells that receive color-opponent inputs should behave in a different way. They should respond well to all color stimuli regardless of their luminance contrast. These cells should not have a "null" response for any of the chromatic stimuli in this experiment.

We ran this experiment on 33 cells for which we had previously established the preferred azimuth in our color space. Fig. 5 shows three representative examples of responses. The cell in Fig. 5A is typical of a luminance cell, which sums cone inputs with a slightly different ratio than the photometric standard. Its response curve with chromatic stimuli is parallel to that of the purely luminance curve, and it has a null shifted to the right of the isoluminant point (0 on the abscissa). The cell in Fig. 5B also has a null close to photometric isoluminance, but it hardly responded to the purely luminance gratings. Furthermore, its responses to the chromatic stimuli depended strongly on the relative phase between the luminance and the purely chromatic components. This is typical of a cell that does not linearly sum the cone inputs, and this cell is indeed one that had a narrow tuning in color space (Fig. 2C). Finally, the cell in Fig. 5C has no null, it responds to all color-luminance combinations used in this experiment, and thus has the signature of a true color-opponent cell.

To quantify the responses of each cell in this experiment, and to determine how the addition of chromatic contrast changed the responses to luminance, we computed for each cell a facilitation index (*FI*). It is defined as the ratio between the averaged responses to the chromatic stimuli (luminance and color) and the averaged responses to the achromatic stimuli (luminance only). A value of *FI* close to 1 indicates that responses depend mostly on

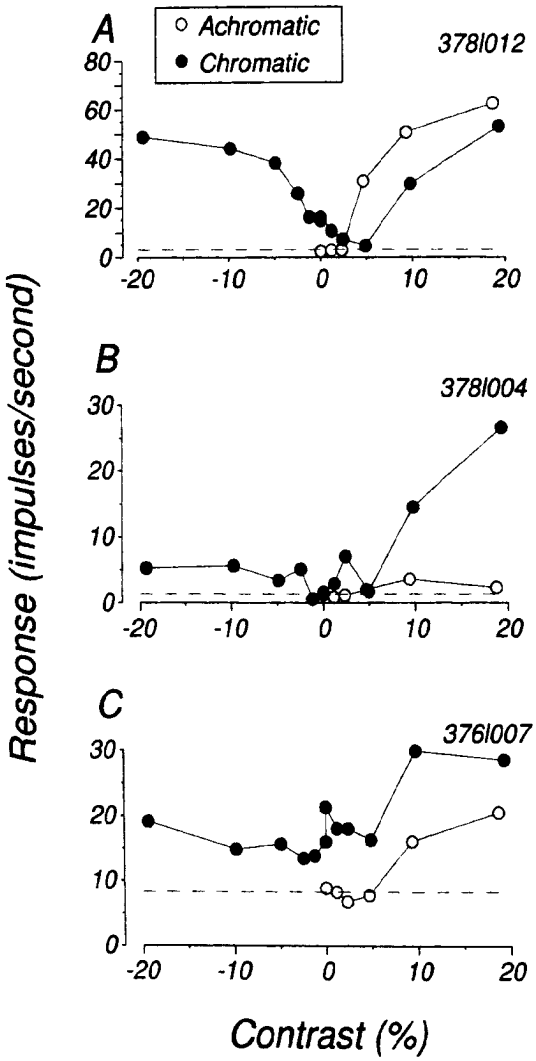

Fig. 5. Representative responses of three V2 cells to two sets of stimuli differing in chromatic contrast. The open circles show the responses to purely luminance gratings at increasing contrasts. The filled circles show the responses to gratings with the same luminance contrasts but that also contain chromatic information, selected in each cell's preferred azimuth. The horizontal dashed line shows the baseline response. (A) Cell from a thick stripe with a preferred azimuth close to 0 deg. It is a typical example of a cell whose responses are dominated by the luminance component of the stimulus. It has a null plane slightly off the photometric plane of isoluminance. Spatial frequency was 0.75 cycles/deg, temporal frequency 7.0 Hz. (B) Cell located in a thin stripe with a preferred azimuth close to 0 deg. This cell also has a null close to isoluminance, but hardly responded to the purely luminance grating. Spatial frequency was 0.5 cycles/deg, temporal frequency 3.5 Hz. (C) Example of a color cell, which did not have a null in this experiment. This cell was located in an inter-stripe and its preferred azimuth was 30 deg. Spatial frequency was 0.75 cycles/deg, temporal frequency 1.75 Hz.

the achromatic components of the stimuli, as for the cell shown in Fig. 5A (*FI* = 1.02). A value of *FI* higher than 1 means that the response curve for chromatic responses lies significantly above the curve for the achromatic responses, as for the cell shown in Fig. 5C (*FI* = 3.4). Finally, if a cell does not respond to luminance at all, *FI* becomes very high or indeterminate, as for the cell shown in Fig. 5B (*FI* = 9.7). A histogram for the indices for the 33 cells in our sample is shown in Fig. 6. Different levels of gray indicate different CO compartments. For about half of the cells (17 of 33,

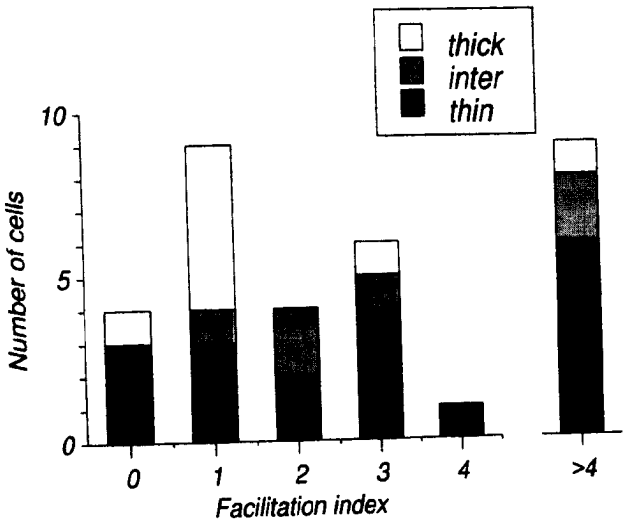

Fig. 6. Stacked histogram of the facilitation indices (see text) distribution for 33 cells, according to their location in the three CO compartments. Different shades of gray indicate different CO compartments (thick: white, inter: gray, thin: black) All the cells with a facilitation index larger than 4 are grouped together in the rightmost column.

52%), the chromatic component had little effect on the magnitude of the responses ($FI < 2.5$). For the other half we found a significant enhancement of the responses. There was no statistically significant difference between the different CO compartments, neither when tested by an analysis of variance ($F_{2,30} = 0.72$, $P > 0.1$) nor by a nonparametric median test ($\chi^2 = 1.52$, $df = 2$, $P > 0.1$).

Despite the above, the majority of cells (22 of 33, 67%) had a clear response null for one or more of the chromatic gratings, where the response was less than 10% of the maximum response to any of the achromatic gratings. Either these cells were luminance cells with a clear single response null, or they were otherwise inhibited for some of the chromatic stimuli, like the cell in Fig. 5B. These response minima did show some variation—not all cells had their minimum at photometric isoluminance. Since psychophysical experiments using isoluminant stimuli typically use photometrically isoluminant stimuli, it is of great interest to determine the overall response of cells for that particular stimulus. For 14 of 33 cells (42%), the response at isoluminance was less than 10% of the maximum response to any of the achromatic gratings. The median response at isoluminance was at 19.1% of the achromatic maximum.

These characteristics are also visible in the population average response, shown in Fig. 7A. The response to the chromatic stimuli exceeded that to the achromatic stimuli at all the contrasts we used. Moreover, the response curve to the chromatic stimuli does not have a null, although it has a minimum near photometric isoluminance. Even though individual null points are shifted leftward or rightward, the average curve is centered at photometric isoluminance (dashed vertical line). These averaged responses illustrate the fact that the chromatic content of visual stimuli does contribute significantly to the responses of cells in V2 and that there exists no single color-luminance combination that can totally silence the responses of area V2 as a whole. At photometric isoluminance, the population response in area V2 is at 44.04% of the maximum response to any of the achromatic stimuli. For reference, the highest achromatic contrast we used in this experiment was 18%.

The same holds for individual CO compartments. Fig. 7B shows the response relative to the highest luminance response (at 18% contrast) of populations of neurons from the three different CO compartments. The population average response at isoluminance was at 46.25% of the maximum achromatic in the thick stripes ($N = 8$), at 43.65% in the thin stripes ($N = 6$). In all compartments the chromatic component has a facilitative effect on the population response. For comparison, in area MT, an area with predominantly magnocellular input, the average response at isoluminance is at 27% of the luminance response (Gegenfurtner et al., 1994; Gegenfurtner & Hawken, 1996). Fig. 7C shows the same average responses as in Fig. 7B without the normalization.

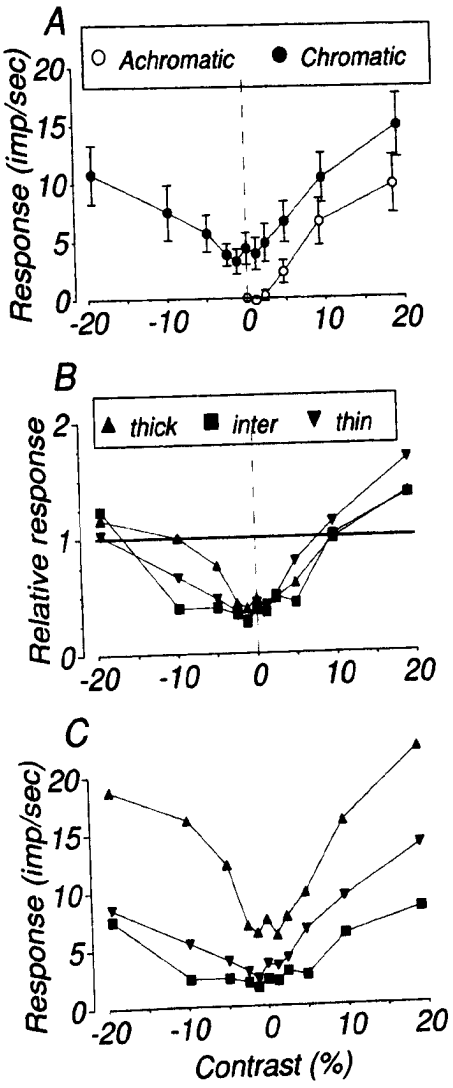

Fig. 7. (A) Averaged responses of 33 cells from all three CO compartments to two sets of stimuli differing in their chromatic contrast only. The average responses to purely luminance gratings are shown by the open circles, those to the gratings containing both luminance and chromatic components by the filled circles. The average baseline response has been subtracted from both sets of data. The error bars represent the standard deviation of the 33 responses at each contrast level. The vertical dashed line shows the location of the photometric isoluminance plane. (B) Averaged responses to chromatic stimuli relative to the highest luminance response (at 18% contrast, shown by the horizontal line) of populations of neurons from the three different CO compartments, thick (upward pointing triangles), thin (downward pointing triangles, and inter-stripe (squares) regions. (C) The same responses as shown in B, without the response normalization.

Spatiotemporal tuning at isoluminance

Having obtained a significant population response at isoluminance, we investigated whether the tuning characteristics of individual cells would be different for achromatic and chromatic stimuli. For 20 cells that gave significant responses to isoluminant stimuli, we measured the cell's tuning for orientation, spatial frequency, and temporal frequency, as well as its contrast–response curve using isoluminant gratings. For orientation, spatial frequency, and temporal frequency, the contrast of these gratings was always the maximum we could achieve on our monitor in the particular color direction (azimuth) the cell preferred. We then compared these measurements to the earlier measurements using achromatic black-and-white gratings of maximum contrast (near 100%). An example is shown in Fig. 8. Even though the responses of this cell, located in a thin stripe, were lower to the isoluminant gratings than to the high contrast luminance grating, its tuning characteristics were virtually identical for both types of stimuli. This was characteristic for our sample of cells.

Fig. 9A shows a scatter plot of the optimal orientations for each cell for luminance (x-axis) and isoluminant (y-axis) stimuli. The correlation coefficient between these two measures was 0.97 and the mean difference was 5.8 deg. Similarly, as shown in Fig. 9B, selectivity for orientation, as determined by an orientation index (Gegenfurtner et al., 1996), was not significantly different for both types of stimuli ($t_{20} = 1.2$, $P > 0.1$) and correlated highly ($\rho = 0.68$). The orientation index was defined as

$$ORI = 1 - \frac{\text{Response in orthogonal orientation} - \text{Baseline}}{\text{Response in optimum orientation} - \text{Baseline}}.$$

Orientation half-bandwidth at half-height was also not significantly different for luminance (mean 31.58 deg) and isoluminant (mean 39.55 deg) stimuli ($t_{20} = 1.1793$, $P > 0.1$). Also, for 19 cells, the median peak spatial frequency at isoluminance was 1.16 cycles/degree and 1.03 cycles/degree for luminance. This small difference was not statistically significant ($t_{18} = 1.47$, $P > 0.1$). The correlation between the peak spatial frequencies was high ($\rho =$

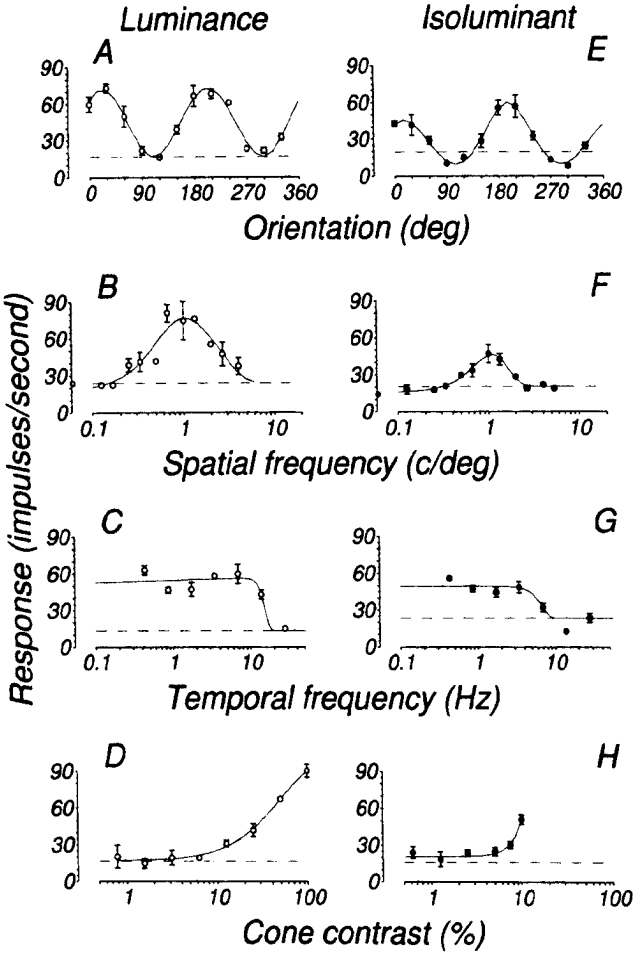

Fig. 8. Orientation, spatial frequency, temporal frequency, and contrast responses for one cell located in a thin stripe, using luminance gratings (left column) and isoluminant gratings (right column). The error bars represent standard errors. The chromatic gratings used in these experiments always had an azimuth of 45 deg and an elevation of 0 deg. Contrast is specified as the root-mean-squared contrast in the L- and M-cones. Note the similarities in orientation, spatial, and temporal tuning obtained with these two sets of stimuli.

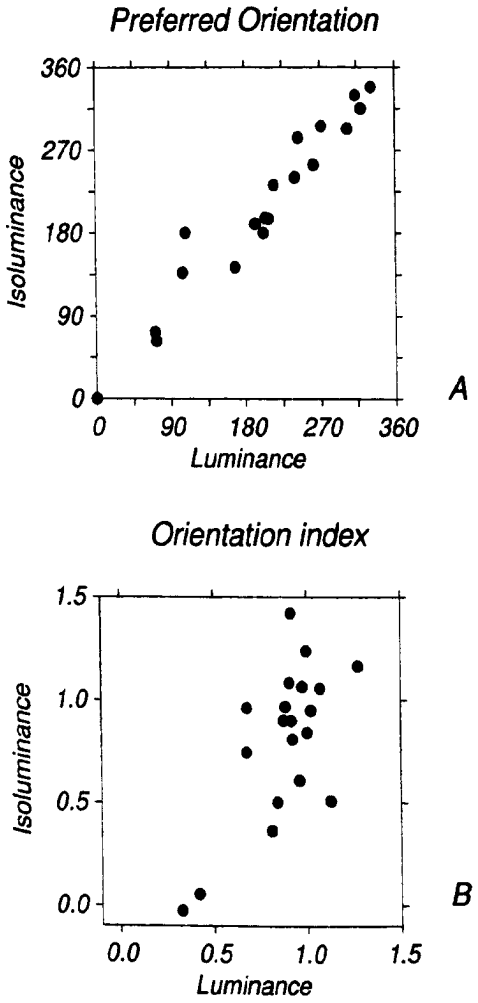

Fig. 9. (A) Scatter diagram of the preferred orientation of 20 cells for chromatic gratings versus luminance gratings. The preferred orientations were derived from the fits to the data (see Methods). The correlation coefficient for preferred orientations was 0.97. (B) Scatter diagram of the orientation indices (see text) for the same cells. The correlation coefficient between indices obtained with isoluminant versus luminance gratings was 0.68.

0.87). Similarly, there was no difference in the peak temporal frequency in the responses to both types of stimuli. The median peak was 2.25 at isoluminance and 2.69 for luminance. Furthermore there was no difference in the bandwidth of tuning, neither for spatial nor for temporal frequency. We were able to measure contrast–response curves to both types of stimuli for only nine cells. For these, no systematic differences in the steepness or shape of the contrast–response curves were observed.

Double opponency

The existence of so-called double-opponent cells is one of the most controversial issues in cortical color processing at the moment (Livingstone & Hubel, 1984; Vautin & Dow, 1985; Michael, 1978*a–c*, 1979; Ts'o & Gilbert, 1988; Lennie et al., 1990). We measured complete spatial-frequency tuning curves in several color directions for 25 cells. In addition to luminance and red–green isoluminance, we also measured responses to gratings in the directions isolating the three cone types, L-, M-, and S-cones. Double-opponent cells are defined as being chromatically opponent in center and surround. Thus, they are spatially opponent as well. A red–green, double-opponent cell should have a bandpass spatial-frequency tuning for both L- and M-cone isolating stimuli, and the response phase should be reversed for the two cone types. This points to the problem of determining double opponency for complex cells, where the response is independent of the stimulus phase. Since both L- and M-cone isolating stimuli have a luminance component as well, a spatially opponent cell responsive to luminance contrast would give such a response. However, if the cell also responds at isoluminance, or if the cell responds poorly to luminance, then it is a good indication for double opponency. Fig. 10 shows two such cells, the only ones out of our sample of 25 cells. Both show bandpass tuning characteristics in all color directions tested. Responses to S-cone isolating stimuli are not shown here, since they were not significantly above the baseline response. When tested with gratings which selectively modulate the activity of L- or M-cones they retained their bandpass characteristics. This suggests that their complex receptive fields contain subregions that alternatively receive excitatory and inhibitory inputs from these two classes of cones.

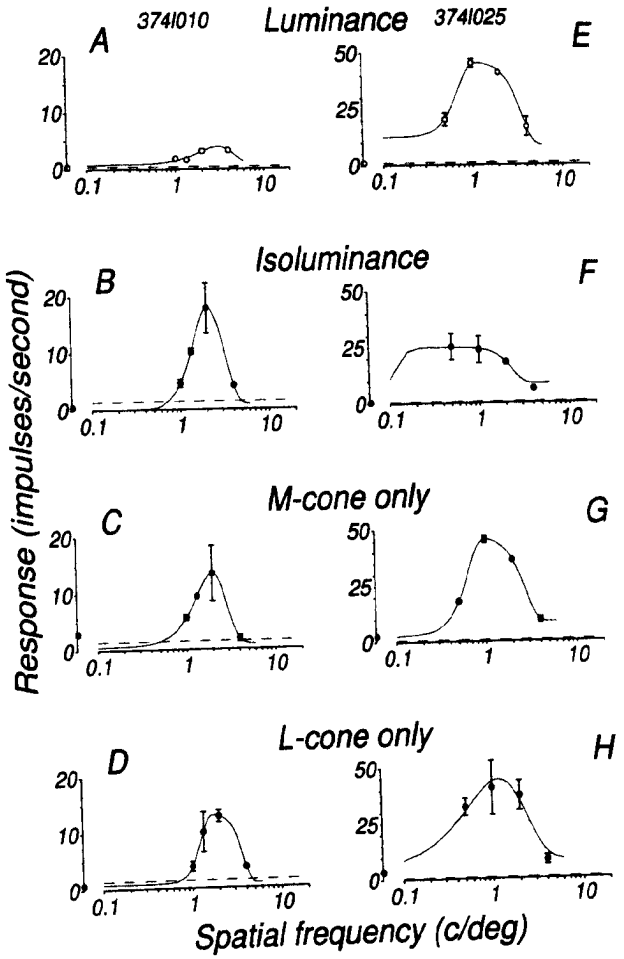

Fig. 10. Spatial tuning for two double-opponent cells, using luminance, red–green, M-cone isolating and L-cone isolating stimuli. The cell shown in the left column was located in a thick stripe, the cell to the right in an inter stripe. The horizontal dashed lines represent the cell's baseline response. The data plotted on the ordinate show the cell's response to full-field modulation.

Discussion

Our results show that there is a subpopulation of V2 neurons that show narrow tuning to stimulus color. Color has a strong facilitation effect on the responses of about 50% of all V2 neurons from all three CO compartments. There is no population response null at isoluminance, and the relative population responses are very similar in the three different CO compartments. Tuning characteristics for luminance and isoluminant stimulation were also quite similar for individual cells. In particular, no differences in the tuning to orientation or spatial frequency were apparent. Finally, we did find a minority of cells that showed indication of a double-opponent, receptive-field organization.

Color-specific mechanisms in the visual cortex

Our results reveal a significant population of V2 cells (35%) that exhibit responses specific to a limited range of colors. Comparable experiments in area V1 have only rarely shown this type of cell. Lennie et al. (1990) found only six out of 305 neurons (2%) that showed narrow color tuning. They might have missed some narrowly tuned cells, since their chromatic stimuli were rather broadly spaced in azimuth (45 deg). But even with a coarser spacing of chromatic stimuli of 45 deg, Levitt et al. (1994*a*) found significant deviations from the linear model in V2 cells. This makes it highly unlikely that Lennie et al. (1990) missed a large number of narrowly tuned V1 cells. The proportion of these cells in V1 is therefore probably much smaller than in V2.

In several studies the chromatic bandwidth of neurons at a later stage (V4) was investigated. Zeki (1980) reported that many cells in V4 were narrowly tuned for color. Even though some of these results can be criticized on methodological grounds (de Monasterio & Schein, 1982), the bandwidths reported by Zeki (1980) are close to what was later reported by Schein and Desimone (1990). In all of these experiments bandwidth was measured on a wavelength scale using monochromatic stimuli, so the results are not directly comparable with ours. However, when we converted our broadband stimuli to a wavelength scale using the dominant wavelength, the bandwidth of our narrowly tuned cells was at or below 20 nm (half-width at half-height), similar to the most narrowly tuned cells reported in V4 (Zeki, 1980; Schein & Desimone, 1990). The interpretation of these results is complicated by the fact that

narrow wavelength tuning might occur at even earlier stages in the cortex, or even in retinal ganglion cells, as was reported by de Monasterio and Schein (1982). Since the spectral bandwidth also critically depends on the peak wavelength (de Monasterio & Schein, 1990), a comparison across visual areas or even across different neurons is complicated, unless the comparison is made for cells preferring the same range of wavelengths.

The results by Derrington et al. (1984) and by Lennie et al. (1990) show that the responses of LGN and V1 neurons can be characterized as a linear summation of cone inputs. The resulting chromatic tuning in the color space of Krauskopf et al. (1982) is sinusoidal, independent of the cell's chromatic preference. In a strict sense, this model is not valid for the nonlinear cells in our sample, since their tuning curves clearly deviate from the model's predictions. However, the deviations show a systematic pattern, namely a narrowing of the chromatic tuning, independent of the cells' preferred azimuths. Although the exact chromatic bandwidth might not be well defined for these cells, it is certainly true that their tuning is significantly narrower than that of cells in the LGN or in V1. Furthermore, narrowly tuned cells in V2 often showed an inhibition of their responses to stimuli in the color direction opposite to their preferred direction, a characteristic also present in many cells of area V4 (Schein & Desimone, 1990), but not seen in the LGN or V1. These results suggest that narrowly tuned cells in V2 could provide the input to the color-selective cells in V4.

The fact that cells with narrow color tuning occur at a stage earlier than V4 in the visual system has important implications. It has been found that different CO compartments of V2 have different target areas (Shipp & Zeki, 1985; DeYoe & Van Essen, 1985). Whereas thin stripes and interstripe regions project predominantly to area V4, thick-stripe neurons project mostly to area MT, which is assumed to play a major role in the processing of visual motion. Our results imply that higher order color mechanisms are available to all processing streams in extrastriate cortex. This agrees with recent psychophysical results by Krauskopf et al. (1996), who presented evidence for higher order color mechanisms in the perception of coherently moving, colored, sine-wave plaids.

Segregated functional streams in area V2

Our data show that color facilitates the response of neuronal populations in all CO compartments in a similar way. No "isoluminant" stimulus can silence the populations of neurons in any CO compartment. Note that this does not mean that the response in all compartments is identical. Relatively small differences in the relative responses to luminance and isoluminant stimuli such as shown in Fig. 7B can be used to identify CO compartments in optical imaging, for example (Roe & Ts'o, 1995). However, the fact that responses are never abolished completely has a very strong implication for behavioral experiments which try to use color as a means of isolating neural pathways. There are good reasons to assume that isoluminant stimuli indeed mostly stimulate parvocellular LGN neurons (Shapley, 1990), even though some magnocellular neurons might show a frequency-doubled response to isoluminant stimuli (Schiller & Colby, 1983; Derrington et al., 1984). But given the large extent of mixing of parvocellular and magnocellular signals in V1 and V2 (Lund & Boothe, 1975; Blasdel et al., 1985; Fitzpatrick et al., 1985; Rockland, 1985; Lachica et al., 1992; Yoshioka et al., 1994; Nealey & Maunsell, 1994; Levitt et al., 1994*b*), it is not surprising to see little segregation of color processing at the level of V1 (Leventhal et al., 1995) and V2 (Levitt et al., 1994*a*; Gegenfurtner et al., 1996).

Our results show that isoluminant stimuli cannot be used to isolate different functional streams at the level of cortical area V2. This is consistent with results from quantitative psychophysical experiments, indicating that the primate color system is capable of supporting analysis of form and motion (for a review see Gegenfurtner & Hawken, 1996).

Double opponency

The question of the incidence of double-opponent cells, or even of their existence in macaque V1, has been highly controversial. Double-opponent cells have a receptive-field organization with a reverse chromatic antagonism in center and surround. For example, a cell could be tuned excitatory to red and inhibitory to green in the center and have the reverse arrangement in the surround. Cells like that had been reported initially in the goldfish (Daw, 1968), and later in the macaque monkey striate cortex (Dow, 1974; Michael, 1978*a–c*, 1979; Livingstone & Hubel, 1984). Other investigators have failed to find a sizeable proportion of these cells in macaque V1 (Ts'o & Gilbert, 1988; Lennie et al., 1990). The importance of double-opponent cells lies in the fact that they give a response to relative chromatic contrast, independent of the absolute color of the stimuli. It has been shown (Rubin & Richards, 1982; Valberg & Seim, 1983; Gershon et al., 1986) that this could form the basis for a response to color that is independent of the illumination color.

A double-opponent, receptive-field organization has some clear implications for simple cells. Their spatial-frequency tuning should be bandpass for isoluminant stimuli and for cone-isolating stimuli. Responses to red and green should be in opposite phase. The response should be abolished to black-and-white luminance stimuli. In V2, most cells (approximately 80%) are complex-like, that is, their response is independent of stimulus phase. Thus, it is not straightforward to extend this definition to complex cells. We found that many cells had a spatial bandpass tuning to isoluminant stimuli. But most of them also responded well to luminance stimuli and were bandpass for L-cone and M-cone isolating stimuli as well. Cells that respond mostly to luminance contrast, but have their null point shifted away from photometric isoluminance, could fulfill all these criteria. If they have a spatially antagonistic center-surround organization, they could respond to isoluminant and L- and M-cone isolating stimuli simply based on the residual luminance contrast contained in these stimuli (relative to that cell's isoluminant point). For a cell to be classified as double opponent, it needs to be shown that the response is mostly determined by chromatically opponent inputs. The response to luminance gratings should be abolished, or significantly lower than the response to isoluminant and L- and M-cone isolating gratings. Only very few of the cells in our sample fulfilled all of these requirements, and it is doubtful whether these few cells could form the basis for perceptual color constancy.

Conclusions

It has been firmly established in the past that area V2 contains a high proportion of cells responding selectively to color (Baizer et al., 1977; Zeki, 1978; Burkhalter & Van Essen, 1986; Hubel & Livingstone, 1987; Levitt et al., 1994*a*; Roe & Ts'o, 1995; Gegenfurtner et al., 1996). On the other hand, the functional properties of these color-selective cells have not been extensively studied. Animals with V2 lesions showed little deficit in chromatic contrast sensitivity (Merigan et al., 1993). In contrast, our results indicate that visual area V2 in primates could be an important stage in the

hierarchy of processing of color information. Whereas in V1 and at earlier stages color signals are mostly processed in a linear fashion, area V2 contains a significant subpopulation of neurons that show narrow tuning to specific color combinations and thus respond specifically to certain colors. Since surface color is an important intrinsic property of objects, these cells are ideally suited to discriminate objects from a textured background, a possibility that has recently gained importance in computer image segmentation (Healey, 1989).

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