Cone Inputs in Macaque Primary Visual Cortex

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Johnson, Elizabeth N., Michael J. Hawken, and Robert Shapley. Cone inputs in macaque primary visual cortex. J Neurophysiol 91: 2501–2514, 2004. First published January 28, 2004; 10.1152/jn.01043.2003. To understand the role of primary visual cortex (V1) in color vision, we measured directly the input from the 3 cone types in macaque V1 neurons. Cells were classified as luminance-prefering, color-luminance, or color-prefering from the ratio of the peak amplitudes of spatial frequency responses to red/green equiluminant and to black/white (luminance) grating patterns, respectively. In this study we used L-, M-, and S-cone–isolating gratings to measure spatial frequency response functions for each cone type separately. From peak responses to cone-isolating stimuli we estimated relative cone weights and whether cone inputs were the same or opposite sign. For most V1 cells the relative S-cone weight was &lt;0.1. All color-prefering cells were cone opponent and their L/M cone weight ratio was clustered around a value of −1, which is roughly equal and opposite L and M cone signals. Almost all cells (88%) classified as luminance cells were cone nonopponent, with a broad distribution of cone weights. Most cells (73%) classified as color-luminance cells were cone opponent. This result supports our conclusion that V1 color-luminance cells are double-opponent. Such neurons are more sensitive to color boundaries than to areas of color and thereby could play an important role in color perception. The color-luminance population had a broad distribution of L/M cone weight ratios, implying a broad distribution of preferred colors for the double-opponent cells.

INTRODUCTION

This communication is about color processing in the macaque primary visual cortex (striate cortex, or V1). The neural processing of color in the brain depends on how signals from the L-, M-, and S-cone classes are combined in different visual neurons. Previously, indirect methods have been used to estimate the cone inputs to macaque striate (Lennie et al. 1990) and extrastriate visual neurons (Gegenfurtner et al. 1996, 1997). Color-modulation stimuli that isolate signals from each of the cone types provide a direct way to study cone inputs to neurons (Conway 2001; Estevez and Spekreijse 1982; Reid and Shapley 1992, 2002). This paper reports new findings about color processing in V1 based on the direct approach.

We used cone-isolating stimuli to measure the cone inputs of 247 neurons in macaque V1. For simple cells, we determined whether cone inputs were additive (cone nonopponent) or subtractive (cone opponent), based on the temporal phases of L- and M-cone responses. For complex cells we gauged whether they were cone opponent or nonopponent from color-exchange experiments described in detail below. Relative cone weights were estimated from the response amplitudes for cone-isolating stimuli.

Previously, from the ratio of the amplitudes of responses to red/green equiluminant and to black/white luminance grating patterns, respectively (Johnson et al. 2001), we grouped V1 cells as luminance-prefering, color-luminance, or color-prefering. Our new results are that 73% of cells classified as color-luminance cells are cone opponent. Most cells (88%) classified as luminance-prefering cells are cone nonopponent. All color-prefering cells are cone opponent. These results support our previous conclusion that the color-luminance cells are double-opponent (both for color and space) based on the finding that they are spatially tuned for both achromatic and chromatic stimuli (Johnson et al. 2001).

Some of our results on V1 cone weights are unique, some confirm conclusions of other studies, and some differ greatly from previous conclusions. For the first time, we establish that the L/M cone-weight ratio in the color-luminance population has a broad distribution, implying that there is a broad distribution of preferred colors for such cells. Another new finding is that the distribution of the L/M cone-weight ratio for color-prefering cells is clustered around a value of −1, which is roughly equal and opposite L and M cone signals. Our results agree with those of Lennie et al. (1990), but disagree with those of Cottaris et al. (1998), that in most V1 cells the relative S-cone weight is &lt;0.1. There is a striking disagreement regarding the characteristics of luminance-prefering cells between our work and that of Lennie et al. (1990). We find a large population of luminance-prefering cells that are cone nonopponent, unlike Lennie et al. (1990), but in agreement with recent work from the same lab (Solomon et al. 2004). In the DISCUSSION we propose how color-prefering, color-luminance, and luminance-prefering cells could all contribute to the perception of color, in different ways (cf. Schluppeck and Engel 2002).

METHODS

Animal preparation

Acute experiments were performed on adult Old World primates (Macaca fascicularis) in strict compliance with the guidelines for humane care and use of laboratory animals published by National Institutes of Health and PHS. Animals were initially tranquilized with acepromazine [50 μg/kg, intramuscularly (im)]. After about 15 min, we anesthetized the animal with ketamine (10 mg/kg, im). Additional ketamine was given as needed during the initial phase of surgery. Local skin regions in the leg and neck were infused with long-lasting local anesthetic (lidocaine hydrochloride, 1%). A broad-spectrum antibiotic (bicillin, 50,000 IU/kg, im) and an antiinflammatory steroid (dexamethasone, 0.5 mg/kg, im) were given during the initial surgery and every day during the recording period. A venous cannula was present address and address for reprint requests and other correspondence: E. Johnson, Dept. of Neurobiology, Duke University Medical Center, Box 3209, Durham, NC 27710 (E-mail: johnson@neuro.duke.edu).
placed in a superficial vein in each leg to infuse drugs intravenously during the experiment. A tracheotomy was also performed. Subsequent surgery and preparation were performed with the animal under opioid intravenous (iv) anesthesia (sufentanil citrate, 6–30 µg·kg\(^{-1}\)·h\(^{-1}\) in an infusion of 5% dextrose dissolved in heparinized saline), with the animal artificially respired. Anesthesia level was determined by continuous monitoring of the electrocardiogram, the electroencephalogram, the expired \(\text{CO}_2\), and noninvasive blood pressure. The animal was kept in a continuous state of light anesthesia as judged by intermediate-amplitude EEG waveforms that lacked either alpha, spindle waves or high-frequency low-amplitude desynchronized waveforms.

The animal was placed in a stereotaxic frame designed especially for visual experiments. A small craniotomy (≤5 mm) was made to cut in one hemisphere posterior to the lunate sulcus (10 mm anterior to the occipital ridge; 10–20 mm lateral to the midline). The dura was cut to provide access for the recording electrode. A cylindrical chamber was constructed from bone wax around the craniotomy. The microdrive with a recording electrode was then placed at the cortical surface for a penetration normal to the cortical surface. The chamber around the craniotomy was then filled with warm agarose gel (2–4%) to help stabilize the recording. All of the surgical procedures were conducted before paralysis so that we could observe any signs of discomfort.

For recording, suftentanil anesthesia was continued, and the animal was then paralyzed with either pancuronium bromide (0.1 mg·kg\(^{-1}\)) or vecuronium bromide (0.1 mg·kg\(^{-1}\)·h\(^{-1}\), iv) in an infusion of 5% dextrose dissolved in heparinized saline. The artificial respirator’s rate was adjusted to maintain the expired level of \(\text{CO}_2\) at close to 5%. Body temperature was maintained at 37.5°C. Experiments typically lasted 4–5 days and were terminated by iv injection of a lethal dose of sodium pentobarbital (60 mg/kg).

**Optics**

Ophthalmic atropine sulfate (1%) was initially administered to the eyes to dilate the pupils. A topical antibiotic solution (gentamicin sulfate, 3%) was then applied to the eyes. For the duration of the experiment, the eyes were protected by clear, gas-permeable contact lenses. The foveae were mapped onto a tangential screen using a reversing ophthalmoscope (Eldridge 1979). The visual receptive fields of isolated single neurons were then mapped onto the tangent screen, keeping reference to the foveae. Each eye was corrected optically with external lenses placed in custom-designed lens holders. Adjustments to the ophthalmic refraction were made during the recording session by stimulating a responsive cell with a sinusoidal grating composed of intermediate-amplitude EEG waveforms that lacked either alpha, spindle waves or high-frequency low-amplitude desynchronized waveforms.

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**Extracellular recording**

We recorded single units with a glass-coated tungsten microelec
trode (5–10 µm tip size). The electrode advanced through the cortex by a stepping motor (1-µm step size) mounted to a microdrive (Narashige, Kyoto, Japan). The electrophysiological signal was ampli
dified using a Dagan (Minneapolis, MN) EX4–400 differential ampli
er and band-pass filtered (0.1–10 kHz). For some experiments, impulses triggered by each action potential were detected with a Bak Electronics (Germantown, MD) DDS-4 dual window discriminator and were time-stamped with 1-ms precision and stored by a CED-1401+ (Cambridge, UK) data acquisition system. In more recent experiments, spikes were discriminated and time-stamped with 1-ms accuracy by means of custom-designed software running on a Silicon Graphics O2 computer. Strict criteria for single-unit recording were used, including fixed shape of the action potential and absence of spikes during the absolute refractory period.

**Visual stimulation**

The visual stimuli were generated on a Silicon Graphics O2 R5000 computer. The software for stimulus presentation was written by Dr. D. L. Ringach. Stimuli were displayed on a Sony Multiscan 17se II color monitor measuring 31.4 cm wide and 23.5 cm high, with a resolution of 800 × 600 pixels. The refresh rate of the monitor was 100 Hz and its mean luminance was 53 cd/m\(^2\). The International Commission on Illumination ([CIE (Commission Internationale de l’Eclairage)]) chromaticity coordinates of the “white” background were \(x = 0.288, y = 0.294\). All color modulation was around this white point. A few experiments were performed with a Sony GDM F520 monitor measuring 40.5 cm wide and 30.5 cm high, with a resolution of 1,024 × 768 pixels. The refresh rate was 100 Hz and the mean luminance was 75 cd/m\(^2\). The CIE chromaticity coordinates of the “white” background for this monitor were \(x = 0.292, y = 0.320\). The stimuli were viewed at a distance of 115 cm.

**Monitor calibration**

The monitor calibrations for luminance were based on the human spectral sensitivity function \(V_\lambda\), and were determined photometri
cally. We used the 10° \(V_\lambda\) function because (as stated below) all neurons studied had receptive fields far enough from the fovea that the macular pigment had a negligible effect on spectral sensitivity. Cone excitations were calculated as the dot product of the cone absorption fundamentals (Stockman and Sharpe 2000) and the spectral energy distribution of the cathode ray tube (CRT) gun primaries at 2-nm resolution measured with a Photo Research spectroradiometer (model number 703A). Calculating cone-isolating stimuli using the Stockman and Sharpe (2000) cone fundamentals, rather than other commonly used cone fundamentals, yields the smallest amounts of artifacts (Cottaris 2003).

**Searching for cells**

The electrode was advanced through the cortex in 2–5 µm steps while stimulating the eyes by back-projecting light onto a translucent tangent screen, 115 cm from the animal’s eyes. The projected light consisted of bright bars on a dark background or dark bars on a bright background. Colored bars were produced by interposing filters (red, green, blue, and yellow). It was possible to quickly change the orientation, drift direction, length, width, and color of the spots and bars. Multiunit activity ("hash") could be heard over the audio ampli
er, and it was possible to determine, by ear, the rough receptive field parameters for the neurons in the vicinity of the electrode. Once a single unit was isolated, the position of the receptive field relative to each fovea was determined. A mirror was placed in front of the animal to center the receptive field approximately on the CRT screen. The center of the receptive field on the CRT was determined very precisely with a computer-controlled mapping program developed in our labor
atory by Dr. D. L. Ringach.

**Characterization of receptive fields**

Each cell was stimulated monocularly through the dominant eye with the nondominant eye occluded. Receptive fields were located between 1° and 6° eccentric from the fovea. Therefore the effect of macular pigment on spectral sensitivity of the photoreceptors was negligible (Cottaris 2003; Snodderly et al. 1984a,b). For each cell we characterized the receptive field’s optimal parameters for orientation, temporal and spatial frequency, and area, and measured a contrast-
response function, using conventional drifting sinusoidal luminance gratings. The optimized values from the standard characterization...
were used throughout the specific experiments in this paper. For example, drifting gratings were windowed in a circular aperture of optimum area.

Each cell was categorized as simple or complex based on its response to sinusoidal drifting grating input. Linear systems respond to a sinusoidal input with a sinusoidal output without changing the frequency. Using sinusoidal gratings, we temporally bin the action potentials and average the responses relative to the temporal period of the grating to form poststimulus time histograms. These histograms were Fourier analyzed to calculate the average firing rate (DC), as well as the amplitude and phase of the fundamental stimulus frequency (F1). Cells were classified as simple if the ratio of the first harmonic response to the DC response was >1 (Skottun et al. 1991). Complex cells had a ratio ≤ 1.

The stimulus strength for all luminance sinusoidal gratings was measured in units of Rayleigh contrast

\[
\text{Contrast} = (L_{\text{max}} - L_{\text{min}})/(2L_{\text{mean}})
\]

For each cone we calculated the cone contrast from the effective max-, min-, and mean photon catch for that cone type, and formed the Rayleigh contrast ratio for that cone (cf. Shapley and Hawken 1999). By convention, we specify the contrast of red/green equiluminant stimuli as the root mean square (rms) of the L- and M-cone contrasts.

**Color-sensitivity index**

Many V1 cells respond to both black-and-white and pure color modulation. To describe the range of preferences to color and luminance, we devised a chromatic sensitivity index based on the ratio of each neuron’s peak response to luminance and equiluminant gratings, termed the **color-sensitivity index** (Johnson et al. 2001)

\[
\text{Color sensitivity index} = \frac{\text{response}_{\text{max(luminance)}}}{\text{response}_{\text{max(equiluminance)}}}
\]

Some cells showed little or no response to equiluminance, but responded well to luminance, and thus had low sensitivity indices (index < 0.5; luminance-prefering group). Other cells gave comparable responses to equiluminant and luminance gratings, having sensitivity indices of about 1 (0.5 ≤ index ≤ 2). We classified these neurons as **color-luminance** cells. The last group of cells gave larger responses to equiluminant gratings and little or no response to luminance gratings, yielding sensitivity indices > 2 (color-prefering group).

Cells that did not give a response of ≥10 spikes/s above the mean spontaneous rate to either luminance or red/green equiluminant gratings (or to both in the case of color-luminance cells) were excluded from analysis. Three cells (out of a population of more than 300 V1 cells) produced a maximal response to S-cone–isolating stimuli of ≥10 spikes/s, but did not respond to luminance stimuli or to red/green equiluminant stimuli. Because they were so rare, these 3 “pure blue-yellow” cells were not included in the population analyzed in this paper.

**Cone-isolating stimuli**

Spatial frequency tuning responses were measured for the 3 cone-isolating directions (L-, M-, and S-cone), as described previously (Johnson et al. 2001). The stimuli were drifting sinusoidal gratings. The grating patch on average consisted of 4 spatial cycles, and was drifted at a rate of 4–8 Hz. Over the 4-s period of measurement there were therefore 16 to 32 stimulus cycles over which the response was averaged. For a subset of neurons (n = 89), the entire spatial frequency experiment was repeated 3 times, yielding 48 to 96 stimulus cycles over which the response was averaged. The cone contrasts for the cone-isolating stimuli were 13, 15, and 24% (for L-, M-, and S-cone–isolating stimuli, respectively). All stimuli were of the same mean luminance as the background. As stated above, all stimuli were presented on a white background with a mean luminance of 53 cd/m² and chromaticity coordinates of x = 0.288, y = 0.294, or in a few recent experiments on a different monitor with a white background of mean luminance 75 cd/m² and chromaticity coordinates of x = 0.292, y = 0.320.

**Determining relative cone weights**

For ease of comparison, the maximum amplitude response for each cone-isolating response was normalized by the contrast of the cone-isolating stimuli. This was done to correct for the minor differences between the cone contrasts of the L-, M-, and S-cone–isolating stimuli. Thus all weighting functions are normalized in units of (spikes/s)/(unit contrast)

\[
\begin{align*}
\text{w}_L &= \frac{\max(I_{\text{cone-isolating response}})}{R_0}/13 \\
\text{w}_M &= \frac{\max(M_{\text{cone-isolating response}})}{R_0}/15 \\
\text{w}_S &= \frac{\max(S_{\text{cone-isolating response}})}{R_0}/24
\end{align*}
\]

In Eqs. 1–3, R_0 is the mean spontaneous activity of the neuron; R_0 = 0 for simple cells. \(w_L, w_M\), and \(w_S\) are the absolute weights with which the cell receives cone input. To make direct comparisons across the neuronal population, it is necessary to normalize for any variations in overall sensitivity by determining the **relative weight** (strength) of each cone input (\(W_L, W_M, W_S\)). This is obtained by dividing each weight calculated in Eqs. 1–3 by the sum of the weights for all 3 classes of cones

\[
\begin{align*}
W_L &= w_L/(w_L + w_M + w_S) \\
W_M &= w_M/(w_L + w_M + w_S) \\
W_S &= w_S/(w_L + w_M + w_S)
\end{align*}
\]

**Statistical analysis**

To make quantitative comparisons, Student’s t-tests were performed to examine whether the relative cone weights differed from each other (L-cone vs. M-cone; L-cone vs. S-cone; and M-cone vs. S-cone), as well as for different groups of cells (simple vs. complex; color-luminance vs. color-prefering; color-luminance vs. luminance-prefering; etc.). The significance level in all tests was \(P < 0.05\). To determine whether each cone weight distribution was flat or concentrated around the mean, the distributions were analyzed for peakedness/flatness by measuring the kurtosis. The kurtosis of a Gaussian distribution is zero. Distributions that are sub-Gaussian (flat) will have a negative kurtosis, and those that are super-Gaussian (spiky) will have a positive kurtosis.

**Data analysis**

Cellular responses were analyzed on-line and off-line using LAB (Mathworks, Natick, MA), S-plus (Insightful, Seattle, WA), and custom software written specifically for this purpose on an Intel personal computer. All fitting procedures discussed here were done with the MATLAB optimization toolbox using the CONSTR and FMINCON nonlinear least-squares functions.

**Histology**

At the end of the recording session, 3 to 5 electrolytic marking lesions (2–3 μA for 3 s, electrode tip negative) were made along the length of each penetration to reconstruct the recording sites with respect to the laminar boundaries of the cortex [as described in Hawken et al. (1988)]. Although the sections were stained for the mitochondrial enzyme cytochrome oxidase (CO), the procedure we
used did not give enough definition of the CO pattern in the supragranular layers after 5 days of acute recording to enable us to quantify unambiguously whether cells were located inside or outside of CO patches.

**RESULTS**

We measured L-, M-, and S-cone–isolating spatial frequency response functions for 247 neurons, including neurons from all layers of primary visual cortex. The spatial frequency tuning properties of 167 of these cells were described previously (Johnson et al. 2001). We classified 127 (51%) as simple cells and 120 (49%) as complex cells. In addition, we classified 139 as luminance-prefering (56% of all cells studied; 70 simple cells, 69 complex cells), 84 as color-luminance (34% of all cells studied; 35 simple cells, 49 complex cells), and 24 as color-prefering (10% of all cells studied; 22 simple cells, 2 complex cells), using the color-sensitivity index (see Methods and Fig. 2 in Johnson et al. 2001).

**Determining spatial symmetry**

We analyzed receptive field symmetry for a subset of the V1 neurons we studied. Symmetry of the receptive field is important because only for even-symmetric cells is it meaningful to assign a net sign for a cone input—in the even-symmetric case, one is justified in calling the sign of the cone input to the even-symmetric field’s central region its net sign [as in lateral geniculate nucleus (LGN) cells; Derrington et al. 1984; Reid and Shapley 2002]. If a neuron’s spatial profile is odd-symmetric or asymmetric, there is no meaningful assignment of signature to a cone’s input. This is because the cone input is both on-excitatory and off-excitatory in different spatial regions of an odd-symmetric or asymmetric receptive field. In such asymmetric or odd-symmetric cases, the only meaningful signature is the relative signature of a pair of cone inputs: are they opponent (opposite sign) or nonopponent (same sign)?

If the spatial profile is an even function, and we approximate the spatiotemporal receptive field as a linear, separable function of space and time, then we can predict the phase versus spatial frequency curve (cf. Dawis 1984; Johnson 2002). The phase will be proportional to spatial frequency as follows

$$\phi(k) = -kx_0 + \phi_0(\omega)$$

where k is spatial frequency, $x_0$ is the offset of the receptive field middle from the center of the coordinate system of the stimulus screen, and $\phi_0(\omega)$ is the temporal phase at the temporal modulation frequency $\omega$ (for a drifting grating $\omega = 2\pi \times$ the temporal modulation frequency in bars/s). Equation 7 means that the phase as a function of spatial frequency is a straight line with slope $-x_0$ that intersects the phase axis at $\phi_0(\omega)$ for $k = 0$.

For an odd-symmetric spatiotemporal sensitivity $h(x, t)$, one can derive that

$$\phi(k) = -kx_0 + \text{sgn}(k) \times 90^\circ + \phi_0(\omega)$$

so an indication of odd symmetry is an offset of $\pi$ in the zero spatial frequency intercepts of the straight-line phase versus spatial frequency functions in the optimal and opposite-to-optimal (optimal $+ 180^\circ$ in orientation) directions. For an asymmetric receptive field (which can be expressed as a weighted summation of odd- and even-symmetric receptive fields) the offset between positive and negative intercepts of the phase versus spatial frequency lines will lie between 0 and $90^\circ$, or between $90$ and $180^\circ$.

We applied such spatial phase analysis to a subset of our simple cell data ($n = 26$ color-luminance cells, $n = 22$ luminance-prefering cells, $n = 6$ color-prefering cells). For this subset of simple cells, the first harmonic amplitude and phase responses were measured with high-contrast luminance gratings for a range of spatial frequencies drifting in both directions at the preferred orientation. Because an accurate spatial phase analysis requires significant responses to drift in both the optimal and opposite-to-optimal directions, cells that were strongly direction-selective were not analyzed for spatial phase. Direction-selective neurons were included in all other analyses.

For the spatial phase analysis, we assigned positive spatial frequencies to the optimal direction, the one that elicited the largest response. By convention, negative spatial frequencies correspond to data collected with stimuli drifting in the opposite-to-optimal direction. The phase curves for each direction of drift were determined by fitting the measured phases with a linear regression from zero spatial frequency. The slope of the positive spatial frequency phase data and the slope of the negative spatial frequency data depend on the spatial offset from the origin of the spatial profiles. In our case, the origin is the upper left of the display and the center of the receptive field is usually near the center of the screen. Consequently, the number of cycles from the origin to the receptive field determines the slope of the phase versus spatial frequency line. Figure 1 shows data from 2 color-luminance cells, one even-symmetric (Fig. 1A) and one asymmetric (Fig. 1B). When we analyzed the color-luminance and luminance cells as in Fig. 1, they were often asymmetric or odd-symmetric. We concluded from this analysis that only relative cone signature from cones, not net cone sign, was significant for color-luminance cells and for luminance-prefering cells in V1. This spatial frequency analysis is consistent with the more extensive analysis of receptive field spatial symmetry by Ringach (2002), which showed that most V1 cells were odd-symmetric or asymmetric.

The color-prefering cells we examined were even-symmetric, approximately, so one could have plotted their signed, net cone weights. However, for this paper we have not done that but rather have used the relative cone weight exclusively, to facilitate comparison between cells in the 3 different groups. Therefore in subsequent figures, we graph the cone weight data on a triangle that depicts magnitude of the cone weight and relative cone opponency (Figs. 3, 4, 7, and 10) and not on a diamond-shaped plot that would assign a net sign to each cone weight (as for instance in Lennie et al. 1990).

**Objective determination of chromatic opponency**

If a neuron receives antagonistic input from both L- and M-cones, the color responsiveness assessed by the method of color-exchange (as described in Johnson et al. 2001; Shapley and Hawken 2002) is very different from the color responsiveness of a neuron that adds its cone inputs. In the color-exchange experiments, the red CRT gun contrast was held constant at 1.0 (100%), whereas the green gun contrast varied from 0 to $-1.0$, with the green and red modulation $180^\circ$ out of phase. This produces
sinusoidal heterochromatic red/green gratings. The sinusoidal gratings were drifting at the optimal orientation, temporal frequency, and spatial frequency for the cell determined from the standard receptive field characterization. The response of a neuron was then measured at each green gun contrast over a range from below to above equiluminance of the green and red stripes of the grating (as illustrated in Fig. 2). If cells receive additive same-sign input from both L- and M-cones, they will show a response minimum near the red/green equiluminant modulation value (Fig. 2C). This is typical of LGN magnocellular neurons (Shapley and Hawken 1999, 2002). If cells receive subtractive (antagonistic) input from L- and M-cones, they will show no minimum, or null (Fig. 2A). This is typical of LGN parvocellular (pLGN) neurons (Shapley and Hawken 1999, 2002). Thus red/green color-exchange provides a method for determining whether the L- and M-cone inputs are chromatically opponent. If the amplitude as a function of the gain of the green CRT gun was a function with a clear dip, as in Fig. 2C, this is a sign of a nonopponent neuron. If on the other hand, the amplitude function is a flat or sloping line, as in Fig. 2A, this is evidence for cone opponency. We used a $\chi^2$ test to classify complex cells as opponent or nonopponent, based on whether their color-exchange curves were well fit by a straight line, as in Fig. 2A. If the value of $\chi^2$ was less than a criterion value ($P \approx 0.05$), we classified the cells as opponent. If it exceeded the criterion value ($P < 0.05$), we classified the cell as nonopponent. All the cells we studied fell into clear nonoverlapping groups with this statistical classification procedure.

In addition, it is possible to determine color opponency for all simple cells by analyzing the phase difference at the peaks of the L- and M-cone–isolating spatial frequency responses. Complete chromatic opponency would mean that the cone signals were 180° apart. Nonopponency would mean that the phase difference would be 0°. Simple cells were classified as opponent if the color-exchange experiment had no null and the phase difference was $>90°$ (see Fig. 7 in Johnson et al. 2001).

There was good agreement between the phase test and the color-exchange test of cone opponency when they were compared in simple cells. Out of 127 simple cells, there was agreement between the phase and color-exchange tests in 121
Relative cone weights for the entire V1 population

The relative cone weights were calculated for all cells in our sample (n = 247). The relative weights sum to 1.0, so they can be represented on a plot of \( W_L \) against \( W_M \). In this type of plot, the S-cone weight \( W_S \) is proportional to the distance between each point and the edges of the triangle. The data from all neurons in the sample suggest that the majority of V1 cells receive primarily L- and M-cone input, as can be observed in Fig. 3.

Because most cells receive little or no S-cone input relative to the L- and M-cone input, neurons tend to lie near the triangle’s edges. Cells that receive input from only one cone are shown at the vertices of the triangle. As discussed above, because most V1 cells have asymmetric or odd-symmetric receptive fields, it is only appropriate to illustrate cone weights in a triangle (as in Fig. 3), where the cells are divided into 2 main classes, color-opponent and nonopponent. To separate the color-opponent and nonopponent neurons in our plots, the relative L-cone weight was multiplied by \(-1\) for all cells that are opponent by the color-exchange and/or phase difference analysis described above. When \( W_L = 0.5 \) and \( W_M = 0.5 \), the relative strengths of the L- and M-cone inputs are equal and nonopponent. When \( W_L = -0.5 \) and \( W_M = 0.5 \), the relative strengths of the L- and M-cone inputs are equal and opposite (opponent). The cone weights of red/green pLGN neurons cluster around equal and opposite values for L- and M-cones (Derrington et al. 1984; Reid and Shapley 2002). Although Fig. 3 shows that the relative L- and M-cone weights of V1 cells vary continuously, there is some evidence of clustering at the \( W_L/W_M = 0.5 \) intersection. We will discuss this further in the sections about color-preferring and color-luminance cells. The mean cone weights for all simple and complex cells are shown in Table 1.

It is necessary to determine whether the large variation of relative L- and M-cone weights found for both the color-opponent group and the nonopponent group is significant, or whether the variation could be accounted for simply by noise in the estimates of the peak response amplitudes. To do this, we calculated the relative SD of each cone weight from repeat measurements of the spatial frequency responses to each cone-isolating stimulus. This calculation was done on a subset of neurons for which we had enough stimulus repetitions (n = 89). The mean of the results for each cone type is shown in Table 1. It is clear from the table that the variance in cone weight estimates is considerably larger than the noise in the measurement of the neural responses. Therefore “noise” in the measurements does not account for the observed broad distribution of relative L- and M-cone weights.

Color-luminance population

The relative cone weights for color-luminance cells are plotted in Fig. 4. Of the 84 neurons that we classified as color-luminance cells from the color-sensitivity index, 13/49 complex cells and 10/35 simple cells (27% of all color-luminance cells) were not chromatically opponent by color-exchange (complex cells) or phase-difference analysis and color-exchange (simple cells). These neurons are examples of what Gegenfurtner and colleagues have called “miscalibrated photometers” (Gegenfurtner et al. 1994). The relative weights of
The color-luminance cells that are nonopponent are plotted on the right (the nonopponent) side in Fig. 4. All the remaining color-luminance cells, the large majority of this group (73%), were cone opponent and they are plotted in the left side of the cone weight triangle in Fig. 4.

The distributions of the relative cone weights for opponent simple and complex color-luminance cells are shown in Fig. 5. A surprising finding from our cone weight results is that there is a salient difference between the distribution of L- and M-cone weights in the color-luminance simple cells and the color-luminance complex cells. The L- and M-cone weight distributions for the simple cells are broad and flat (kurtosis = -0.47 L-cone, -0.84 M-cone) (Fig. 5A). However, the distributions of L- and M-cone weights for the complex cells are clustered around the means (~0.5) (kurtosis = 0.13 L-cone, -0.01 M-cone) (Fig. 5B). The histogram distributions of the \( W_L/W_M \) ratios are shown in Fig. 6 (Fig. 6A shows the distribution of the ratio for simple cells, kurtosis = -0.35; Fig. 6B shows the distribution of the ratio for complex cells, kurtosis = 2.34; note that the median and kurtosis calculations were done after excluding cells that showed only one cone input). When \( W_L/W_M = 1 \), the L- and M-cone inputs are equal. Values < 1 indicate stronger input from M-cones, and values > 1 indicate stronger input from L-cones. The diversity of cone inputs to the simple color-luminance cells suggests that functionally these neurons will have different color preferences. The geometric mean and median of the \( W_L/W_M \) ratio for the color-luminance neurons are: mean ± SD = 0.74 ± 3.47, median = 0.93. The mean and median are near unity, indicating approximate equality of the average input from L- and M-cones.

**Luminance-preferring population**

The relative cone weight data for the luminance-preferring cells are shown in Fig. 7. Of the 139 neurons that were classified as luminance-prefering, a small fraction (12%) showed signs of chromatic opponency and are plotted in the cone-opponent half of the cone-weight triangle. These cone-opponent, luminance-prefering neurons often receive dominant input from one cone type or they have chromatic sensitivity indices near 0.5 (i.e., they lie near the boundary of the luminance-prefering population and the color-luminance group). However, the large majority of luminance-prefering neurons were cone nonopponent, as can be seen from the location of the bulk of the points in Fig. 7 in the nonopponent half of the cone-weight triangle.

The distributions of the relative cone weights for simple and complex luminance-prefering cells are shown in Fig. 8. Cells that were classified as nonopponent color-luminance cells (miscalibrated photometers, as described above) were added to the luminance-prefering population. Luminance-prefering cells that showed chromatic opponency were kept in the luminance-prefering group. Both the simple and complex luminance-prefering neurons have quite flat L- and M-cone distributions (Fig. 8) (kurtosis (simple cells) = -1.13 L-cone, -1.17 M-cone; kurtosis (complex cells) = -0.89 L-cone, -0.74 M-cone). As indicated in the cone-weight triangle, there is little or no S-cone input to the majority of luminance cells when the responses are scaled by the effective cone contrast to obtain the weights.

Figure 9 graphs the \( W_L/W_M \) ratios for the luminance-prefering group [Fig. 9a shows the distribution of the ratio for simple cells (kurtosis = -0.67); Fig. 9B shows the distribution of the ratio for complex cells (kurtosis = 1.06)]. The geometric mean and median of the \( W_L/W_M \) ratio for the luminance-prefering cells are: mean ± SD = 0.93 ± 3.80, median = 0.98.

**Color-prefering population**

The cone-weight plot for color-prefering neurons is given in Fig. 10. All cells are in the opponent area with some indication

<table>
<thead>
<tr>
<th>Cell Type</th>
<th>Mean ( W_L )</th>
<th>( W_L ) Variance</th>
<th>Mean ( W_M )</th>
<th>( W_M ) Variance</th>
<th>Mean ( W_S )</th>
<th>( W_S ) Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simple</td>
<td>0.46 ± 0.25</td>
<td>0.06 ± 0.03</td>
<td>0.51 ± 0.26</td>
<td>0.13 ± 0.07</td>
<td>0.03 ± 0.06</td>
<td>0.01 ± 0.02</td>
</tr>
<tr>
<td>Complex</td>
<td>0.46 ± 0.25</td>
<td>0.05 ± 0.04</td>
<td>0.49 ± 0.23</td>
<td>0.06 ± 0.04</td>
<td>0.06 ± 0.07</td>
<td>0.01 ± 0.01</td>
</tr>
</tbody>
</table>

**TABLE 1. Mean cone weights for all cells in the sample (n = 127 simple, n = 120 complex) and mean cone weight variances (± SD) for a subset of cells in the sample (n = 44 simple, n = 45 complex)**

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of clustering. It is notable that almost all the color-preferring cells were classified as simple (22/24, 92%), suggesting that this is a unique class of V1 cells. The distributions of the relative cone weights for the simple color-preferring cells are shown in Fig. 11. From the histograms, it is clear that the distributions of L- and M-cone weights are clustered around the means for the color-preferring population (the kurtosis for these distributions = 0.12 L-cone, −0.53 M-cone). The clustering of cone weight is illustrated more directly in Fig. 12, which graphs the $W_L/W_M$ ratios for the color-preferring group (Fig. 12 shows the distribution of the ratio for simple cells; kurtosis = 0.52). The clustered distribution of L- and M-cone weights for color-preferring neurons is similar to the distribu-

![Graph showing relative cone weights for simple and complex color-luminance cells.](http://jn.physiology.org/)

**FIG. 4.** Scatter diagram showing the relative weights of cone input for simple and complex color-luminance cells in the population ($n = 84$). Weight of the L-cone input is multiplied by −1 for cells that are opponent by phase analysis (simple cells) or by color-exchange (complex cells) to differentiate opponent and nonopponent neurons.

![Histograms for simple and complex color-luminance cells.](http://jn.physiology.org/)

**FIG. 5.** Histograms of the relative (unsigned) L-, M-, and S-cone weights for the color-opponent color-luminance neurons ($n = 77$). Luminance-prefering neurons that were found to be opponent by color-exchange or phase analysis were added to this group. A: histograms for the simple color-luminance cells ($n = 30$). B: histograms for the complex color-luminance cells ($n = 47$). Bin width for the L- and M-cone weights is 0.1, but 0.05 for the S-cone weights.

![Distribution of the ratio of the relative (unsigned) L- and M-cone weights.](http://jn.physiology.org/)

**FIG. 6.** Distribution of the ratio of the relative (unsigned) L- and M-cone weights for simple and complex color-opponent color-luminance cells. A: histogram of simple color-luminance cells ($n = 27$, median L:M ratio = 0.55). B: histogram of complex color-luminance cells ($n = 44$, median L:M ratio = 0.93). Histograms show the ratio $W_L/W_M$. Distributions do not include cells that had $W_L$ or $W_M > 1$. 

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tion of cone weights described for neurons in the parvocellular layers of the LGN (Derrington et al. 1984; Reid and Shapley 2002). The geometric mean and median of the $W_L/W_M$ ratio for color-prefering neurons are: mean $\pm$ SD = 0.88 $\pm$ 1.85, median = 0.97.

Laminar reconstruction

Of 247 cells, 217 (88%) could be assigned to a laminar position after histological reconstruction of the electrode penetrations. Forty-one cells (17%) were in layers 2/3, 3 cells (1%) were in 4A, 52 cells (21%) were in 4B, 35 cells (14%) were in 4C, 14 cells (6%) were in 4D, 33 cells (13%) were in layer 5, and 39 cells (16%) were in layer 6. Color-luminance cells

**FIG. 7.** Scatter diagram showing the relative weights of each class of cone input for all simple and complex luminance-prefering cells in the population ($n = 139$). Weight of the L-cone input is multiplied by $-1$ for cells that are opponent by phase analysis (simple cells) or by color-exchange (complex cells) to differentiate opponent and nonopponent neurons. Note that few cells show opponency by phase and/or by color-exchange. These neurons are shown on the opponent side ($L^-$).

**FIG. 8.** Histograms of the relative L-, M-, and S-cone weights for the nonopponent luminance-prefering neurons ($n = 146$). Color-luminance neurons that were found to be nonopponent by color-exchange or phase analysis were added to this group. A: histograms for the simple luminance cells ($n = 75$). B: histograms for the complex luminance cells ($n = 71$). Bin width for the L- and M-cone weights is 0.1, but 0.05 for the S-cone weights.

**FIG. 9.** Distribution of the ratio of the relative (unsigned) L- and M-cone weights for simple and complex nonopponent luminance-prefering cells. A: histogram of simple luminance-prefering cells ($n = 72$, median $L:M$ ratio = 1). B: histogram of complex luminance-prefering cells ($n = 68$, median $L:M$ ratio = 1.15). Histograms show the ratio $W_L/W_M$. Distributions do not include cells that had $W_L$ or $W_M$ $>1$.2509

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were found in all layers except 4A, but they were concentrated especially in superficial layers 2/3 (21/84; 25% of all color-luminance cells). The majority of all cells encountered in layers 2/3 were color-luminance cells (21/44; 51%). Layers 2/3 are important in the output of visual information from V1; thus it is likely that color-luminance cells project to many visual cortical areas. Many cells that responded preferentially to color were found in layers 2/3 (5/24; 21%), 5 (5/24; 21%), and 6 (4/24; 17%). Cells that responded preferentially to luminance were most often located in layers 4B (34/139; 24%), 4α (29/139; 21%), and 6 (26/139; 19%), and the majority of cells in layer 4α and layer 6 were dominated by luminance. The laminar position for 167/247 of these neurons was illustrated previously (see Figs. 2 and 3 in Johnson et al. 2001).

Cells with significant S-cone input

Ten neurons had an S-cone weight ≈ 0.2. Seven neurons were color-luminance cells and 3 were luminance-prefering. The majority (8/10) were complex cells. It was possible to assign a cortical depth and layer by histological reconstruction of the electrode track (see Methods and Hawken et al. 1988) for 8 of these neurons. Five cells were in layer 5, 2 were in layer 6, and one was in layers 2/3. Six out of 10 neurons were spatial frequency selective to S-cone-isolating stimuli, with a mean spatial frequency preference of 2.12 ± 0.79 cycles/deg. The other 4 gave low-pass spatial frequency-tuning responses to S-cone-isolating stimuli, and 3 of these 4 also gave low-pass responses to red/green equiluminant color.

Discussion

Using spatial frequency-tuning responses to cone-isolating stimuli, together with a combination of spatial receptive field measurements and color-exchange measurements, we were able to determine how V1 cortical neurons combine signals from L-, M-, and S-cones. This enabled us to make direct empirical measurements of the relative strength of the cone inputs instead of deducing them from indirect measurements. If the cortex were entirely linear in the way it combined cone inputs, the direct approach and the indirect approach would be equivalent. However, there is abundant evidence of nonlinear signal summation in V1 neurons, so the results with the direct approach more straightforwardly answer the question of the nature of cone inputs.

As in our previous work on color in V1, we categorized neurons into color processing groups by calculating a color-sensitivity index (Johnson et al. 2001). Although V1 neurons are distributed continuously in the color-sensitivity index, the fact that there were only a small number of cells categorized in the luminance-prefering group that exhibit cone opponency in the color-exchange experiments suggests that assigning the boundary between the luminance-prefering group and the color-luminance group at a color-sensitivity index of 0.5, as we did, was a good choice. Furthermore, the uniformity of properties of the color-prefering cells indicates that the upper boundary we chose to divide the color-luminance and color-prefering cells, with an index = 2, also is a good choice. It is also important to point out that cells in the upper range of the color-luminance group (i.e., having a color-sensitivity index near 2) do not share the spatial properties of the color-prefering group. Only one neuron near the upper boundary of the color-luminance group gave a low-pass spatial response to equiluminant chromatic gratings (see Fig. 2 in Johnson et al. 2001). These results suggest that it is reasonable to compare and contrast the visual responses of cells in each classification.

Color-luminance cells and double opponency

It is important to point out that most color-luminance cells are cone opponent, whereas most cells classified as luminance-prefering are nonopponent. This suggests that color-luminance neurons are indeed part of a color pathway because they perform a computation on the inputs from cones that would allow them to react to a wide range of color modulation. We showed in a previous paper (Johnson et al. 2001) that the color-luminance cells were spatially tuned for cone-isolating as well as for equiluminant stimuli. Taken together with the present results on cone opponency, this suggests that these neurons must be double opponent—cone-opponent neurons that also receive spatially opponent drive from each cone type. Our results are consistent with and extend the pioneering work of Thorell and colleagues on this type of V1 neuron (Thorell et al. 1984). The functional consequence of the double opponency of color-luminance cells is that these cells have the visual properties that would make them capable of supporting color induction and color constancy (cf. Wachtler et al. 2003). They
will be less sensitive to large colored regions than to an optimal colored spatial pattern—possibly an edge or a grating. Our results suggest that complex color-luminance cells may detect the presence of color boundaries, but that simple color-luminance cells could detect the boundaries as well as distinguish the different hues that make up that boundary because of their sensitivity to the stimulus phase. Such neurons could be important in providing some constancy in color responses as the color of an illuminant changes—the well-known perceptual phenomenon of color constancy.

Our results and conclusions about color-luminance cells as the double-opponent neurons in V1 do not agree with the conclusions of recent work by Conway (2001) and Conway et al. (2002). These recent papers explicitly argue for the controversial idea that double-opponent cells have a concentric, even-symmetric geometry (Livingstone and Hubel 1984; Michael 1978). We believe the conclusions of Conway and co-workers (Conway 2001; Conway et al. 2002) are incorrect on methodological grounds. They used cone-isolating stimuli produced by placing highly colored spots on highly colored backgrounds. However, the background for their L+ cone map is not the same as for M+ or M− cone maps, and not even the same color as for the L− cone map. Highly colored backgrounds could cause significant chromatic adaptation in the retina and in the LGN. Nonlinearities like chromatic adaptation could certainly change or distort the spatial maps of cone influence. Simply adding the maps together, as done by Conway (2001), is based on an assumption of linearity across all the different colored adapting backgrounds, and this linearity assumption is very likely to be incorrect. Any significant nonlinearity from retina to cortex would make it invalid to compare the spatial maps obtained on one intensely colored background from those obtained on another (De Monasterio et al. 1975).

It is worth noting that, by their selection criterion, Conway and co-workers elected to study only neurons that were color-prefering, and so the conclusions in their recent papers are equivalent to the claim that a significant fraction of V1 color-prefering neurons are double-opponent cells. Contrary to this conclusion, one of our strongest results is that V1 color-prefering neurons are almost all single opponent (Johnson et al. 2001). Our conclusion is based on the data that V1 color-prefering neurons respond best to the lowest spatial frequencies of colored patterns (Johnson et al. 2001; Solomon et al. 2004). This qualitatively refutes Conway et al.’s hypothesis that color-prefering cells are double-opponent.

Others previously concluded that V1 did not contribute to color contrast or color constancy but that such properties emerged in V4 or other extrastriate visual areas (Zeki 1983). As we have pointed out elsewhere (Shapley and Hawken 2002), this may have been a mistaken conclusion based on a selection bias for color-prefering cells in V1. Results reported by Zeki (1983) on color-prefering cells completely support our assertions above, that they are single-opponent neurons. By studying only V1 color-prefering cells in his experiments, Zeki may have omitted to study the V1 neurons that are double-opponent—the color-luminance neurons. It is entirely plausible that signals from V1 color-luminance cells provide...
input that ultimately drives the color-contrast sensitive neurons in V4. Studies with functional MRI in humans (e.g., Hadjikhani et al. 1998; McKeefry and Zeki 1997) that use the difference between color and luminance responses as a measure of color sensitivity may have generally underestimated the contribution of V1 to color vision. A recent review by Schluppeck and Engel (2002) presents a similar view.

Our results on receptive field symmetry support the concept that color-luminance cells could be sensitive to color boundaries. The odd symmetry of receptive fields could be a mechanism by which the visual system performs edge detection (Field and Tolhurst 1986; Hamilton et al. 1989; Hubel and Wiesel 1968; Pollen and Ronner 1981). Our results on spatial symmetry suggest that color-luminance and luminance-preferring V1 simple cells both may have odd-symmetric and asymmetric receptive fields (cf. Ringach 2002). There are prior results supporting this hypothesis, Girard and Morrone (1995) inferred from their results on human visual-evoked potentials (VEPs) to gratings modulated in either luminance or red/green color that both color and luminance mechanisms have receptive fields that include asymmetric spatial substructure.

The color-prefering cells could also have an important role to play in color vision. They will respond to large colored areas, and will give information about the color of enclosed regions. However, they will not adjust their color signals when illumination changes because they do not respond to color contrast but only to local color modulation.

Luminance-prefering cells

A significant new result of this study is that a large fraction of V1 cells, the luminance-prefering class, are cone nonopponent. This is significant because it shows that cone opponency is not as widespread as had been suggested previously (Lennie et al. 1990). Recall that Lennie et al. calculated that almost all neurons in V1 were cone opponent, and on the basis of this calculation they made the suggestion that cone opponency might have no functional significance for color vision. This quotation comes from their 1990 paper, as follows: “The fact that virtually all neurons in striate cortex are chromatically opponent revives the question (raised earlier by our work on l.g.n.) of whether chromatic opponency per se is of any functional significance” (Lennie et al. 1990). Figure 12 from the Lennie et al. (1990) paper shows that they calculated that most of the cells they studied were in the opponent quadrants of their diamond-shaped graphs. We have offered evidence that contradicts this important calculation, and it is worth considering why our results are so different from those of Lennie et al. (1990).

There are several reasons why we obtained different results about the luminance-prefering cells, and they all can be traced to different experimental methodologies between this study and that of Lennie et al. (1990). One reason is that we measured responses to cone stimuli directly and did not depend on a linear model to calculate the cone weights. Nonlinearities in cortical responses could have given mistaken estimates of the relative sensitivity of the luminance-prefering cells to different color directions. Another reason is that we did not use such high luminance contrast as was used in the Lennie et al. (1990) study, and this also will lessen the impact of contrast nonlinearity on our measurements. Perhaps the most important difference is that we used spatial stimuli that were of optimal size, whereas Lennie et al. (1990) used large grating stimuli that were often larger than optimal for the neurons. As we now know, many luminance-prefering neurons are located in layer 4B (Johnson et al. 2001), and layer 4B neurons have the strongest end inhibition and surround inhibition in V1 cortex (Sceniak et al. 2001). Thus the responses to luminance stimuli of many of the luminance-prefering cells in the population of V1 cells studied by Lennie et al. (1990) were likely to be small and noisy because of the large size of the stimuli that were used. However, by using optimal size stimuli that generated robust responses, we found a large population of cone nonopponent cells in V1. Therefore reasoning that cone opponency is not functionally important because all cells are cone opponent is probably incorrect. Cone opponency is most likely a sign that a neuron is involved in color processing, as originally supposed (DeValois 1965).

The luminance-prefering population was quite diverse in the ratio of L/M cone weights. This means that the luminance-prefering population will have different response distributions to different colors, and could contribute to color vision somewhat through the diversity in the population response. However, these nonopponent neurons usually produce weak responses to highly colored red/green stimuli because the L and M cones are connected to them with the same sign, and they do prefer achromatic stimuli.

Magnitude of S-cone weight

A significant result of our study is the relatively weak S-cone weight in most V1 cells compared with the input from the L- and M-cones. Recent results from other investigators suggest that the relative S-cone input to V1 is as much as 20–30% of the total (Chatterjee and Callaway 2002; Cottaris and De Valois 1998; De Valois et al. 2000). In addition, these studies suggest that the S-cone response contribution doubles from LGN to V1. Our results indicate that the S-cone response is about 2–8% of the total response to all 3 classes of cone. This range of S-cone input is similar to the range seen in the LGN (Derrington et al. 1984; Reid and Shapley 2002). Although we find weak S-cone input in the majority of the V1 cells in our sample, our results also indicate that S-cone inputs are significantly weaker in luminance-prefering, nonopponent cells than in either variety (color-luminance or color-prefering) of cone-opponent cells. The most obvious difference in technique between the experiments presented here and other studies in V1 is that we used a much lower S-cone contrast (24% vs. 83% or greater). S-cone-isolating stimuli can be presented over a much larger range of contrasts than L- and M-cone-isolating gratings because of the spectral response curves for each cone (the L- and M-cone spectral response curves overlap substantially, whereas the S-cone spectral response curve is quite separate). However, high S-cone contrasts potentially possess luminance artifacts as recently analyzed in detail by Cottaris (2003). It is possible that the S-cone input has a higher contrast threshold. Nevertheless, this still indicates that the S-cone input to V1 is less effective than L or M input. The primary goal of this study was to make direct measurements of cone input with cone-isolating stimuli of matched cone contrast, and the cone contrasts for the L- and M-cone-isolating stimuli were sufficient to drive robust responses in V1.
Magnitude of L- and M-cone weights

Our results also suggest that V1 color-luminance, cone-opponent neurons, especially simple cells, have specific color preferences, as demonstrated by the wide distribution of cone weights in the color-luminance population (Fig. 4). In their study of LGN cells, Derrington et al. (1984) deduced that many parvocellular LGN cells received roughly equal opponent input from L- and M-cones. More direct evidence that many pLGN neurons received balanced, opponent signals from L- and M-cones came from a study by Reid and Shapley (2002), which measured LGN cell responses to cone-isolating pseudorandom white-noise stimuli (m-sequence grids). Our quantitative results about relative cone weights suggest that simple color-luminance cells may have varied preferences for color, whereas complex color-luminance cells appear to have cone-weight distributions that are more clustered around an L/M ratio of $-1.0$, like most pLGN cells.

One possible explanation for the different cone-weight results for color-luminance cells and color-prefering neurons could be found in the different pLGN inputs these neurons receive because of their different spatial-tuning properties. The cited results on unity L/M ratios in pLGN cells are based on experiments with full-field stimulation (Derrington et al. 1984) or calculations of what would be the response to such stimuli (Reid and Shapley 2002). However, when Reid and Shapley (2002) measured the cone weights of the center regions of pLGN cells, they found a wide diversity of L/M weights. The optimal spatial stimuli for color-luminance and color-prefering cells are quite different. Color-prefering cells, being single-opponent, low-pass spatial neurons, were tested in our experiments with stimuli that would be equivalent to “full-field” in the pLGN experiments, and their cone weights were clustered around the values of pLGN cone weights for such stimuli. The stimuli we used to study cone weights in color-luminance cells were of higher spatial frequency because these neurons are double-opponent and respond suboptimally to “full-field” stimuli, if at all. The optimal stimuli for the color-luminance cells probably were similar spatially to stimuli that yielded a broad distribution of cone weights in the Reid and Shapley (2002) experiments. Thus the difference between the cone-weight distributions we observed could be attributable to the different spatial selectivities of the color-prefering and color-luminance neurons, and the different patterns of cone-weight distributions of pLGN cells for different kinds of spatial stimuli. This has the functional consequence that the neuronal population that responds to color boundaries and colored spatial patterns is much more diverse in its color properties (because of the diversity in relative cone weights) than the color-prefering population that is clustered around an L/M cone weight ratio of $1$.

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REFERENCES


