Spatial and chromatic processing in layers 2+3 of primate striate cortex

R.C. Reid and D.Y. Ts'o
The Rockefeller University
Laboratory of Neurobiology
New York, NY 10021

Running title: Spatial and chromatic processing in V1
Total pages: 48
Figures: 10
Tables: 0
Number of words in Abstract: 255
Number of words in Introduction: 586
Number of words in Discussion: 1498

Correspondence: R. Clay Reid
Harvard Medical School
Department of Neurobiology
220 Longwood Ave., GB2-203
Boston, MA 02115
(617) 432-3621; fax: (617) 734-7557
clay_reid@hms.harvard.edu

Key words: primate, macaque, vision, visual cortex, striate cortex, V1, color, double-opponent, cone, photoreceptors, receptive field, white noise

Acknowledgments: This work was supported by National Institutes of Health Grants 5F32EY06393, EY08240; ONR grant N00014-91-J-1865; The Whitaker Foundation and the Revson Foundation.

Dr. Ts’o’s present address: SUNY Health Sciences Center, 750 East Adams St., Syracuse, NY 13210
ABSTRACT

Four classes of unoriented color-selective neurons have been described. Two broad classes have been described. Double-opponent cells respond best to contrasting colors, while modified type II cells are inhibited by light of any color in the surround. We have studied these types of center/surround interactions in a population of unoriented, color-selective cells in layer 2+3 of macaque striate cortex. Optical imaging was used to target electrode penetrations to regions (presumed cytochrome oxidase blobs) with a high concentration of these neurons. Receptive fields mapped with spatiotemporal noise (m-sequences) composed of cone-isolating colors. The responses to these stimuli allowed us to make separate receptive-field maps due to each class of cones: long, middle, and short wavelength-sensitive (L, M, and S). Receptive-field centers and surrounds were considered separately in order to analyze both spatially and chromatically opponent processes.

Chromatic mechanisms in the receptive-field centers were either predominantly red-green (L-M) or blue-yellow (S-(L+M)) opponent. In marked contrast to cells in the lateral geniculate nucleus, however, many red-green opponent cortical cells received significant S-cone input.

Responses in the receptive-field surrounds were more heterogeneous. Roughly 1/4 (10/37) of the neurons were suppressed by luminance in the receptive-field surround (modified type II cells). Three cells, all with S-cone input, were double-opponent: receptive-field maps due to one cone were on-center/off-surround, while maps due to an opponent cone class were off-center/on-surround. For all cells, surround responses were strongly nonlinear: responses to achromatic stimuli were poorly predicted by the cone-isolated responses.
INTRODUCTION

A population of neurons in layers 2+3 of primate striate cortex (V1) have unoriented and color-selective receptive fields. Several studies have localized these neurons to the cytochrome oxidase blobs (Livingstone and Hubel, 1984; Ts'o and Gilbert, 1988; Landisman and Ts’o, 2002). Previous studies, however, have presented different accounts of the spatial and chromatic organization of the receptive fields of these neurons. Some studies have reported a predominance of so-called double-opponent cells, while others have reported a heterogeneous distribution of cell types that exhibit a range of center/surround interactions. To address this controversy, we have combined the two techniques to map receptive fields: binary noise stimuli (m-sequences) and cone isolation with the method of silent substitution. Color properties were studied with silent substitution, a method for isolating the contribution of the three cone classes: long, medium, and short wavelength-sensitive, or L, M, and S (Estevez and Spekreijse, 1974, 1982). A receptive-field map (or spatial weighting function, see Materials and Methods) obtained with a cone-isolating stimulus therefore represents, for each point in space, the signature and magnitude of the influence of that cone class (Reid and Shapley, 1992). Together, these two techniques provide a quantitative characterization of the chromatic signature of both center and surround.

Figure 1 Color-selective receptive-field types near here.

Although studies have differed in their methods of classification, as many as four classes of unoriented, color-selective neurons have been described in the superficial layers of macaque V1: type I, type II, double-opponent, and modified type II (fig. 1). A type I neuron is both spatially and chromatically opponent; a typical example is a red-on center, green-off surround cell (fig. 1A). A type II neuron (fig. 1B, also red-on/green-off) is chromatically but not spatially opponent. Both type I and type II cells are selective for the color of a stimulus that covers the entire receptive field, but they differ in their responses to achromatic stimuli. Type I cells have opponent
center/surround responses to achromatic stimuli, while type II cells are insensitive to the spatial structure of the stimulus (fig. 1A,B; far right). A double-opponent receptive field is chromatically opponent in both the center and surround (Daw, 1968; Michael, 1978). Unlike either type I or type II cells, double-opponent cells are classically described as being most responsive to spatial stimuli defined by contrasting colors, such as a red spot on a green background (fig. 1C). Finally, a modified type II cell (fig. 1D; Ts’o and Gilbert, 1988) is chromatically opponent in the center but either a chromatic or achromatic stimulus in the surround suppresses it, decreasing both excitatory and inhibitory responses evoked by stimulation of the center.

While these four types of color-opponent neurons have been described by some authors, there has been disagreement in the literature over whether they are all represented in the superficial layers of V1 and, if so, in what proportions (H+L, T+G, C). The present study was undertaken to examine this question by characterizing separately the influence of the three cone classes on the receptive-field centers and surrounds of these neurons. These quantitative descriptions of the receptive fields have allowed us confirm the original observations, based largely on qualitative techniques, that there is a heterogeneity of receptive-field structures amongst the color-selective neurons in layer 2+3 of V1.
MATERIALS AND METHODS

Surgery

Adult cynomolgus monkeys, *Macaca fascicularis*, were anesthetized with ketamine HCl (10 mg/kg, intramuscular). Sodium thiopental was then administered, first intravenously (20 mg/kg) then intraperitoneally as maintenance (2 mg/kg/hr). The animal was intubated and placed in a stereotaxic apparatus. Temperature, EKG, EEG, and expired CO₂ were monitored continuously throughout the experiment. Eyes were dilated with 1% atropine and protected with clear contact lenses. The refractive error was measured with a slit ophthalmoscope and corrected with contact lenses of the appropriate curvature.

All surgery was performed on a sterile field. The skin over the skull was shaved and cleaned with Betadine. A 5-10 mm craniotomy was made over the operculum; the anterior border was from 0-15 mm posterior to the lunate sulcus and the medial border from 3-15 mm from the midline. In this region of V1, receptive fields ranged from 1.5° to 7° eccentric. All but a few receptive fields were between 3° and 7° eccentric and were between 0.5° and 1.0° in size.

Once all surgical procedures were complete, animals were paralyzed with vecuronium bromide (0.2mg/kg/hr, intravenous) and ventilated mechanically. Proper depth of anesthesia was ensured throughout the experiment by 1) monitoring the EEG for changes in slow-wave/spindle activity, and 2) monitoring the EKG and expired CO₂ for changes associated with a decrease in the depth of anesthesia. In some animals, the paralytic agent was withdrawn in order to test whether the above criteria adequately indicated the depth of anesthesia.

Action potentials of single neurons in the cortex were recorded with glass coated (Alan Ainsworth, London) or plastic coated (Hubel, 1957) tungsten microelectrodes. Action potentials from individual neurons were discriminated with the Discovery recording system (Datawave Systems, Longmont, CO). In some cases, two neurons could be recorded simultaneously from the same electrode and were discriminated by their amplitude and waveform.
Eight animals were used in the present study, as well as other studies not described here. Thirteen experiments were performed, again some of which were partially devoted to other studies. For nine of the thirteen experiments, the animal was recovered within sixteen hours from the beginning of surgery. In these experiments, about 6-12 hours were available for recording. The remainder of the time was used for surgery and optical imaging. In the non-survival experiments, animals were euthanized with an overdose of barbiturate. In these experiments, cytochrome-oxidase histology was performed. In the survival experiments, it would have been difficult to correlate the recording sites with cytochrome-oxidase histology performed at a later date; penetrations were therefore presumed to be in the blobs from the optical imaging alone (see below).

Before recovery, a piece of clear, sterile dural substitute (Tecoflex) was placed over the exposed region of cortex and the dura was sutured. The bone was replaced and secured with cyanoacrylate glue. Finally, the skin was sutured and thoroughly rinsed with an antibiotic solution. In the days following recovery, animals were treated with antibiotics (Bactrim or Tribrissen) and narcotic analgesia. Subsequent experiments were performed at least two weeks following recovery. All experimental procedures were approved by the Rockefeller University standing committee on animal care and conformed to NIH guidelines.

**Optical imaging**

In nine of thirteen experiments, the exposed patch of cortex was optically imaged before electrophysiological recording (Blasdel and Salama, 1986; Grinvald, et al, 1986; Ts’o et al., 1990). First, electrophysiological recordings were made in the corners of the exposed region of cortex to ensure that the stimulus monitor (see below) covered the retinotopic locations represented in the imaged patch. During optical imaging, the visual stimulation protocol consisted of eight parts. Each eye was stimulated separately with gratings of one of four different orientations. Of particular interest were maps of ocular dominance (fig. 2A), which were made by subtracting all images of the cortex during left eye stimulation from images during right eye stimulation. Dark regions in these
images were more active when the right eye was stimulated. Ts’o et al. (1990) have shown that the regions with the strongest signals in these ocular dominance maps correspond very closely to the cytochrome oxidase rich blobs found in layer 2+3 (Wong-Riley 1979; Horton, 1984). Electrode penetrations (fig. 2A-C, +) were most often made in the regions of the strongest monocular signal in the optical images (fig. 2B, dark patches). In several experiments, regions of color selectivity were also mapped with optical imaging. In these images (fig. 2C), the dark regions of cortex (‘color patches’) were more active when stimulated with red-green gratings than with achromatic gratings (Landisman and Ts’o, 1992). The color patches have been found to be loosely correlated with the blobs, but not equivalent to them (Landisman and Ts’o, personal communication). When images of color patches were available, we targeted penetrations to regions that were both within a color patch (fig. 2C, +) and within a presumed blob from the ocular dominance map (fig. 2B, +).

**Figure 2 Optical image near here.**

The location of unoriented color-selective cells in layer 2+3 is a disputed topic (see Lennie et al., 1990; Leventhal et al., 1995). The present study was not designed to address this issue. Although these cells were targeted using the technique of optical imaging, a quantitative analysis of the efficacy of targeting was not attempted here (but see Landisman and Ts’o, 1992). Nevertheless, our strategy to target presumptive blob locations yielded a high proportion of cells with unoriented receptive fields, many of which were chromatically opponent.

**Laminar position of cells**

All recordings were done in the superficial layers of visual cortex. Since the experiments were semi-chronic, electrolytic lesions were not made during most penetrations. The electrode position could therefore not always be confirmed histologically, so great care was made to confine penetrations to layers 2+3. Electrode penetrations were perpendicular to the cortical surface. Electrodes were advanced through a thin layer of agar, so that the cortical surface was quite visible and there was little doubt when an electrode entered the cortex. All but two of the reported
recordings were made within 625 µm of the cortical surface. The two remaining neurons were at 800 µm. In the terminal experiments, lesions were placed and electrode tracks were reconstructed in order to ensure the accuracy of the electrode depth estimated during the experiment.

**Selection of neurons to study**

Neurons were studied only in columns in which unoriented, color-selective cells were encountered within the first several hundred µm. If highly oriented cells were encountered, no cells would be studied in that penetration. No attempt was made to obtain a uniform sampling of all cells in layers 2+3. Instead, cells were chosen that have been found to be typical of the cytochrome oxidase blobs (Livingstone and Hubel, 1984; Ts’o and Gilbert, 1988). Only color opponent cells were included in this study, as defined by the following criteria: 1) the cells were obviously color-selective when studied with the narrow-band stimuli and 2) the receptive fields (or spatial weighting functions, see below) as assessed by the cone-isolating stimuli were cone-opponent. That is, there were two cones classes that evoked responses of the opposite sign, one on and the other off (for instance a red-selective neuron is L-on and M-off).

**Hand-plotting of receptive fields**

All units were characterized with a hand-held projector before quantitative study with spatiotemporal noise stimuli. First, a white bar was swept through the receptive field at various orientations. If the cell’s responses to this stimulus were strongly oriented, no quantitative data were collected and the electrode was moved to a new position. If the receptive field was unoriented, its center was then located with a small spot of broadband light. Receptive-field size was mapped as the minimal response field and tended to be somewhat smaller than the center sizes measured with the spatiotemporal noise stimuli. Color tuning was next assessed with small and large spots of light projected through narrow-band filters that each transmitted roughly the same energy. The center wavelengths of the filters were spaced every thirty nm, from 450 to 630 nm.
Narrow-band spots were presented on backgrounds of variable luminance, from dark to roughly equal luminance with the spot itself.

The hand-held projector and narrow-band filters were used to characterize cells into three categories: Types I, II (Wiesel and Hubel, 1966), and surround-suppressed or modified type II (Ts’o and Gilbert, 1988). No attempt was made to systematically analyze double-opponency with the narrow-band stimuli, although several double-opponent cells were encountered and were characterized with the computer-generated stimuli. Some cells were not characterized by hand. This was usually the case when there were two neurons recorded simultaneously with the same electrode. The larger unit would be mapped by hand with color filters and the only the retinotopy of the smaller spike would be determined.

**Binary noise stimulus (m-sequence technique)**

The white-noise stimuli consisted of two types. In both types of stimuli, spatial regions were modulated by a binary temporal sequence, called an m-sequence (maximal length shift register sequence; Sutter 1987, 1992; Reid et al. 1997) whose temporal spectrum was white (all temporal frequencies in a given range were equally represented). In some experiments, cells were studied with a stimulus that consisted of 16 by 16 grid of squares: an “m-sequence grid”. Individual pixel size ranged between 0.19° and 0.31°. This stimulus is spatiotemporal white noise: it is uncorrelated in both space and time, at least to the resolution of the pixel size and the frame rate.

One difficulty with studying color-selective cells in visual cortex is that many of them are strongly and tonically suppressed by light of any wavelength in the surround (modified type II cells, Ts’o and Gilbert, 1988). Since the spatiotemporal noise stimulus (either luminance or cone-isolating) is necessarily modulated around some mean luminance, these cells were often tonically inhibited by the stimulus. In some experiments, therefore, an m-sequence was used to modulate a small circle surrounded by either 15 or 31 concentric annuli (fig. 1E). The annular configuration was designed as a more powerful stimulus for concentrically organized cells than the grid stimulus,
which had been used in a similar study of receptive fields in the LGN (Reid and Shapley, 1992). With the concentric stimulus, the area of each successive annulus increases, thereby increasing its effectiveness through spatial summation. The widths (radii) of the annuli were usually 0.13°, but were 0.06° or 0.08° in four cases. This stimulus is temporally white at each position, but spatially correlated. To test that the two methods gave similar results, four cells were studied with both the grid and the annular stimuli.

When the concentric stimulus was used, great care was taken to ensure that the central circle was located in the receptive-field center (and that the outer annuli extended beyond the receptive field). The receptive field was centered on the CRT with a small flashing spot that could be moved under keypad control. If there were two cells being studied at once, data from the second cell were used only if the two receptive fields were judged to be superimposed from their responses to the flashing spot. The stimuli were created with a PC video graphics card (Pepper Graphics System, Number Nine Computer Corporation) presented on a CRT monitor (Barco, CCID 7351). During any frame of the stimulus, each region took on one of two values. The video frame rate was 60 Hz and a new spatial stimulus was presented every two video frames, or every 33 msec. The two stimulus values were either black and white, or two different colors. The colors were chosen so that each pairselectively modulated a single cone type, but were indistinguishable to the other two cone types (silent substitution, see below). At each time, the color or luminance was determined by the binary m-sequence (Sutter 1987, 1992; Reid and Shapley 1992; Reid et al. 1997).

For the 16 by 16 grid, an m-sequence of length $2^{15}-1=32,767$ was used. Each region was modulated by the same m-sequence, but there was a relative delay of 128 frames (4.3 sec) between each successive region, as described elsewhere (Sutter 1987, 1992; Reid et al. 1997). When concentric annuli were used, which had only 16 or 32 regions, the m-sequence was $2^{13}-1=8191$ stimulus frames in duration. For the 16 by 16 grid configuration, each m-sequence took ~18.2 minutes to complete; the annular stimulus took ~4.6 minutes to complete. With two exceptions, cells were studied for at least 4.6 minutes with each of five different types of stimuli: achromatic; L,
M, and S-cone isolating; and red-green equiluminant (data not shown). In practice, most cells were held for over an hour in order to complete the entire protocol, including hand-mapping and centering on the screen.

**Chromatic calibration and cone-isolating stimuli**

The spectrum of each of the three phosphors (R, G, and B) was measured as a function of wavelength in 2 nm increments between 430 and 690 nm (Photo Research Spectrascan, PR 793A). These spectra were used to create cone-isolating stimuli by the procedure outlined by Estevez and Spekreijse (1974, 1982). The cone absorption spectra used to calculate the cone-isolating pairs were obtained from psychophysical data obtained from human subjects lacking one or more photopigment (Smith and Pokorny, 1972; Smith et al., 1976; no such data are available for the macaque). The Smith-Pokorny fundamentals include pre-retinal absorption due to the optical media of the eye (which are not as well studied in the macaque), in addition to the cone absorption spectra themselves. The cone absorption spectra are quite similar between human and macaques (Schnapf et al., 1988) and between individual macaques (Baylor et al., 1987).

It is important to note that the problem of imperfectly known absorption spectra is not unique to the cone-isolating technique, but affects any study of color processing. With cone-isolating stimuli, however, no transformations of the data are necessary to interpret the results in terms of cone classes. Thus no additional assumptions, such as linear summation, are necessary. Especially when studying mechanisms that have significant nonlinearities, the use of cone-isolating stimuli assures that no additional noise is added, for instance by interpolation between measurements that do not isolate cone responses at the photoreceptor level (e.g., Lennie et al., 1990).

The contrast of each cone-isolating stimulus is limited by the requirement that the physical contrast of any phosphor cannot exceed 1.0, since negative luminances are impossible. For L and M cone-isolating stimuli, the red phosphor was the limiting factor. For the S cone, the blue phosphor was limiting. The maximal contrasts obtainable in this study (determined by phosphors and white
point) were, 0.19, 0.16, and 0.80 for the L, M, and S cones respectively. The contrast for any cone was defined as the deviation from the mean level of excitation for that cone, divided by its mean level of excitation.

Receptive-field calculation: reverse correlation and the spatiotemporal weighting function

The rationale behind receptive-field mapping with spatiotemporal noise stimuli has been described in detail by us and by others (Reid et al., 1997; Reid and Shapley, 1992; Emerson et al., 1987; Jacobson et al., 1993). The approach is very similar to the reverse-correlation method (Jones and Palmer, 1987). Spatiotemporal weighting functions, often called receptive-field maps, were calculated by the method of reverse-correlation (Jones and Palmer, 1987), which is in this case comparable to the first-order (linear) kernel in the Wiener kernel expansion (Marmarelis and Marmarelis, 1978).

The weighting functions, \( K(r_j,t_k) \), are functions of both space, \( r_j \), and time \( t_k \), which is quantized at the update rate of the stimulus: \( \tau = 33 \) msec. For example, if \( K(r_j,t_k) = 2 \), then on the average, in the interval between \( k\tau \) msec and \((k+1)\tau \) msec after the presentation of a positive stimulus in region \( r_j \), the neuron tended to fire 2 spikes/sec more than the mean firing rate. If \( K(r_j,t_k) = -2 \), then the neuron tended to fire 2 spikes/sec less following the positive stimulus. The positive stimulus is defined as the brighter phase (positive contrast) for each condition: lighter gray for luminance, and red, green, and blue/purple respectively for the L, M, and S cone-isolating stimuli. The negative stimulus is black for luminance, and green, red, and yellow/green for the L, M, and S stimuli. It is perhaps useful to note that the L cone stimulus consists of a brighter red and a darker green, while the M cone stimulus consists of a brighter green and a darker red (schematically shown in fig. 1E). For ease of comparison, all weighting functions are normalized, in units of (spikes/second)/(unit contrast) (Reid and Shapley, 1992). For instance, the L-cone weighting is divided by the contrast of the L-cone stimulus, 0.19. Given this normalization, the 'linear' hypothesis is that the sum of the L, M and S-cone weighting functions should be equal to the
weighting function obtained with an achromatic stimulus at 100% contrast (black and white). This is because a pure black and white stimulus modulates all three cone classes simultaneously with 100% contrast (the mean luminance was the same for all stimuli).

Although the neurons we studied did not behave strictly linearly by this criterion, reverse correlation nonetheless provided a detailed and informative picture of their receptive fields. By analogy, reverse-correlation elucidates the spatial and temporal properties responsible for direction selectivity in simple cells of cat striate cortex, even though the mechanism is only partially linear (McLean and Palmer, 1989).

**Time course of responses: the temporal weighting function**

The spatiotemporal weighting function, $K(r_j, t_k)$, can be presented as either a function of time or of space. Spatial weighting functions (similar to receptive-field maps) can be made for any delay between stimulus and response; they are proportional to the average spatial stimulus that preceded each action potential with a delay of $t_k$. Alternatively, for any region of the stimulus, $r_j$, a temporal weighting function (analogous to the impulse response) is the time-series proportional to the average stimulus that tended to precede each action potential, as a function of the delay, $t_k$. More intuitively, the temporal weighting function can be thought of as the average deviation in firing rate at time $t_k$ following presentation of the bright stimulus in region $r_j$.

In order to analyze the sign (on or off), strength, and time-course of the responses, we first separated the weighting functions into two spatial regions: center and surround. In most cases the center and surround themselves were defined using the strongest (largest amplitude) of the four spatial weighting function obtained with the cone-isolating or luminance stimuli. In a few cases the luminance weighting function had a clearly opponent center and surround, but the strongest weighting function was non-opponent; in these cases, the luminance weighting function was used to define center and surround. Regions (pixels or annuli) were included in the center if the responses 1) were of the same sign as the strongest response, 2) were greater than two standard deviations
above the measurement noise, and 3) formed an area that was contiguous with the peak region. The noise was estimated by examining the calculated reverse-correlation at long delays between stimulus and response (>233 msec), when any correlation was spurious. The surround of the weighting function was defined as all regions that were in a ring around the center, with a width of four pixels or annuli. Finally, the temporal weighting functions, $C(t_k)$ and $S(t_k)$, were calculated by summing over all regions in center and surround at each time point, $t_k$. These functions of time are written in boldface to distinguish them from the scalar response weights, $C$ and $S$, defined in the Results section. Separate temporal weighting functions were calculated for the three cone-isolating stimuli and for the luminance stimulus. Recall that all weighting functions were divided by the cone contrast of the stimulus used to measure them (0.19, 0.16 and 0.80, for L, M and S cones respectively), so that the units were (spikes/sec)/(unit contrast).
RESULTS

The receptive fields of 37 unoriented, color-selective cells in layers 2+3 were mapped successfully with the spatiotemporal noise stimuli: 14 with the grid stimulus alone, 19 with the concentric annular stimulus, and 4 with both. Thirty-one cells had antagonistic input from L and M cones: that is, they were red-green opponent. Of these, 14 were selective for red stimuli (L+/M-) and 17 were selective for green stimuli (M+/L-). The remaining six were blue-on/yellow-off cells (see fig. 8 below). Three separate sets of the cone-isolating spatiotemporal noise stimuli were employed in order to study independently the L, M, and S cone inputs to these receptive fields. The cells were also studied with an achromatic (black and white) spatiotemporal noise stimulus.

We recorded from 25 unoriented cells not included in this study. Five color-selective cells were unresponsive to the noise stimuli. In addition, we made quantitative maps of 20 cells that were not color opponent, although most were encountered in the same penetrations as color-selective cells, as noted in previous studies (see Livingstone and Hubel, 1984; Ts’o and Gilbert, 1988).

Red-Green Opponent Neurons

Figure 3 Red-green opponent spatial weighting functions near here.

We first illustrate spatial weighting functions of cone inputs for three green-selective neurons, two type I green-on/red-off cells (fig. 3A, B) and a type II red-off/green-on cell (fig. 3C). For each neuron we show five panels, each representing different aspects of the receptive field. The first three panels show the spatial weighting functions measured separately with the L, M, and S-cone isolating stimuli. The fourth panel is the sum of the first three, L+M+S. This sum represents the expected response to the black and white (Lum) stimulus, assuming that inputs from the three cone types add linearly (see Materials and Methods). The fifth panel shows the actual spatial weighting function as measured with a black/white, luminance-modulated stimulus.
The degree to which the last two panels, $L_{um}$ and $L+M+S$, are similar provides a rough test of linear summation of the inputs from the three cone types.

The luminance spatial weighting function for the first type I cell (fig. 3A, $L_{um}$) will be used to introduce the plotting conventions. Spatially, the stimuli consisted of a grid of square pixels, 0.31° on a side. The plot is a color-coded version of the spatial stimulus that tended to precede each action potential, between 67 and 100 milliseconds before each action potential (three frames before the spike at 30 Hz). Color codes for response sign (red for on responses, blue for off), and brightness codes for response strength. The isolated red region, the receptive-field center, corresponds to the area where the neuron was excited by a lighter phase of the stimulus. The brighter the red, the more strongly the neuron was excited. The diffuse dark blue region, in the surround, corresponds to an area where it was weakly excited by a darker stimulus. Black corresponds to areas where the neuron was unaffected by the visual stimulus, or equally affected by light and dark. The black grid outlines the locations of the pixels. When mapped with a luminance stimulus (either with spatiotemporal noise, shown here, or by hand) this neuron had a classical on-center/off-surround spatial weighting function. The luminance response of this neuron was particularly weak, so the scale used to plot it was eight times lower than that used for the cone-isolating responses.

The first panel of Figure 3A illustrates the L-cone weighting function of the same type I neuron. Over the entire receptive field, this neuron responded to the off phase (dark green) of the L-cone stimulus. The second panel shows the M-cone weighting, which is slightly smaller and exclusively on. The center of this receptive field gave weak on responses to the S-cone stimulus, shown in the third panel. Finally, the fourth panel in Figure 3A shows the sum of the three cone-isolated spatial weighting functions, L+M+S. Again, the degree to which this map approximates the luminance spatial weighting function provides a good measure of the linearity of chromatic summation for this neuron. The off surround in the luminance response is mirrored in the L+M+S map, but the center shows up as a hole in this off response, rather than as an on region. The L
and M responses of this neuron were very well balanced, as reflected both in their numerical near-equivalence and also in the fact that the luminance response was quite weak. It is perhaps not surprising that the sum of a large positive response (M-on) and a large negative response (L-off) was somewhat noisy. Qualitatively, the L+M+S and the luminance maps have similar features, but there are some clear differences. In Figures 4 and 10, below, we show quantitative comparisons between these two measurements that cannot be appreciated from the spatial receptive field maps.

The second type I neuron (fig. 3B) was mapped with the annular stimuli. In this experiment, an m-sequence function was used to modulate the luminance or color of a circle surrounded by 15 concentric annuli. When mapped with the black and white (Lum) stimulus, this neuron gave on responses in the central circle and the first annulus, but gave off responses in the surrounding annuli (fig. 3B, Lum). The M-cone response was strongly on in the central regions. The S-cone response was also on, but weaker. Finally, the L-cone stimulus evoked off responses in the central regions, but weak responses extended out to a slightly larger diameter. Therefore, the summed L, M, and S responses in panel four has the same on-center/off-surround configuration seen in the luminance response. In summary, this neuron was an M(+S)-on/L-off (blue and green-on/red-off) type I cell that exhibited qualitatively linear summation of cone inputs in both center and surround.

The third set of spatial weighting functions (fig. 3C) are from a red-off/green-on type II cell. Again, these data are from an experiment with annuli that were modulated with binary noise. Qualitatively the L and M cone responses were the same as those seen for the type I neurons in Figure 3A and B, L-off and M-on. The luminance response, however, was entirely off. This lack of spatial opponency is the hallmark of type II cells. Similarly, the L+M+S spatial weighting function in the fourth panel was almost entirely off, since the L-off responses were stronger than the M-on responses. The apparently on response in the small central circle ($\frac{1}{2}$ the area of the first annulus) was weak and almost certainly due to noise. Again, the predicted luminance responses
(L+M+S) were the noisiest because they were the sum of nearly balanced positive and negative terms (see fig. 4 below).

**Figure 4. Red-green temporal weighting function near here.**

The spatial weighting functions (fig. 3) represent the average spatial stimulus that preceded each action potential at the delay that gave the strongest response. The spatial representation of the data gives a qualitative picture of receptive-field structure, but a poor sense of response magnitudes. In order for both strong and weak receptive-field structures to be visible (given the limitations of color reproduction), some of the luminance or L+M+S weighting functions were scaled, as noted in the legend. The quantitative aspects of the receptive field are better appreciated when the spatial data are collapsed into two components—center and surround—and the temporal responses are plotted as a function of time. These temporal weighting functions have the added benefit that the response dynamics can also be seen.

Temporal weighting functions are illustrated (fig. 4) for the same neurons whose spatial weighting functions are shown above (fig. 3B,C). First, the pixels that correspond to center and surround were defined (see Materials and Methods). Then, for each frame of the spatiotemporal weighting function, the responses due to all annuli (or pixels) in these regions were summed. These summed temporal weighting functions for center \((C(t_k))\), thick lines, and surround \((S(t_k))\), thin lines, are plotted for stimulus/response delays, \(t_k\), up to 466 msec. The summed temporal weighting functions are given in terms of \((\text{spikes/second})/\text{(unit contrast)}\).

Several aspects of the responses of the type I neuron can be readily appreciated from the temporal weighting functions (fig. 4A). The luminance plot indicates that on response in the center (thick line) was in fact weaker than the off response in the surround (thin line). Both responses were quite weak, on the order of a few spikes per seconds, compared to the L and M responses, which were around 40 spikes per second after the normalization. The L, M, and S cone responses also reflect the fact that the spatial antagonism was due to interactions between
cone-classes, not within any class. For each cone class, the center and surround had the same sign of response (on or off) and a similar time-course. Finally, the predicted luminance response, $L+M+S$, was qualitatively similar to the actual luminance response, but smaller by more than a factor of two. The large amount of noise results from the fact that the $L$-off and the $M$-on responses subtract, so that the luminance prediction was much smaller than either measurement.

For the type II cell, the responses in the surround were qualitatively different. Since this cell had no spatial antagonism, the region defined as the “center” by our algorithm included most of the receptive field, almost 2° in diameter. The integrated response strength for the L and M cone inputs was much stronger than for the type I cell: between 150 and 200 (impulses/sec)/(unit contrast). The $L+M+S$ and the actual luminance responses also showed no opponency. As with the type I cell, the $L+M+S$ prediction was larger than the luminance response by more than a factor of two. This is a general phenomenon; the predicted luminance responses in the centers and, even more so, the surrounds were consistently overestimated by the linear prediction (see fig. 10, below). In other words, nonlinear mechanisms act to decrease the responses to achromatic stimuli.

**Modified type II neurons**

A total of 10 modified type II neurons (as characterized by hand) were successfully mapped with the annular stimulus. They were color-selective when tested with small, narrow-band stimuli on a dark background. When the stimuli were enlarged to include more than just the central region (or when the background luminance was increased) they were less responsive, or unresponsive, to stimuli of any wavelength. Three such cells were sufficiently surround-suppressed that they could not be mapped with the annular stimuli.

In Figure 5, we present data from a red-on/green-off modified type II cell. When mapped with handheld stimuli, the receptive-field center was roughly 0.5° and gave on responses for spots of light between 570 to 630 nm, off responses for 510 and 540 nm. It was unresponsive to all
larger stimuli. The neuron was then studied with noise stimuli that had a central spot and annuli with widths (radii) of 0.08°. We show the responses to the central eight regions, which correspond to a total diameter of 1.25° (fig. 5A). The peak response to the L-cone stimuli had an *on* center that included the center circle and the first annulus (0.31° in diameter) and a weak *off* surround. The M-cone stimulus produced weak *off* responses over a slightly larger region that included two or three annuli (.47-.63° in diameter). The luminance stimulus also evoked weak *off* responses. Qualitatively, this modified type II cell gave the same sort of responses that are illustrated in the model receptive field in Figure 1. The center mechanism was color opponent (L-*on*/M-*off*) but the surround non-opponent (L-*off*/M-*off*).

**Figure 5. L-*on*/M-*off* modified type II cell near here.**

The term “¾ double-opponent” (Livingstone and Hubel; 1984) has been used to describe color-selective receptive fields for which one cone type is center/surround opponent (the L cone in fig. 5A), but the other cone type (the M cone in fig. 5A) is spatially non-opponent. The spatial weighting functions of modified type II cells often were of this type when mapped with noise stimuli. Although the spatial weighting functions may therefore indicate some association between modified type II cells and ¾ double-opponent cells, they do not illustrate the defining characteristic of modified type II cells: that luminance in the surround strongly suppresses (or vetoes) any response to center stimulation. Our stimulus protocol that yielded the spatial weighting functions (fig. 5A) was not well suited to a thorough analysis of the interactions between center and surround. Because only one cone class was tested in each experimental run, interactions between cone inputs could not be determined. We therefore subjected this cell and a few others to an exhaustive test of center/surround interactions.

The interaction protocol involved independently modulating a central spot and a peripheral annulus. For the cell illustrated, the spot had a diameter of 0.31°, the size of the red-*on* center. The peripheral annulus had a diameter of 2.5 degrees. The center was alternated at 1.0 Hz
between two values: either a cone isolating pair (L, M, or S) or luminance at 100% contrast (black and white). Simultaneously, the surround was modulated between two values either in phase with the center (bright center with bright surround, dark with dark; fig. 5B, top row) or in anti-phase (fig. 5B, bottom row). Finally, extra cases were added in which the center or surround were not modulated, but were kept at either the mean luminance or black (fig. 5B, column 5). Therefore, for both the spot and the annulus there were six stimulus types: four modulated stimuli and two unmodulated. These were presented independently in the spot and the annulus, either in phase or anti-phase. There were thus a total of 6x6x2=72 configurations. They were presented in 8-second trials (8 cycles) and repeated in a random order through a number of iterations.

Cells that were not strongly surround-suppressed (type I or II cells) responded to a large number of different pairings in this stimulus matrix. Further, these responses could be qualitatively predicted from the spatial weighting functions obtained with the noise stimuli (data not shown). This modified type II cell illustrated in Figure 5, however, responded well to only a few specific stimulus configurations. By far the strongest responses were obtained when a red spot was presented concurrently with the annulus changing from white to black (fig. 5B, thick arrows), as would be expected from the original description of modified type II cells. There were two such configurations: L-cone spot with a luminance annulus (in anti-phase: L-off paired with luminance-off), or M-cone with luminance (in phase: M-off with luminance-off). Both of these stimuli gave similarly strong responses. In other words, this cell responded best to a red spot on a black background, whether the red signal came from on responses of the L cones or an off response of the M cones. The importance of the background in these pairings can be seen by comparing these two strong responses (fig. 5B, thick arrows), with the responses above or below them. In each case, when the red stimulus was presented at the same time as the black-to-white transition in the surround, there was no response (fig. 5B, asterisks in columns 2 and 3).

It might be argued that the very strong responses to red-on-black stimuli (fig. 5B, columns 2 and 3) are caused by linear summation of excitatory (or disinhibitory) responses from the center
and surround. The hallmark of modified type II cells, however, is a sub-additive suppression of center responses. In order to assess this idea, one can examine the cases in which central spot was paired with constant stimuli in the surround (fig. 5B, column 5), either black (top) or gray (bottom). If the neuron summed its inputs linearly, the M-cone stimulus in the center would have evoked the same response (that is, the same modulation from the mean rate). Instead, the excitatory response to the dark red (M-off) stimulus on a black background (thin arrow) was much stronger than the excitatory response on the gray background (asterisk). The gray background also suppressed, or vetoed, the inhibitory response to the green (M-on) phase of the M-cone stimulus: there was a very strong off response on the black background (fig. 5B, column 5, top) but only a weak off response on a gray background (fig. 5B, far right, bottom). Luminance in the surround thus suppressed, or vetoed, both the on and off responses evoked in the center of this modified type II cell.

Finally, we tested multiple conditions in which this neuron could be assessed for double-opponency. These conditions included each of the eight pairings of L or M-cone stimuli, in either center or surround, and with center and surround either in-phase or anti-phase. None of these stimuli evoked strong responses. We illustrate only the responses evoked by an M-cone spot and L-cone annulus (fig. 5B, column 5; none of the other pairings evoked stronger responses). For this pairing, the M-off response was very weak either for the in-phase case, which should have been strong if the cell were double-opponent (top, double asterisk) or the anti-phase case (bottom, asterisk).

In summary, this neuron had some of the features of the ¾ double-opponent cell (Livingstone and Hubel, 1984)—color-opponent in the center, non-opponent in the surround—when tested with stimuli that modulated only one cone type at a time (fig. 5A). More exhaustive testing of center/surround interactions (fig. 5B) showed that this cell in fact had the characteristic feature of modified type II cells (Ts’o and Gilbert, 1988)—suppression, or a veto, of all center responses by luminance in the surround.
Neurons with strong S-cone input

Figure 6. Receptive fields with S-cone input near here.

Neurons that received strong S-cone input are illustrated with two examples, a classic blue-on/yellow-off cell and a double-opponent cell. For the blue yellow cell (fig. 6a), the responses to the cone-isolating stimuli were entirely as would be predicted. The L-cone and the M-cone both evoked off responses, while the S-cone stimulus evoked on responses. As was true for all six of our standard blue-on/yellow-off cells, the (L+M)-off responses were stronger than S-on response (fig. 6A, L+M+S; see fig. 7C below); these cells were therefore off-center when mapped with the luminance stimulus (fig. 6A Lum, see fig. 9D, below).

The second cell with S-cone input (fig. 6B) was also characterized as blue-on/yellow-off by hand; it responded to the onset of small spots of 450 and 480 nm light on a dark background, was unresponsive to 510 nm light, and responded to the offset of light at 540 nm and above. Unlike the other S-on cell (fig. 6A), however, this cell also showed a significant amount of surround suppression. Both the on and the off responses were abolished when tested with stimuli greater than one degree, and responses to small spots were weaker on a bright background. Color antagonism between center and surround was not tested with narrow-band stimuli. When mapped with the cone-isolating stimuli, however, this cell showed true double-opponent responses. The L-cone weighting function was off-center/on-surround and the S-cone weighting had the opposite configuration: on-center/off-surround. The M-cone responses were weaker than the L or S, but were also on-center. As a result, the luminance response of this neuron was dominated by the S-on, M-on components.

In our sample of 37 concentric cells, three were clearly double-opponent. Interestingly, all three cells received strong S-cone input, the one illustrated above and, in a different experiment, a pair of neurons that were recorded simultaneously. The L and S cone-isolating weighting were qualitatively similar for all three neurons, but the M-cone inputs were different. The receptive
field illustrated above was (S+M)-on/L-off in the center, (S+M)-off/L-on in the surround. The two neurons recorded simultaneously were both (L+M)-off/S-on in the center, L-on/S-off in the surround.

**Responses strengths of cone inputs to center and surround**

So far, we have characterized receptive fields either with functions of space—the spatial weighting functions (figs. 3, 5, and 6)—or functions of time: the temporal weighting functions (fig. 4). Below, we will characterize the responses of both the center and the surround each with a single number. These numbers, the *response strengths*, were the sum of the temporal weighting functions from a delay of zero up until the first zero crossing. If there was no zero crossing, the sum was taken for the first 133 msec for the center and 167 msec for the typically slower surround. Lennie et al. (1990) designated similar parameters \( w_R, w_G \) and \( w_B \) for the strengths of the R, G, and B (L, M and S) cone inputs. Here, the response strengths are designated

\[
\begin{align*}
c_L, c_M, c_S, s_L, s_M, \text{ and } s_S
\end{align*}
\]

for the center and surround, respectively. As noted in the Materials and Methods, these values were normalized by the effective contrast of each stimulus: 0.19, 0.16, and 0.80 for L, M and S-cones, respectively. If the neurons summed their inputs linearly, these six parameters would give a comprehensive measure of the cone inputs to the center and surround. In order to test linearity, similar values (\( c_A \) and \( s_A \), for achromatic) were calculated from the temporal weighting functions obtained with the luminance stimuli. The remaining four figures will explore the relations between these parameters.

**Figure 7. Histograms of normalized cone inputs near here.**

In order to group neurons in terms of cone-opponent mechanisms, we normalized the response strengths for each cone type. Following Derrington et al. (1984) and Lennie et al. (1990), the response strength for a given cone class was normalized by the sum of the absolute values of the responses strengths for all three. For instance:
$C_L = \frac{c_L}{(|c_L| + |c_M| + |c_S|)}.$

These values, $C_L$, $C_M$, and $C_S$ will be referred to as weights (dimensionless) to distinguish them from the strengths, $c_L$, $c_M$, and $c_S$, which have units of $\text{(spikes/sec))/(unit\ contrast)}$. The type of color opponency for each neuron was determined by the relationships among these three normalized weights.

When the cone weights for the 37 color-selective cells in the study are shown as histograms (fig. 7), the most salient feature is that the L and M cone weights cluster near 50% and -50%. The S-cone weights are comparatively weaker. For 19 cells, the S-cone inputs were less than 8% of the total. It should be recalled that all the response weights are calculated by first normalizing by the contrasts of the cone-isolating stimuli. Since the S-cone stimulus had a contrast of 0.80, the measured responses are multiplied by a factor of 1.25. The L and M-cone responses are multiplied by factors of 5 and 6, respectively. Therefore, a very robust S-cone response may yield a small percentage. For instance, weights of 50% M and 10% S would correspond to exactly the same raw response magnitudes. Similarly, we found that cells that had S-cone weights even between 10 and 20% would respond vigorously to narrow-band stimuli at 450 and 480 nm.

Of the cells that received over 8% of their inputs from S cones, 15 were S-on and 3 were S-off. This is consistent with the prevalence of blue-on cells found in retina (de Monasterio and Gouras, 1975), LGN (Wiesel and Hubel, 1966; De Valois et al., 1966) and V1 (Livingstone and Hubel, 1984; Ts'o and Gilbert, 1988; but see Lennie et al., 1990).

Figure 8. Cone weight plots for center and surround near here.

The sum of the three normalized cone weights always adds up to 1.0, so it is possible to see the relationship between all three parameters on a single two-dimensional plot. Again following Derrington et al. (1984) and Lennie et al. (1990), we have plotted the M-cone weights versus the L-cone weights. In these plots (fig. 8), the S-cone magnitudes (but not sign) can be
evaluated by the distance from the four diagonal lines determined by the equation: $|C_L| + |C_M| = 1.0$. Separate plots are shown for the cone weights calculated for both center and surround.

When plotted in this manner (fig. 8A), the cone weights of the receptive-field centers cluster into a number of distinct groups. Each cell is marked with a colored symbol that represents the cell class. The cell classes were defined by the clustering of points in Figure 8A, along with the sign of the S-cone input (which cannot be determined from the location of data points). The cells with S-on responses are color-coded by blue/purple; S-off cells are color-coded by yellow. The same symbols are used in all subsequent figures.

There are three broad clusters in Figure 8A, the first of which is in the second quadrant (II), where the M weights are positive and L negative. These 17 neurons are primarily selective for green stimuli. The second cluster is in the third quadrant (III), where both L and M weights are negative. These points lie a significant distance from the line $M+L=-1.0$, which means they receive strong S-cone input. For all six of these cells, the S-cone input was positive. These are therefore classical blue-on/yellow-off neurons. The third cluster is in the fourth quadrant (IV), where the L input is on and the M input is off. These 14 neurons are primarily selective for red stimuli (note that there were roughly equal numbers of red-sensitive and green-sensitive neurons).

It is interesting to note that all six of the classical blue-on/yellow-off cells (those we term L-M-/S+) were encountered in only two of the sixteen penetrations from which we present data. In one of these penetrations, all four cells were blue-on/yellow-off. In the other penetration, two cells were blue-on/yellow-off and the only other two had the strongest S-off input encountered in this study. While our sample size was certainly not large enough to perform meaningful statistics, these findings are consistent with the clustering of blue-yellow cells reported by Ts’o and Gilbert (1988).

Upon closer inspection, both the red-selective and green-selective neurons fall into several groups. First, there are the points that fall on or very near the two lines $M-L=1.0$ and $L-M=1.0$. 
These correspond to the cells that received little or no S-cone input: the classical red-green cells. These cells further fall into four groups, depending on whether the L or the M cones evoked stronger responses. The 13 cells dominated by the L cones are plotted as circles. The centers of these circles are colored in order to specify whether the L cone input is *on* (bright red) or *off* (dark green). The colors are intended to approximate the light and the dark phases of the L-cone-isolating stimulus. The borders of the symbols are colored in dark red and bright green in order to specify the sign of the M cone input. The centers are associated with the stronger cone input, the border with the weaker input. The seven cells dominated by M cone input are plotted as squares. Again, the colors of the centers and the borders specify the sign of the cone inputs: M-*on* centers with L-*off* surrounds in the second quadrant and M-*off* centers with L-*on* surrounds in the fourth.

Although we have characterized four classes of red-green opponent cells from their clustering in the second and fourth quadrants of the cone-weight plot (fig. 8), many other cells that cluster nearby also receive weak but significant input from S-cones. Similar plots of data from LGN cells (Derrington et al., 1984; Reid and Shapley, personal communication) show no such cells with weak S-cone input. For LGN cells, points fall either exactly on the diagonal borders of the plot or are at a significant distance; there is strong S cone input or none at all. In the cortex, however, we have found a continuous gradation from no S cone input up to fractions of 20% or more (fig. 7), particularly in the second quadrant of Figure 8A (green-selective cells). A similar blurring of the categories was also seen by Lennie et al. (1990), although most of their color cells were not in layers 2+3, but instead in layers 4 or 6 (see also Cottaris and De Valois, 1998; De Valois et al., 2000; Conway, 2001).

We have rather arbitrarily set the cutoff for "significant" S-cone input at 8% (see figure 7). All cells with a value larger than this are represented with triangles in Figures 8-10. Since the spatial extent of S-cone inputs tended to be larger than either the L or M inputs, the borders of the triangles indicate the sign of the S input: again, blue/purple represents S-*on* input; yellow
represents S-off. The classical (L+M)-off/S-on cells in the third quadrant are shown as triangles with dark blue centers and purple surrounds.

The presence S cone input to cells in the first and third quadrants mixes the classical red-green and blue-yellow opponent axes. These cells are predominantly red-green opponent, but they get significant S-cone input as well. Although there we did not study enough of these cells to determine whether they fall into distinct classes, we have put them into four categories. In the second quadrant, we found L-/M+ (S+) and M+/L- (S-) cells. In the fourth quadrant, we found M-/L+ (S+) and L+/M- (S-) cells.

One of the more striking patterns in figure 8 is that in the second quadrant (II; green-selective neurons) there are more cells with some S-cone input than in the fourth quadrant (IV; red-selective neurons). This is particularly true for the cells that had stronger L-off input (L+/M- cells). Further, all of these points have a positive S-cone input ($W_s > 0$). This brings up the concern that S-cone input may be an artifact, in particular that the S-cone isolating stimulus weakly excited the M cones. This is unlikely for two reasons. First, the amount of S-cone input did not vary with the relative amount of M-cone input. More importantly, for six of the predominantly red-green cells with S-cone input, the S-cone was opposite in sign to the M-cone: M-/L+S+ and M+/L-S-. In fact, the only constant finding was that the S-cone input was always opposite in sign to the stronger of the other two cone inputs (L or M). In other words, the S-cone had the sign that would tend to minimize the response to achromatic stimuli ($|L+M+S| < |L+M|$). The S-cone responses were unlikely to be luminance artifacts, however, since their magnitudes were not correlated with the luminance responses.

Although the plot of L and M weights for the receptive-field centers (fig. 8A) is nicely clustered, the plot for the surround weights (fig. 8B) is quite disordered. There are two explanations for this lack of clustering. First, there is the trivial explanation that some of the surround responses are quite weak for all cone classes. For instance type II cells by definition
have center, but no surround. Any "surround" responses can be thought of as spillover from the true center mechanism. In this case the normalized weights are quite noisy.

A more important reason for the scatter in the plot of surround cone-weights is that color-selective cells have a variety of surround types. For instance, most of the red-green cells have the same gross color preferences in the center and surround; i.e., most of the cells that mapped in the second (or fourth) quadrant in the center plot (fig. 8A) remained in the second (or fourth) quadrant in the surround plot (fig. 8B). This finding was also true for the great majority of cells in a similar study of the LGN (Reid and Shapley, personal communication). Most of the cells in the present study that changed quadrants (that is, they had different color specificities in center and surround) were modified type II cells. Because the cone-weights in these plots are normalized, however, no distinction can be made between strong and weak (noisy) responses. For this reason, we also plot the data in an un-normalized form (fig. 9).

**Figure 9. Center/surround opponency of cone inputs and luminance responses near here.**

In order to examine further the relations between the cone inputs to center and surround, we have also plotted the relation between center and surround strengths (as opposed to the normalized weights) separately for each cone type (Fig. 9A-C). The abscissa in each of these plots gives the strength of response to center in (spikes/sec)/(unit contrast), positive for on responses and negative for off. The ordinate gives the strength of the response in the surround. Thus for points in the first quadrant of such a scatter plot (Fig. 9A, I), the response was on in both the center and surround: the weighting function has no center/surround opponency. For points in the third quadrant (Fig. 9A, III), there were off responses in both center and surround. For points in the second or fourth quadrants (Fig. 9A, II, IV), however, there was center/surround opponency: off-center/on-surround in the second quadrant, the opposite in the fourth quadrant.
When plotted in this fashion, the data from almost all parvocellular LGN cells demonstrate spatially opponent luminance responses (second and fourth quadrants) and spatially non-opponent single-cone response (first and third quadrants; Reid and Shapley, 1992). In the present study, almost 1/3 of the cortical cells fall in the first and third (spatially non-opponent) quadrants in the plot of luminance response strengths (fig. 9D). Most of these were type II cells. Perhaps more interestingly, many cells were center/surround opponent when mapped with cone-isolating stimuli (fig. 9A-C), which almost is never seen in the LGN (Reid and Shapley, 1992). In our sample of cortical cells, this center/surround opponency for a single cone type was seen typically in modified type II cells and in double-opponent cells. Most modified type II cells were opponent for one cone class (3/4 double-opponent: Livingstone and Hubel, 1984) and the double-opponent cells for two or three cone classes.

**Figure 10. Linearity of chromatic summation near here.**

In order to examine the degree to which these receptive fields add up their chromatic influences linearly, we compared the luminance responses of these cells with the prediction from the cone-isolating responses (L+M+S). If all cells added their input linearly, the points in the scatter plot would fall along the line of unit slope. A similar comparison has been done for parvocellular geniculate cells (Reid and Shapley, personal communication). For the parvocellular receptive-field centers, chromatic summation was found to be quite linear: the slope of the scatter plot was 0.75 and the correlation coefficient was 0.96. The surrounds in the LGN were less linear: the slope was 0.40 and correlation coefficient 0.72. In the cortex, chromatic inputs to both center and surround summed less linearly. The luminance responses of receptive-field centers were correlated with the L+M+S prediction (r=0.60), but the slope was quite low 0.35 (fig. 10A). In the surround, the two values were related, but the slope was only 0.06 and the correlation coefficient r=0.20 (fig. 10B).
In summary, the measured luminance responses in most cases were qualitatively predicted by the cone-isolated responses (the sign, on versus off, was correct), but the amplitudes were poorly predicted. Because of well-matched opponent inputs from two or often all three cone types, the sum of these inputs (the linear predictions) was always smaller than the individual chromatic responses seen to cone-isolating stimuli. The actually observed luminance responses, however, were even smaller than the prediction. It appears that these neurons employ both linear (additive) and nonlinear mechanisms to ensure that the responses to luminance stimuli are smaller than the responses to the optimal range of chromatic stimuli.

Responses to achromatic, luminance-modulated stimuli in the center were quite weak, the result of both linear and nonlinear mechanisms. The antagonistic cone inputs to most cells were well balanced; that is, the sum of the cone-strengths was usually close to zero. If cone signals were simply added, then this sum would predict the response to a luminance-modulated stimulus. In fact, the actual responses to achromatic stimuli were consistently smaller than the linear prediction from the cone-isolating stimuli (fig. 10). This finding is somewhat at odds with the finding of Lennie et al. (1990), who reported that chromatic integrating in most cortical neurons was linear (although the six cells in their study that ‘showed unusually sharp chromatic selectivity’, Lennie et al., 1990: figure 10) may be equivalent to those we have studied). This discrepancy may be related to the difference in laminar sampling between the two studies. The present study was directed specifically towards unoriented, color-selective cells in the supragranular layers, while most of the color-selective cells in the study of Lennie et al. were in layers 4Cβ and 4A. Derrington et al. (1984) found linear chromatic integration in the LGN, as did Reid and Shapley (1992, 2002) in a study using similar methods to the present study. Because layer 4Cβ and 4A neurons receive a dense projection from parvocellular geniculate afferents, it might be expected that they would integrate their chromatic inputs in a more linear fashion than neurons in layers 2+3, which receive predominantly intracortical input (and a sparser input from the koniocellular layers of the LGN, reviewed in Hendry and Reid, 2000).
DISCUSSION

If these cell types can be seen as members of a hierarchy (type I, type II, double-opponent and/or modified type II), then there are representatives of all levels in this hierarchy within layer 2+3. This finding is at odds with the recent report that virtually all unoriented color-selective receptive fields in V1 (with the exception of type I cells in layer 4Cβ) are double-opponent. (Conway, 2001). One potential source of the discrepancy is that our study was performed with stimuli on a mean gray background, while Conway’s study for the most part used stimuli on strongly adapting red or green backgrounds, in order to achieve higher contrast cone-isolating stimuli.

Hubel and Wiesel (1968) described unoriented color cells in layer 4 “a very few” of which were double-opponent (p. 224-5). Later studies (Gouras, 1974; Michael, 1978) claimed a higher proportion of double-opponency among unoriented color cells, but again these cells were virtually all found in layer 4. In our study, which concentrated on layers 2+3, we found three of 37 cells with a clear double-opponent signature in their responses to the white-noise stimuli. Although our small sample size was too small to draw strong conclusions, this value is intermediate between the values found in other studies of color-selective, unoriented cells in layers 2+3 (Livingstone and Hubel, 1984: 86/133 = 65%; but see H+L 1987, p. 3381; Ts’o and Gilbert, 1988: 5/292 = 1.7%). Another recent study (Johnson et al., 2001) found a large number of cells that had spatially opponent chromatic interactions, as do DO cells, but most of these cells responded strongly to achromatic stimuli and were often oriented as well. As such, they represent a different population to those studied here.

The fraction of modified type II cells (13/40 = 32% of those mapped by hand), however, was similar to that seen by Ts’o and Gilbert (121/292 = 41%).
Color mechanisms in the receptive-field center

The color mechanisms exhibited by the centers of unoriented receptive fields were highly stereotyped (Figure 8A): all cells fell into three categories that have been well noted in both the LGN and visual cortex. The largest two groups were those that showed red-green opponency: the L-on/M-off cells (14/37) and the M-on/L-off cells (17/37). Six of the 37 cells had classical blue-yellow opponency: S-on/(L+M)-off. Unlike in the LGN, however, we found that many red-green opponent cells also received considerable input from the S cones. Most of these cells received S-on input and were quite responsive to narrow-band light at 450 or 480 nm. Lennie et al. (1990) also found a similar mixing of color axes (from the canonical red-green and blue-yellow) in their population of color-selective cells, which were primarily in layers 4 and 6 (see also Cottaris and De Valois, 1998; Conway, 2001). Qualitatively, some of these hybrid cells, particularly the (M+S)-on/L-off cells, behave quite similarly to the more standard blue-yellow cells: they show on responses to short wavelength light and off responses to longer wavelengths. We did not systematically explore the relation between the shape of the spectral response curves and the cone-isolated receptive-field measurements, but anecdotally it appeared that the mixed (M+S)-on cells retained their on response up to higher wavelengths than the S-on cells.

Color mechanisms in the receptive-field surround

While chromatic processing in the receptive-field centers can be grouped into only a few categories, mechanisms found in the receptive-field surround were more heterogeneous. Thirteen cells of the forty we plotted by hand were found to be surround suppressed, or modified type II. Ten of these cells could also be mapped with the spatiotemporal noise, cone-isolating stimuli. The cells that could not be plotted with these stimuli were profoundly suppressed by large hand-held stimuli and could only be driven on a dark background. Many of the neurons that could be mapped with white noise showed the ¾ double-opponent characteristic (Livingstone and Hubel, 1984) shown in Figure 5A: the weighting function as mapped with one cone-isolating stimulus was on-center/off-surround, but the weighting functions for the other cones were non-opponent.
It should be noted, however, that the effect of the surround in modified type II cells is two-fold: it can be transiently driven but it can also tonically suppress any response from the center. For the cell in figure 5, the surround produced transient off response—either with the noise stimulus (fig. 5A) or in the center/surround interaction experiments (fig. 5B, columns 1-3, compare top and bottom). The tonic suppression of both red-on and green-off responses by luminance in the surround (fig. 5B, bottom right), however, is an independent phenomenon that cannot be predicted from the responses to modulated stimuli. As such, it is reminiscent of other suppressive effects seen in visual cortical neurons, such as end inhibition in simple and complex cells of the cat. It should be noted that the double-opponent cells in the present study also had the signature of modified type II cells—they were tonically suppressed by luminance in the surround when tested with hand-held stimuli. The two categories need not be mutually exclusive. The surround can be transiently driven in a cone-opponent fashion (by noise stimuli on a high-luminance background), but still be tonically and nonlinearly suppressed by luminance.

**Consequences of the surround: psychophysics and downstream processing**

The surround specializations in V1—suppression in modified type II cells and double-opponency—both have direct psychophysical correlates. Double-opponent cells could certainly form a substrate of our ability to see stimuli defined by contrasting colors, and as such may play a limited role in color constancy. Color constancy, however, must include long-distance interactions within visual scenes far larger than the surrounds of V1 receptive fields (reviewed in Hurlbert, 1999; see Livingstone and Hubel, 1984; Reid and Shapley, 1988). The achromatic suppression seen in modified type II cells may be related to the psychophysical finding that colored stimuli (spectral lights) appear less saturated on light backgrounds than on dark backgrounds (Abramov et al., 1992). Another possible role of this suppression, which in some cases is quite strong, is that it could act as a gating mechanism. Because we studied responses in anesthetized animals, it is unknown whether this suppression could be modulated, for instance by attention.
It is natural to consider the subsequent stages of color processing in visual cortex, which must derive input from the V1 color cells that we have described here. To date, the spatial integration of color information by cells in visual areas V2 and V4 has not been extensively studied with quantitative cone-isolating stimuli (but see Kiper et al., 1997). Indeed given the difficulties that we encountered with V1 modified type II cells, there is some question as to how successful these methods would be. Reports of the color cells in V2 and V4, however, indicate that the trends we and others have observed in V1 continue in V2 and V4. Specifically among a class of color cells in V2 term “spot cells” (Baizer et al., 1977) or “complex unoriented” (Hubel and Livingstone, 1985, 1987), and their apparent counterparts in V4 (Schein and Desimone, 1990), there are trends towards the mixture of inputs from the two cardinal opponent channels and the increased prominence of a nonlinear suppressive surround. These trends are reminiscent of what we have described for V1 modified type II cells. In addition, these color cells of V2 and V4 have gained a “complexification” or position independence, such that a strong response from the cell may be elicited from a range of positions within the cell’s receptive field as long as the size and chromatic properties of the stimulating spot are optimal. Thus they appear to behave as if they are constructed from the summing of outputs from V1 modified type II cells collected over an area of the visual field (several degrees square for parafoveal eccentricities). This model for V4 color cells was first suggested by Schein and Desimone (1990). In the chromatic domain, several groups have also reported strong interactions between the chromatic properties of center and surround in V4 color cells, first described by Zeki (1983; see Schein and Desimone, 1990) who suggested that such long-range interactions may be important for color constancy. It remains for future studies to determine the degree to which both chromatic and achromatic interactions in the surrounds of V4 cells—whose spatial scale is larger than center-surround interactions in V1—are inherited from V1 color cells (see Wachtler et al, 1999).
REFERENCES


FIGURES

Figure 1.

A-D: Summary of mechanisms and response properties of four types of unoriented color-selective neurons. Left column (Model): diagrammatic representations of receptive fields, shown in terms of the cone inputs. Right columns (Predicted Results): expected spatial weighting functions obtained with binary noise stimuli (see Methods). On responses (+) depicted in red, off responses (-) in blue. E: (Stimuli): representations of annuli modulated by binary noise. Annuli are either luminance modulated (between black and white) or chromatically modulated between cone-isolating hues.

Model: receptive-field types shown in terms of the cone mechanisms responsible for them. A: A Type I red-on/green-off cell is diagrammed in terms of the L-on input to the center (sensitive to the bright red phase of the L-cone isolating stimulus) and M-off surround (sensitive to the dark red in the M-cone stimulus). B: Type II cell is sensitive to the same two cone types, but over a uniform central region. C: A Double-opponent cell is the same as a type II cell in the center, but to is sensitive L-off (here shown as dark green) and M-on (light green) in the surround. D: A Modified type II is the same in the center, but there is a suppressive, non-color-opponent surround: here represented as a divisive input both from the L and M cones. Type I cells are typically red-green opponent, but the three other types can also have S-cone input. For consistency, only red-green opponent cells are shown.

Predicted Results: Spatial weighting functions (receptive fields) measured with L-cone, M-cone and luminance stimuli. False color representation (as in figs. 3, 5, and 6): Red = on responses. Blue = off responses. Black: no response. Type I cells should show spatially opponent responses to a luminance stimulus, but non-opponent on or off responses to the cone-isolating stimuli (L-on center, M-off surround). Type II cells should show no spatial opponency of any kind, but are cone-opponent: L-on center, M-off center. The more balanced the cone inputs, the weaker the response to luminance stimuli. Double-opponent cells should be spatially opponent when probed with cone-isolating stimuli (L: on-center/off-surround; M: off-center/on-surround). Modified type II cells should have similar centers (L-on/M-off) but surround responses would depend on degree of linear summation: subtractive inhibition would yield off responses; divisive inhibition would yield no responses.
Figure 2.

A: Ocular dominance map of 5 by 5 mm region of visual cortex, obtained by optical imaging with a CCD camera. Border between V1 and V2 indicated at left. Map produced by subtracting images of the brain obtained during visual stimulation through left eye from images obtained during stimulation through right eye. Dark stripes (negative values in the difference map) correspond to regions dominated by the right eye; light regions (positive) were dominated by the left eye. B: Monocularity map. Dark regions are those with the largest values (positive or negative) in the ocular dominance map. This map was high-pass filtered to accentuate these regions, which have the appearance of beads on a string. Regions with strongest monocular signals are highly correlated with cytochrome oxidase blobs (Ts’o et al., 1990). C: Map of color patches (Landisman and Ts’o, 1992). Dark patches correspond to regions more active when stimulated with a red-green grating than with an achromatic grating. Electrode penetrations were targeted to regions of highest monocularity (B) and/or to color patches (C). +: Location of penetration in which modified type II cell was encountered (fig. 5).
Figure 3.

Spatial weighting functions from three neurons with green-on, red-off responses, (M+, L-). For each cell (A-C), separate spatial weighting functions are shown for L, M, and S cone stimuli, the sum of L+M+S responses, and for luminance stimuli. On responses are coded in red, off in blue. The brighter the red or blue, the stronger the response. Receptive fields in figure 3A were mapped with pixels, in 3B and 3C with concentric annuli. All three neurons (fig. 3A-C) were inhibited by the L cones, excited by the M cones, and weakly excited by the S cones to a varying degree. A and B: type I receptive fields, spatially opponent (on-center/off-surround) to luminance and chromatically opponent (M -on/L-off). C: type II receptive field, chromatically opponent but not spatially opponent.

Maps in A produced from the responses to a 16 by 16 grid of pixels modulated by binary noise (9 by 9 pixels shown). Pixel locations are outlined in black squares (0.31°). Responses smoothed by a function that falls to 10% at a distance of 1/2 pixel. Maps in B and C from experiments in which a central spot and concentric annuli were modulated by binary noise. As with the grid stimulus, the responses to the annuli are presented in the same configuration as the stimulus itself. The responses to the central 6 and 16 regions are shown, respectively, and the linear extents of the regions depicted are 1.5° and 2.0°. The responses were smoothed by less than the width of a single annulus. Responses shown for the optimal stimulus-response delay: between 67 and 100 msec (A, B), or between 33 and 67 msec (C). The weak L+M+S or Lum responses (right) were scaled relative to single-cone maps (left). A: L+M+S 1.5x; Lum 8x. B: L+M+S and Lum 4x. C: no scaling.

Figure 4.

Temporal weighting functions for receptive fields shown in Figure 3B and C. For each cell, two regions were defined: the center (thick line) and the surround (thin line, see Materials and Methods). All responses in spikes/sec · C, where C is the cone contrast of the stimulus. The fourth plot, L+M+S, is the sum of the first three. Scales on the L+M+S and luminance plots are different from those on the first three, but the interval between tick marks is constant. Each point is for a range of times between stimulus and response (sampled at the stimulus-update rate, or 33 msec; short tick marks). Time labels (long tick marks) are interpolated with respect to the data points (short tick marks). For instance, 0 msec is between the [-33,0] msec bin and the [0,33] msec bin.
Figure 5.

Responses of a modified type II neuron to two stimulus protocols. A: Spatial weighting functions of the responses the cone-isolating binary noise stimuli. The L-cone response was on-center/off-surround. Both the M-cone and the luminance responses were off over entire extent of the receptive field. The neuron was weakly off to the S-cone stimulus. The predicted luminance response (L+M+S) was distinctly on center, the very weak luminance response (shown at 8x scale) was not; thus this neuron exhibited non-linear chromatic interactions. Responses to 8 concentric regions are shown (1.25° total diameter). All responses shown at the same scale.

B: post-stimulus-time histograms (PSTHs) for the same modified type II cell's responses to a variety of square-wave modulated stimuli. Each stimulus (diagrammed above each PSTH) consisted of a spot, equal in extent to the central two regions in the noise stimulus, and an annulus five times wider. Center and surround regions were each modulated between two stimulus values once per second. Ten of the 72 total pairings in the protocol (see text) are illustrated. Columns 1-4 correspond to an in-phase and anti-phase pairing of spot and annulus stimuli. For instance, the second column was for an L-cone-isolating center and a luminance-modulated surround. On top, the bright phase of the spot and the annulus occurred simultaneously (in phase); on the bottom, spot and annulus modulated in anti-phase. This neuron responded most vigorously (arrows) only when the central spot was red, either L-on (column 2) or M-off (column 3), but only when the surround was also black. All other red centers evoked weak responses or none at all (asterisks). All four pairings that would be optimal for double-opponent cells, red-center/green-surround, were ineffective (column 4, double asterisk; other three pairings not shown, see text). When the surround was constant (column 5), the M-off responses were much stronger on a black background than on a mean gray background. The neuron also responded to the full-field luminance-off stimulus (column 1), and S-off on black (not shown). All other stimulus pairings were completely ineffective.
Figure 6.

Two examples of cells with strong S-cone input, mapped with the annular noise stimuli. Conventions as in Figure 3. A: (L+M)-off/S-on type I neuron. The off input from the M cones is localized to a smaller region than the L-off input. S-on input is over a larger region than L- or M-off, and is responsible for the on surround in the predicted luminance response: L+M+S. The luminance response is also off-center/on-surround. B: (S+M)-on/L-off cell double-opponent cell. Both the L-cone and the S-cone receptive fields are center/surround opponent, as is the luminance response (shown at 2x scale). In both A and B, the responses to 8 concentric regions are shown, which corresponds to a total of 2.0° in diameter.

Figure 7.

Histograms of the normalized weights of the cone inputs to the receptive-field centers in the population of 37 color-selective cells (C_L, C_M, and C_S). The absolute values of these weights add up to 1.0 (see text). Negative percentages correspond to off inputs from a given cone class. Separate histograms are shown for the L, M, and S-cone weights. Note that the abscissas for the L and M-cone plots range from -100% to 100% while the S-cone abscissa ranges from -40% to +44%
Figure 8.

Scatter plots of the relation between the L and M cone weights in the center (A) and surround (B) of 37 color-selective cells (C_L and C_M, from data shown in fig. 7). The S-cone weights can be inferred from the distance from the diagonal lines, |C_L| + |C_M| = 1.0. The receptive-field types, classified by the cone weights of the center mechanism, are specified by the color symbols. The colors approximate the cone-isolating stimuli that best excited the receptive-field centers. For cells with S-cone weights greater than +/- 8%, the signature of the S-cone input is given by the color of the symbol border: blue-purple for S-on input, yellow for S-off input. Other symbols are as specified in the legend.
Figure 9.

Scatter plots of the response strengths in surround versus center of all receptive fields studied. Separate plots are given for L, M, S, and luminance measurements performed on all cells. For points in the first and third quadrants (I, III), the receptive-field map is non-opponent (the signature, *on* or *off*, of the center and surround are the same). In the second or fourth quadrants (II, IV), receptive fields are opponent center/surround. Cell classifications and symbols as in Figure 8. Most points in the luminance plot are in the second and fourth (opponent) quadrants, but a significant proportion (mostly type II) are in the first and third. Most points in the single-cone plots (L, M and S) are in the first and third (opponent) quadrants, but a significant proportion (mostly modified type II and double-opponent) are in the second and fourth. Units: spikes/sec · C, where C is the cone contrast of the stimulus. Note that the scales are different, because the L and M response strengths are stronger than the others.
Figure 10.

Scatter plots of the measured luminance response strengths versus the predicted responses (L+M+S, assuming linear chromatic summation). Separate plots are shown for the receptive-field centers and surrounds. Cell classifications and symbols as in Figure 8. Although the L+M+S prediction most often gives the correct sign (on or off), the magnitude is over-estimated, particularly for the surround. If the prediction were numerically precise, a regression line through the points should have a slope of 1.0. The actual regression lines (dashed lines) have slopes of 0.35 and 0.06 for center and surround, respectively, and X-intercepts of -4.0 and 0.1. Correlation coefficients: 0.6 and 0.2. Units: spikes/sec · C, where C is the cone contrast of the stimulus.
<table>
<thead>
<tr>
<th>Model</th>
<th>Predicted Results</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Type I</strong></td>
<td><img src="image1" alt="Predicted Results" /></td>
</tr>
<tr>
<td><strong>Type II</strong></td>
<td><img src="image2" alt="Predicted Results" /></td>
</tr>
<tr>
<td><strong>Double-Opponent</strong></td>
<td><img src="image3" alt="Predicted Results" /></td>
</tr>
<tr>
<td><strong>Modified Type II</strong></td>
<td><img src="image4" alt="Predicted Results" /></td>
</tr>
<tr>
<td><strong>Stimuli</strong></td>
<td><img src="image5" alt="Stimuli" /></td>
</tr>
</tbody>
</table>

Reid and Ts'o Figure 1
Reid and Ts'0 Figure 2
Reid and Ts'o Figure 3

A

<table>
<thead>
<tr>
<th>L Cone</th>
<th>M Cone</th>
<th>S Cone</th>
<th>L+M+S</th>
<th>Lum</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.png" alt="Image A" /></td>
<td><img src="image2.png" alt="Image A" /></td>
<td><img src="image3.png" alt="Image A" /></td>
<td><img src="image4.png" alt="Image A" /></td>
<td><img src="image5.png" alt="Image A" /></td>
</tr>
</tbody>
</table>

M-on/L-off Type I (pixels) 67-100 msec

B

<table>
<thead>
<tr>
<th>L Cone</th>
<th>M Cone</th>
<th>S Cone</th>
<th>L+M+S</th>
<th>Lum</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.png" alt="Image B" /></td>
<td><img src="image2.png" alt="Image B" /></td>
<td><img src="image3.png" alt="Image B" /></td>
<td><img src="image4.png" alt="Image B" /></td>
<td><img src="image5.png" alt="Image B" /></td>
</tr>
</tbody>
</table>

M(+S)-on /L-off Type I (annuli) 67-100 msec

C

<table>
<thead>
<tr>
<th>L Cone</th>
<th>M Cone</th>
<th>S Cone</th>
<th>L+M+S</th>
<th>Lum</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.png" alt="Image C" /></td>
<td><img src="image2.png" alt="Image C" /></td>
<td><img src="image3.png" alt="Image C" /></td>
<td><img src="image4.png" alt="Image C" /></td>
<td><img src="image5.png" alt="Image C" /></td>
</tr>
</tbody>
</table>

L-off/M-on Type II (annuli) 33-67 msec

Reid and Ts'o Figure 4

A

<table>
<thead>
<tr>
<th>L Cone</th>
<th>M Cone</th>
<th>S Cone</th>
<th>L+M+S</th>
<th>Lum</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.png" alt="Image A" /></td>
<td><img src="image2.png" alt="Image A" /></td>
<td><img src="image3.png" alt="Image A" /></td>
<td><img src="image4.png" alt="Image A" /></td>
<td><img src="image5.png" alt="Image A" /></td>
</tr>
</tbody>
</table>

M(+S)-on/L-off Type I

B

<table>
<thead>
<tr>
<th>L Cone</th>
<th>M Cone</th>
<th>S Cone</th>
<th>L+M+S</th>
<th>Lum</th>
</tr>
</thead>
<tbody>
<tr>
<td><img src="image1.png" alt="Image B" /></td>
<td><img src="image2.png" alt="Image B" /></td>
<td><img src="image3.png" alt="Image B" /></td>
<td><img src="image4.png" alt="Image B" /></td>
<td><img src="image5.png" alt="Image B" /></td>
</tr>
</tbody>
</table>

L-off/M-on Type II
Reid and Ts'o Figure 5
**Reid and Ts'o Figure 6**

(A) L Cone  M Cone  S Cone  L+M+S  Lum

(L+M)- off/S-on Type I  67-100 msec

(B) (S+M)-on/L-off Double-Opponent  67-100 msec

**Reid and Ts'o Figure 7**

(A) Number of Cells

Percentage on or off L-cone responses

(B) Number of Cells

Percentage on or off M-cone responses

(C) Number of Cells

Percentage on or off S-cone responses

Percentage on or off L-cone responses
Reid and Ts'o Figure 8
Reid and Ts'o Figure 9
Reid and Ts'o Figure 10