

SPATIAL MAPPING OF MONKEY V1 CELLS WITH PURE COLOR AND LUMINANCE STIMULI

LISA G. THORELL*, RUSSELL L. DE VALOIS and DUANE G. ALBRECHT†
Department of Psychology, University of California, Berkeley, CA 94720, U.S.A.

(Received 14 November 1983)

Abstract—We recorded the responses of single macaque striate cortical cells to color-varying and luminance-varying patterns. We show that (a) the vast majority of primate striate cells respond to pure color stimuli, in addition to responding to luminance-varying stimuli (b) in general, simple cells are color-selective whereas complex cells respond to multiple color regions, (c) most cortical cells show bandpass spatial frequency tuning to pure color-varying gratings, with various cells tuned to each of a wide range of spatial frequencies and (d) the peak spatial frequency and bandwidth of most striate cells is the same for color as for luminance-varying gratings; when they differ, cells tend to be more broadly tuned and peak at lower spatial frequencies for color (e) complex cells, on the average, respond to higher spatial frequencies than do simple cells.

Striate cortex Color vision Spatial frequency Receptive fields Macaque

INTRODUCTION

A major problem in pattern recognition is the relationship between luminance and color information in the form-analyzing mechanisms of the visual cortex. For example, is there any evidence that the visual system can use color for analyzing form? Anyone who has seen the figures in the Ishihara color plates can attest to the perception of such pure color spatial patterns. It follows that, at some level in the visual pathway, spatial mechanisms must exist which abstract these figures composed of purely chromatic differences. In this study, we sought to determine whether the finely tuned spatial preferences for luminance patterns which have been demonstrated for cortical cells exist for pure color patterns as well.

Let us assume that there are color-selective spatial mechanisms: what is the spatial sensitivity of these mechanisms and how does it compare with the luminance-sensitive spatial mechanism? A number of psychophysical experiments have addressed this question by quantitatively measuring the visual threshold for spatial sinusoidal grating patterns modulated in either luminance or chromaticity (van der Horst and Bouman, 1969; Granger, 1973; Granger and Heurteley, 1973; Watanabe *et al.*, 1976). These reports all concur that the visual system possesses low pass tuning for color-varying gratings and bandpass tuning for luminance-varying gratings. Consistent with these psychophysical findings, single cell recordings in the dorsal lateral geniculate nucleus (LGN) (De Valois and Pease, 1971; De Valois *et al.*, 1977) have shown that color information is processed spatially in a quite different way from luminance information: the same LGN cell will tend to have low pass tuning

to color spatial patterns and bandpass tuning to luminance stimuli (von Blanckensee, 1980). In general, these cells respond best to large field (or low spatial frequency) pure color variations and finer gradations (or medium to high spatial frequency) luminance variations.

We have addressed four principal questions: first, what proportion of the units in V1 (area 17) are color cells? Although there have now been a number of investigations of the spectral properties of visual cortical cells, the results are conflicting. The diverse criteria employed in identifying and categorizing color cells have produced a variety of different estimates of the number as well as the types of color cells present at all levels of the pathway thus far examined. One of the more perplexing aspects is the low percentage of color cells reported in the initial cortical studies (Hubel and Wiesel, 1968). Such a low proportion seems very curious because the principal input to striate cortex is via the dorsal lateral geniculate nucleus (LGN), where the vast majority of cells are, in fact, color-sensitive (De Valois and Jones, 1961; De Valois *et al.*, 1966; Wiesel and Hubel, 1966; Padmos and van Norren, 1975).

Secondly, we asked, what types of color cells are present? Since Hubel and Wiesel's pioneering studies (1968) it has been apparent that there are essentially two major functional cell classes in monkey V1 (striate cortex): simple cells, which only respond to spatial patterns placed in certain positions within their receptive fields (RFs) and complex cells, which respond to spatial patterns independent of their positions with respect to the RFs. More recently it has been reported that these cell types also differ in their grating response characteristics (Schiller *et al.*, 1976) and linearity of spatial summation (De Valois *et al.*, 1982). In sum, it seems these cell types carry two distinct transforms of the visual image. We

Present addresses: *2131 Hearst St. Apt 8, Berkeley, CA 94709 and †Department of Psychology, University of Texas, Austin, TX 78712, U.S.A.

wondered if these distinctions existed for the cells' responses to pure color stimuli as well. In particular, we wondered how many V1 cells retained the simple color opponency established at earlier levels and how many (if any) possessed new spectral response properties? Furthermore, while two distinct populations of color opponent cells have been identified in monkey LGN, red-green and yellow-blue types, (De Valois *et al.*, 1966; Lennie *et al.*, 1982), recent studies suggest the existence of only a red-green opponent organization at the cortex (Michael, 1978a, b, c, 1979). This too seems curious since at least some cells in higher cortical regions, whose principal input is from V1, are reported to possess yellow or blue color preferences (van Essen and Zeki, 1978; Schein *et al.*, 1982.)

Thirdly, what is the relation, if any, between the luminance and color processing of V1 cells? Specifically, are these two forms of information carried by two quite different cell populations, as some reports have suggested (Dow, 1974; Michael, 1978, 1979, 1981)? Or are color and luminance information mainly processed by the same cells, as appears to be true at earlier levels of the pathway (Pease, 1975; De Valois *et al.*, 1977)?

Fourthly, what is the relation between the spatial tuning for luminance and color variations? LGN cells show low pass tuning for color. Do cortical cells show bandpass tuning for color patterns as they show for luminance-varying patterns? In other words, are there multiple spatial frequency channels for processing color variations?

A brief report of these findings has been presented elsewhere (Thorell *et al.*, 1978, 1979).

METHODS

Three adolescent Old World monkeys (*Macaca fascicularis*) were used in this study; each animal was run several times giving a total of 31 electrode penetrations: 165 cells were examined from the foveal representation of V1; 51 cells were examined from parafoveal regions (2-5 deg).

1. Stimulus display and calibration

Visual stimuli were generated by a Nova 1220 computer and presented on a Tektronix 654 color television monitor. There were independent inputs to the red (R), green (G) and blue (B) phosphors, whose CIE chromaticity coordinates were (0.645, 0.330), (0.290, 0.600) and (0.150, 0.065), respectively. Reference white for the monitor was factory set to match Illuminant D (approx. 6500 K).

An essential task of this investigation was to distinguish between responses to luminance-varying and color varying stimuli. Thus prior to the experiment color stimuli were equated for luminance by flicker photometry using trained human observers. In the flicker photometric procedure we alternated the separate color phosphors [and combinations of

B + G (cyan), R + B (magenta) and R + G (yellow)] against the fixed 8 ft-L standard white at a 10 Hz rate. Since our intent was to produce equiluminant stimuli for macaques, the measurements were made by an observer whose values provided nearly an identical match to those previously measured on adolescent macaque monkeys (De Valois *et al.*, 1974). Great care was taken to maintain these calibrations.

In addition to black, white, and equiluminant colored bars of various widths, we also used sinusoidal grating patterns. The patterns were drifted across the screen at any desired spatial frequency, temporal frequency and orientation. The mean luminance of both pure color-varying and pure luminance-varying gratings was 16 ft-L. It was also possible to delimit the grating patterns in both the X- and Y-axes to present just a certain number of cycles of a particular length. Color gratings were produced by feeding patterns into the color guns out of phase. For instance, a red-green sine wave grating was produced by feeding a sine wave 180 deg out of phase to the red and green guns. This produced a modulation along the R and G phosphor loci with the voltages so chosen as to maintain equal luminance. The color gratings employed in these experiments were red-green, red-cyan, yellow-blue, blue-green and purple-green.

The oscilloscope was viewed by the animal through a circular aperture in a large white screen. The scope display subtended 6 deg at the viewing distance of 172 cm.

2. Experimental procedure

A week before the first recording experiment, the animal was prepared for chronic neurophysiological recording under deep barbituate anesthesia (sodium pentobarbital, 35 mg/kg/hr). A performed "occipital bonnet" was attached to the animal's skull with screws and dental cement. The animal was then given penicillin (200,000 units, intramuscular) and returned to its cage. On the day of the experiment the monkey was first anesthetized with an injection of a short-acting barbituate (sodium thiamylal, 20 mg/kg) and then transferred to 75% NO₂, 25% O₂ for the duration of the experiment. The animal's body was positioned as comfortably as possible on a rubber pad and the head held by the bonnet. (We therefore did not need to use ear bars.) The animal showed no physiological signs of stress. The animal's head was held in a gimbal arrangement to enable centering of the receptive field of a cell on the stimulus display. We monitored continuously and kept within normal limits the EKG, rectal temperature (37 C) and expired CO₂. The animal was intubated with an endotracheal tube (coated with a local anesthetic, Zylcaine) and artificially respired. At this point a continuous infusion of gallamine triethiodide (Flaxedil 10 mg/kg/hr) and supplemental D-tubo curarine (0.05 mg/kg/hr) in a glucose saline solution minimized eye movements.

The pupils were dilated and accommodation relaxed by applying cyclopentate hydrochloride (Cyclogyl). The corneas were fitted with contact lenses of the appropriate curvature having a 3 mm artificial pupil. The animal was refracted and the appropriate corrective lenses placed before each eye to bring the stimuli in focus on the retinae.

Single units were isolated with glass-coated platinum-iridium microelectrodes whose tips were electrolytically etched to 0.5–1.6 μm in diameter and were exposed for 5–8 μm behind the tip. Extracellular unit activity was amplified and discriminated by conventional means.

To minimize sampling biases, an exhaustive attempt was made to examine every cell encountered. Since cortical cells are notoriously quiescent, we designed a search program which presented drifting gratings and bars whose color as well as spatial, temporal and orientation properties could be controlled manually.

The general paradigm was as follows: once a cell's receptive field (RF) had been located, the optimal stimulus values for that cell were determined: the preferred eye, and the best orientation, direction of movement, spatial frequency and temporal frequency. We obtained some preliminary measures of each cell's RF structure by flashing stationary bright and dark bars at different positions across the field. Cells could thereby be classified as simple or complex, using Hubel and Wiesel's original definitions (1959, 1962, 1968). Our cortical population also included "concentric" and "hypercomplex" RF types. However, based on the results of Gilbert (1977) and De Valois *et al.* (1982), we treat these two cell types as subsets of the major classes of simple and complex RFs. These subsets did not show any different color or spatial frequency preferences from the major classes.

Quantitative response profiles (RF maps) were measured using both achromatic luminance increments and decrements (black and white bars), as well as color bars presented on an equiluminant complementary color background. The computer flashed each black or white bar repeatedly at 9–11 randomly presented locations across the RF. The chromatic RF map was obtained in a similar manner, but in this case a color bar repeatedly replaced a contrasting color background, with no change in luminance. Prior to each RF mapping (and spectral response test), a pre-stimulus bar positioned on the RF center checked whether the eyes had moved.

The stimuli we used to test color responsiveness were produced by shifting from a steady background to an equiluminant bar of a different color presented on the same background. In different experiments, two types of color step were used. For most cells, a color change from a neutral background was used (e.g. gray to red) as well as a color change from one spectral region to its complement (e.g. red to green, yellow to blue, etc.). The color bars and their domi-

nant wavelengths were orangish-red (610 nm), yellow (578 nm), green (547 nm), cyan (495 nm), blue (465 nm) and purple (518 nm). These nominal wavelength values were verified by matching each color against a calibrated monochromator. In addition, bars composed of achromatic luminance increments or decrements were presented on the gray background. The contrast of the black or white bars varied from 1 to 60%. In some cells, we also analyzed responses to color changes combined with luminance increments and decrements.

In all experiments, each test bar was flashed on for 1 sec and repeated 5 times at each position. Where possible, this procedure was repeated several times. For the few cells which would not respond to flashed stationary stimuli, the test bars were moved back and forth across the RF at a constant optimal rate.

Spatial tuning was measured by drifting luminance-varying or color-varying gratings of different spatial frequencies. Spatial frequencies varying from 0 c/deg (full field sinusoidal flicker) to 22 c/deg (in equal logarithmic intervals) were presented; the drift rate was held constant at the optimal temporal frequency for the cell under test. These gratings were presented at each of 2–8 different contrast levels (56, 33, 19, 11, 6.6, 4, 2.4 and 1.4%) in order to determine the sensitivity to color and luminance contrast. The color responses of cells with high luminance contrast sensitivity (cells which might respond to very slight luminance mismatches) were verified by other procedures (e.g. by the luminance masking experiment, and/or by differentiating color from luminance responses on the basis of different spatial preferences, like the cells shown in Figs 12(B) and 15).

After several recording sessions, the animal was sacrificed and the recording sites were determined from histological examination of the electrode tracks in relation to the V1–V2 border and the retinotopic map of Talbot and Marshall (1941). All electrode penetrations were within the foveal and parafoveal representations in V1. Some 52% of the 16 31 penetrations were made in the foveal position. The remaining tracks were medial and posterior to the foveal representation.

3. Data analysis

Analysis of each cell's peri-stimulus time histogram (PSTH) to the stationary and moving bars was computed and printed out on line. The PSTH was collected under computer control by summing spikes into 5 msec time bins and then averaging over 5 repetitions. For stationary bar patterns, the total number of spikes during the stimulus and for equal intervals (1 sec) before and after stimulus presentation were averaged over the repeated stimulus presentations. For moving bar patterns, the total number of spikes was counted for each traverse, over and back, across the RF and each averaged over the stimulus repetitions.

For gratings, the PSTH was collected by summing spikes into 5 msec time bins and then averaging over the 20 temporal cycles. From these data a harmonic Fourier analysis was computed relative to the fundamental temporal frequency of the grating's amplitude (or chromaticity) modulation. This analysis yielded the average firing rate (D.C.) and the amplitude and phase of each of the first five harmonics. The amplitude of the major component (the D.C., 1st or 2nd harmonic) was used as the response measure.

RESULTS

1. Cell classification

In order to assess the relative responsiveness to luminance and color, we performed the following experiment: a narrow bar was centered on the RF and flashed on and off. First, the luminance contrast of the bar was varied, that is, the responses to white bars and black bars were recorded. Then, a series of identical isoluminant bars of various wavelengths were presented. In order to compare the cell responses to color and luminance variations, despite their being along different physical dimensions, we defined color contrast with respect to percentage of maximum distance within CIE space. Therefore a 100% color contrast was defined as the maximum excursion from a spectral color (e.g. 610 nm) to its spectral complement (e.g. 495 nm) and was thus considered equivalent to a 100% luminance contrast. With respect to this maximum, our color stimuli on a neutral background were equivalent to approx. a 33% (mean to peak) color contrast. We therefore compared the color responses to the responses to a 33% luminance contrast.

To quantify the relative responsiveness of cells to our color-varying and luminance-varying stimuli, we took the maximum excitatory response to a 33% luminance contrast (L_{max}) and the maximum excitatory response to our 33% pure color contrast (C_{max}) and computed the following ratio: $C_{max} - L_{max} / C_{max} + L_{max}$. If a cell responds only to color, then the index will equal +1.0. If a cell responds only to luminance contrast, the index will equal -1.0. Obviously, if a cell responds equally to both luminance and color contrast, the index will equal zero.

The distribution of the color response index for all cells is shown in Fig. 1. Dividing the abscissa into three equal parts, we can say that the majority of cortical cells (53%) responded equally well to both color and luminance, while 26% of the cells preferred color stimuli and 21% preferred achromatic stimuli. The latter type are undoubtedly the "luminance sensitive" cells reported by previous studies (Hubel and Wiesel, 1968; Michael, 1978a, b, c; 1979).

For a subsample of our cortical population we also checked the color responses in the presence of luminance increments and decrements. For instance, a 30% luminance contrast would be added to (or

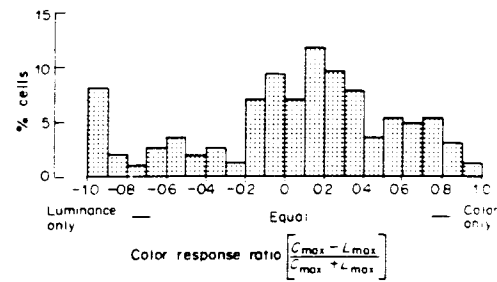


Fig. 1. Distribution of the color response index for the entire population of cortical cells.

subtracted from) the color test bars. The question here was the extent to which a cell's spectral response was maintained in the presence of luminance changes, that is, whether or not the presence of luminance change would mask the response to color. This is an important test because, in the real world, there are both color and luminance variations. Any cell whose color responses could be "masked" by a small luminance change would not serve as a very good color cell.

Of the 50 cortical cells so tested, 30 (76%) showed essentially invariant spectral response characteristics in the presence of a luminance change and 12 showed variable spectral behavior, in which the color response was eliminated by the presence of luminance contrast in the stimulus. Figures 2(a) and 2(b) present data for two cells which showed color responses which were invariant or variant with luminance. The cell in Fig. 2(a) excited to red and inhibited to shorter wavelength bars. When a 30% luminance increment was superimposed on the color bars, the spectral response remained essentially unchanged. In contrast, the color opponent behavior of the cell shown in Fig. 2(b) was eliminated by adding a luminance increment to the bars. Those few cells in which color responses were masked by concurrent luminance variations were also predominantly (10/12) cells which preferred luminance contrast by our conventional measures (i.e. the color-luminance response ratio was less than -0.33).

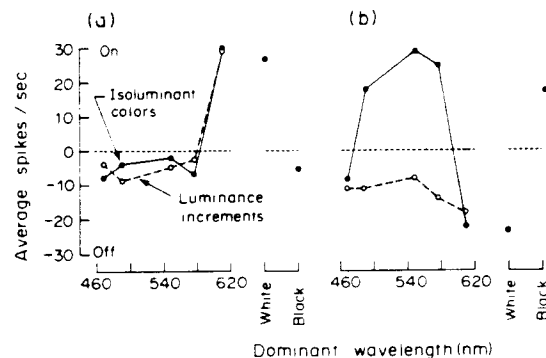


Fig. 2. The spectral response functions of two cortical simple cells tested with pure color bars (solid circles to the left), 33% contrast achromatic bars (solid circles to the right) and their combination (open circles). Data points plotted above the dotted line indicate excitation and data points plotted below indicate off-responses.

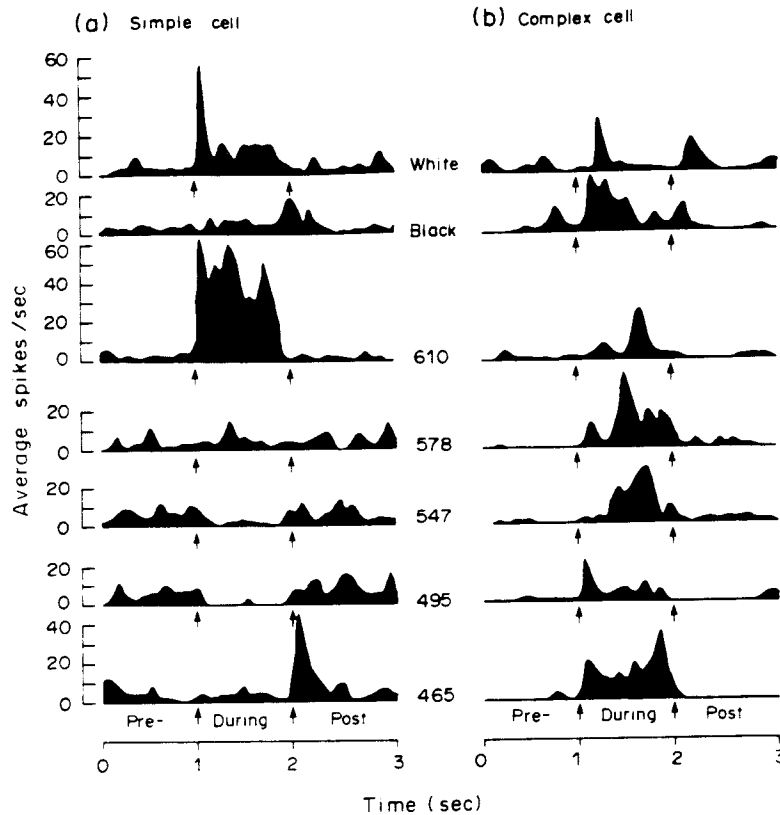


Fig. 3. Examples of the spectral response behavior of a simple cortical cell (a) 21 and a complex cortical cell (b). The PSTH represents the smoothed average response to a stationary color bar flashed repeatedly on the center of the RF. The dominant wavelength of the test bar is shown in the central strip. Arrows indicate the onset of the during and post-stimulus periods.

If we were to adopt a conservative interpretation of these results, we would conclude that the majority of cells preferring luminance contrast are not very responsive to color. If, based on the correspondence between our luminance control experiment and the poor color response index, we completely discount as color cells those which respond preferentially to luminance changes, we would nonetheless conclude that at least 79% ($53 + 26\%$) of our population were bonafide color cells. One might note in passing that this percentage is quite similar to the percentage of color cells reported for the LGN (De Valois *et al.*, 1966; Wiesel and Hubel, 1966). If one were to take a lower criterion for a color cell, such as Padmos and van Norren (1975) and others (De Monasterio *et al.*, 1975a, b, c) have argued that one should take at lower levels, more than 90% of cortical cells should be considered color-responsive cells.

Next, we sought to define the number of functional types of color cells which exist in striate cortex. The responses of a simple and of a complex cell to our equiluminant color stimuli are shown in Figs 3(a) and (b), respectively. The most important feature to note is that both cells responded to pure luminance-varying bars and to pure color-varying bars. However, the manner of response is quite different for these two forms of cortical cell. By definition, the simple cell shown in Fig. 3(a) is selective for contrast

sign: it excites to a white bar and gives a small off-response to a black bar. Conversely, the complex cell is not selective for the sign of the bar's contrast: the cell gives "on" and "off" responses during presentation of both the white and black bars. The spectral responses of the two cells are also quite typical. The simple cell, like color cells described at earlier levels of the pathway, excites to some wavelengths and inhibits, with off-responses, to others. In contrast, the cortical complex cell shown to the right shows virtually no wavelength selectivity: rather, the cell responds robustly to all the isoluminant color changes used. (We should note again that if this cell, like a classical LGN nonopponent cell, could not discriminate color variations, it would respond to none of our color stimuli.)

The chief distinction between simple and complex cortical cells is with respect to phase selectivity. The responses of simple cells are dependent on the spatial phase of the stimulus; complex cells are phase-insensitive. Thus a simple cell will fire maximally to a black-white grating in one position; a 90° phase shift will reduce the response to zero. To a pattern shifted 180° from the position of maximal response, in which the black bars are where the white bars were before and vice versa, the simple cell will be maximally inhibited (Movshon *et al.*, 1978; De Valois *et al.*, 1982). A complex cell, on the other hand, will fire

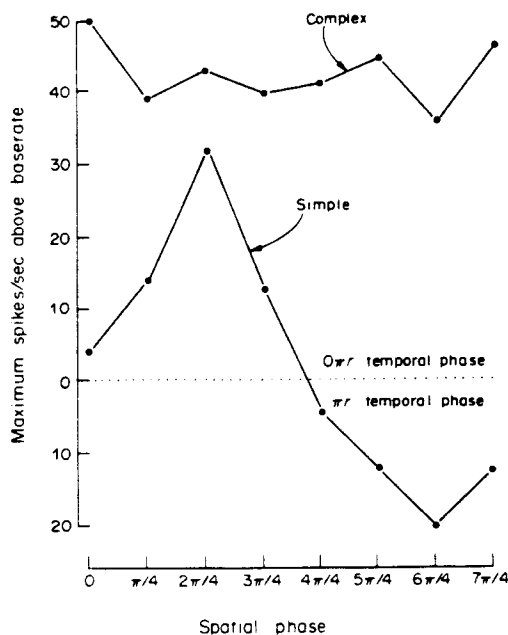


Fig. 4. Spatial phase functions of a simple and complex cell. The abscissa marks the spatial phase of a stationary counterphase modulated color-varying grating. The ordinate indicates the peak response in spikes/sec. Points plotted above the line indicate that the cell's response started within the first temporal half-cycle (first 500 msec for a 1 Hz modulation); points below indicate that the cell's response started during the second temporal half-cycle (second 500 msec for a 1 Hz modulation).

(often with equal vigor) to a stimulus in any phase (De Valois *et al.*, 1982). This same distinction can be seen in these cells' responses to flashed black and white bars: a simple cell which fires to a white bar will be inhibited by a black bar in the same location. A complex cell will fire to either a black or white bar in the same location.

The crucial point that needs to be made here is that the difference between simple and complex cells with respect to phase sensitivity applies not only to luminance-varying patterns, but to color-varying patterns as well. Consider the responses to a stationary red-green counterphase-modulated grating. Figure 4 shows the responses of a simple and complex cell to such a grating presented at different phase angles with respect to the RF. (The stimulus is essentially a chromatic version of the "null phase test" devised by Enroth-Cugell and Robson, 1966.) As can be seen, the simple cell fires best to the grating in one particular location ($2\pi/4$), in this case, when the green "bar" is on the RF center. This simple cell is unresponsive to the same red-green grating shifted 90 degrees in phase, so that the red "bar" now impinges on the RF center. At $6\pi/4$ (180 from $2\pi/4$), the simple cell fails to respond when the red "bar" is centered on the RF center (above the dotted line), but responds when the green "bar" appears in the second temporal half cycle (below the dotted line). This cell was a "double-opponent" + green-red cell much like those first described by Hubel and Wiesel (1968)

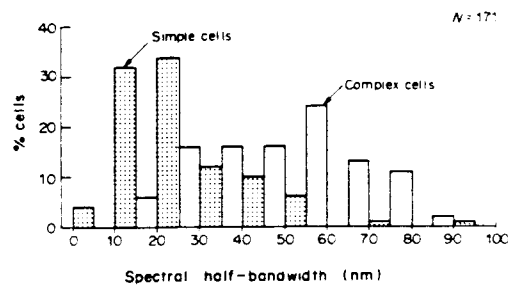


Fig. 5. Distribution of spectral half-bandwidths for all cortical color cells in our sample.

and later studied by Gouras (1974) and Michael (1978a, b).

In contrast, the complex cell responds to the red-green grating in all positions, firing to both red "bars" and green "bars" in any given location. As a consequence, the complex cell's response always began in the first temporal half-cycle (above the dotted line) since either red or green could excite the cell.

This difference between simple cells and complex color cells is also seen in the range of spectral response. Qualitatively, one can see from comparison of Fig. 3(a) and (b) that the complex cell responds over a much larger spectral range than the simple cell. Quantitatively, Fig. 5 shows the distributions of spectral response range (wavelengths eliciting responses equal to or greater than half the maximum response/2) for our cortical population responding to color. As can be seen, simple cells tend to have relatively narrower spectral tuning than complex cells. The mean spectral half-bandwidth for simple cells was 28 nm and for complex cells was 53 nm, a difference which was significant at greater than the 0.001 level. The important point here is that the distribution of spectral half-bandwidths is bimodal. Apparently, primate simple and complex cells can be distinguished not only on the basis of RF structure (Hubel and Wiesel, 1968) and response to luminance-varying gratings (De Valois *et al.*, 1982), but also on the basis of color selectivity.

2. Spatial frequency tuning to pure color and luminance gratings

Consistent with our results with bar stimuli, a substantial proportion of cells responded to both color varying and luminance-varying gratings. Further, most striate cells were selective for the spatial frequency of both luminance-varying and color-varying sinusoidal gratings; each cell had a definite preference for a narrow range of spatial frequency, giving reduced responses at higher and lower frequencies.

Figure 6 summarizes our data on the distribution of spatial frequency preferences for cells tested with luminance-varying and color-varying gratings. It is clear that for chromatic as well as achromatic patterns, cells responded to a wide range of different spatial frequency regions. Thus within a retinal locus, some cells responded as low as 0.5 c/deg and others

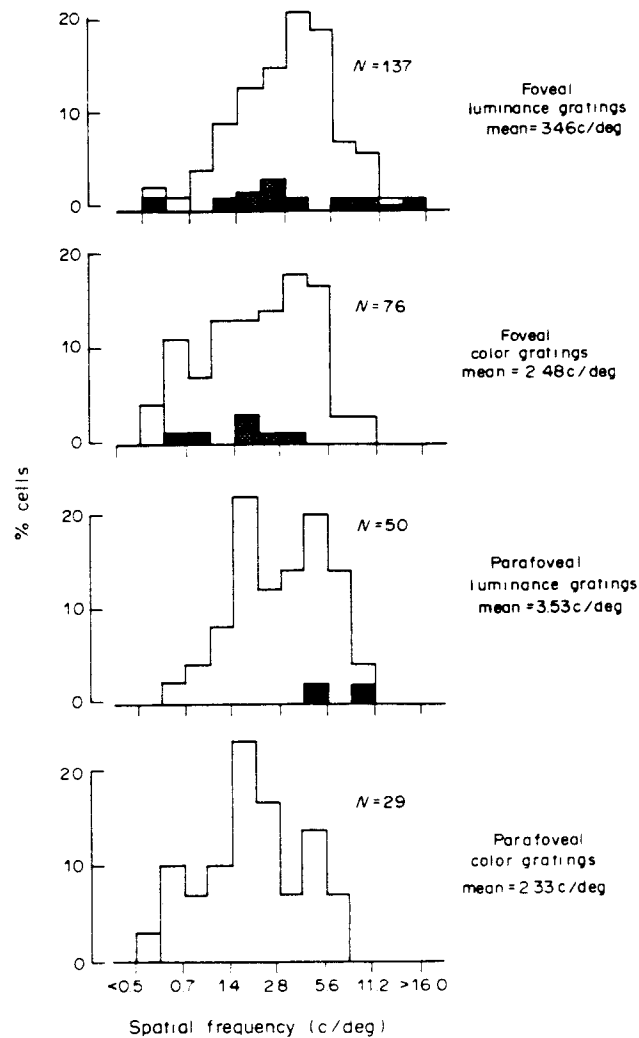


Fig. 6. Distribution of spatial frequency tuning peaks for all cortical cells tested with either luminance-varying gratings, pure color gratings or both. The frequency preferences of cells recorded in foveal cortex for achromatic and chromatic gratings are shown in the first and second histograms, respectively. Frequency preferences of cells recorded in parafoveal cortex for achromatic and chromatic gratings are shown in the two lowermost histograms. Darkened portions denote those cells responding exclusively to luminance-varying or color varying gratings.

peaked as high as 16 c/deg. Perhaps the most interesting aspect of Fig. 6 is that the frequency preferences for color gratings are shifted towards lower spatial frequencies (a trend which was apparent in both foveal and parafoveal samples). In general, we found that only a small percentage of the total cortical population responded exclusively to luminance (20%; 45/216) or exclusively to color gratings (1%; 2/216); these cells are denoted by the darkened portions of the histogram. More typically cortical cells responded to both black-white and pure color variations.

Not all cells were recorded for long enough to study their responses to both forms of information. Figure 7 summarizes our data on the distribution of optimum frequency for 110 neurons for which sensitivity measures were gathered for both types of grating modulation: the peak spatial frequency locus for each cell to luminance and chromatic spatial sine

wave gratings are plotted against each other. As indicated by the number of points scattered along the diagonal, individual cells tend to have similar spatial frequency preferences for color and luminance patterns. However, a considerable number of cells (36%) showed different spatial tuning properties for the two classes of stimuli (i.e. the spatial peaks differed by more than 0.5 octaves). As can be seen, such cells tended to prefer low spatial frequency color gratings; some cells' peak frequency differed by as much as 2 octaves. For the entire cortical population, the mean spatial frequency tuning for luminance gratings was 3.5 c/deg (SD = 2.4) and that for color gratings was 2.63 c/deg (SD = 1.82), a difference which would be expected to occur by chance less than 5 times in 100.

A second question concerns the relative narrowness of tuning shown by cells to color and luminance gratings. Figure 8 plots the spatial frequency bandwidths for the total population of cortical cells.

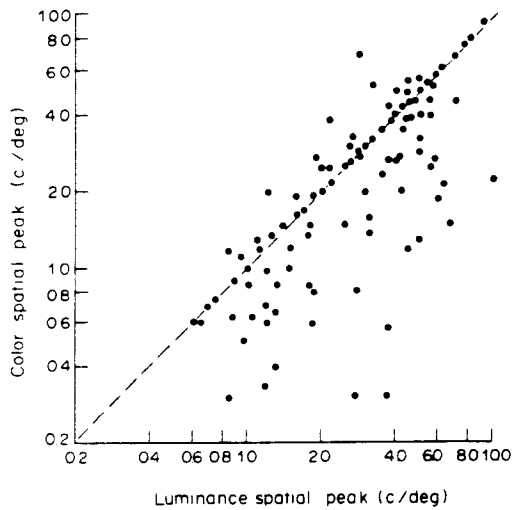


Fig. 7. Scatterplot of peak spatial frequency tuning of cells to color-modulated (Y-axis) and luminance-modulated (X-axis) sine wave gratings. The data are from cells for which both color and luminance spatial tuning functions were obtained. The diagonal indicates the iso-frequency line; cells lying along this line have identical tuning for color and luminance patterns.

(Spatial bandwidth is defined as the distance in octaves between the highest and lowest frequencies to which a cell was half as sensitive as it was to its optimum frequency.) It is clear that cortical cells show narrower spatial tuning than do LGN cells to both color and luminance gratings (see De Valois *et al.*, 1978 and von Blanckensee, 1980 for comparable LGN data). When tested with luminance-varying gratings, cortical cells show a unimodal distribution peaking at quite narrow bandwidths; with few exceptions, cortical cells possess bandpass tuning to luminance variations. In contrast, when tested with chromatic gratings, cortical cells exhibited a bimodal distribution: while some cells, like LGN cells, showed quite broad frequency tuning, a substantial number showed spatial tuning which was as narrow to color patterns as to that seen with luminance patterns.

Figure 9 plots the spatial tuning bandwidths of the same cells shown in Fig. 7. The diagonal here represents those cells which had identical bandwidths for color and luminance gratings. While for most cells the spatial tuning for color variations is the same as that for intensity variations, those cells that deviate from this in general show broader tuning to color than luminance stimuli, as evidenced by the scatter to the left of the diagonal. In the extreme, one observes a situation similar to that in the LGN where a given cell acts as a low pass filter to chromatic spatial patterns, but acts as a bandpass filter to luminance patterns: such cells doubtless make a considerable contribution to the characteristic psychophysical differences found between color and luminance spatial modulation transfer functions (MTFs): bandpass luminance sensitivity vs low-pass color sensitivity. Even if one excludes those cells with low-pass tuning, the mean color spatial bandwidth was 1.56 octaves

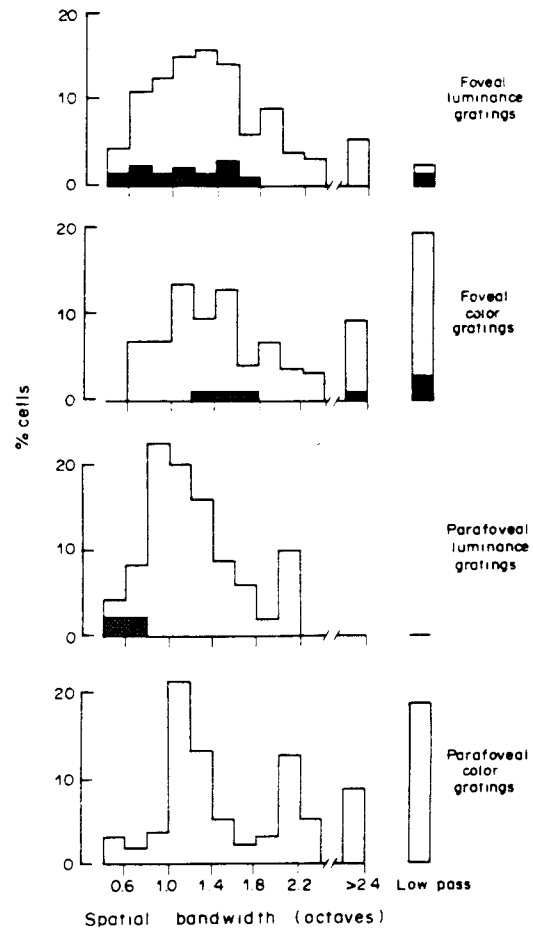


Fig. 8. Distribution of spatial bandwidths of all cortical cells tested with either luminance-varying gratings, pure color-varying gratings or both. The conventions are similar to those used in Fig. 6.

and the mean luminance spatial bandwidth was 1.34 octaves (a difference that would be expected to occur purely on the basis of chance less than two times out

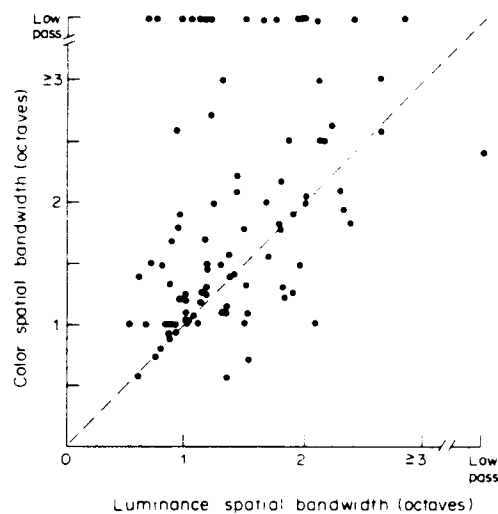


Fig. 9. Scatterplot of the spatial frequency tuning of cells to color-modulated (Y-axis) and luminance-modulated (X-axis) sine wave gratings. The values plotted are the full bandwidths in octaves measured at half-amplitude.

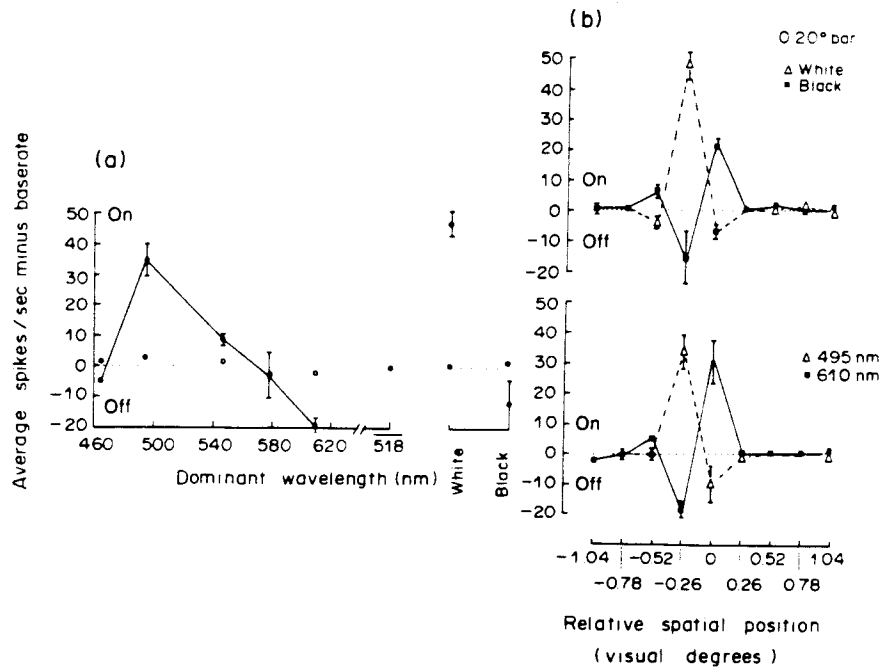


Fig. 10. Spectral response functions and RF maps for the most common type of simple cell seen in visual cortex. The spectral response functions (a) seen to the left show the average response to a variety of colored bars (solid circles) or full field stimuli (open circles) presented on an equiluminant achromatic background. The response to bright or dark achromatic bars (solid circles) and full field stimuli (open circles) is shown to the far right in (a). The RF maps of this same cell are shown in (b). The luminance RF map shows the average response to a 56% contrast white (Δ) or black (\blacksquare) bar flashed repeatedly in each of nine locations across the RF. Excitation is plotted above the dotted line; inhibition (or off-response) is plotted below the dotted line. The same conventions apply to the color RF map shown below. Note that these color stimuli are not incremental flashes, but pure color changes, e.g. the red (or cyan) bar replaces the gray field with no luminance change.

of one hundred). The spatial bandwidths of simple and complex cells were not significantly different.

3. Simple cell RFs: spatial and spectral preferences

We mapped the receptive fields with luminance-varying bars as well as with color-varying bars to compare the RF organization to luminance-varying and color-varying patterns. We obtained complete luminance and chromatic RF maps on a sample of 42 simple cells.

As described in earlier studies, the responses of simple cortical cells to bright and dark bars resembled the behavior of cells at earlier levels of the pathway, in that the cells exhibit discrete excitatory and inhibitory regions. The majority of these cells (34/42; 81%) were oriented cells, while the remainder were non-oriented concentric cells. In both cases, the optimal size of a flashed stationary bar could be qualitatively predicted from the width of the individual response zones. The overall width of the RFs (including all the excitatory and inhibitory subregions) ranged from 0.39 to 3.6 deg; the RF centers ranged from 0.10 to 2.0 deg.

The RFs of most simple cells (34/42; 81%) were divided into two or more regions of opposing color selectivity. These are what have been termed double-opponent cells (Beauchamp and Daw, 1972 in goldfish; Michael, 1973 in ground squirrel; Hubel and

Wiesel, 1968; Dow and Gouras, 1973; Michael, 1978, 1979 in monkey). The spectral response functions and RF maps of one such cell are shown in Fig. 10. To the left is plotted the average response of the cortical cell to a series of stationary flashes of various colors, each of constant luminance. Each pattern was centered on the central flank of the cell's RF: the solid points represent the responses to a narrow color bar; the open points indicate the responses to a full field color change.

Like cells described at earlier levels, the cell shown in Fig. 10 responded to both luminance-varying and color-varying information. The cell is phase-specific for luminance changes as well as for color changes: it excites to green and white and inhibits to red and black. At least in this portion of the RF, the spectral characteristics are reminiscent of +Green-Red cells found in the monkey LGN (De Valois *et al.*, 1966). However, unlike +G-R LGN cells, this cortical cell does not respond well to full field chromatic stimuli.

In other words, the responses to both luminance and color were contingent on the spatial dimensions of the stimuli. This behavior was consistent with the luminance and color RF maps measured for the same cell, shown to the right. When mapped with purely luminance-modulated bars, the cells showed discrete antagonistic subregions within its RF, arranged as an excitatory central zone with inhibitory flanks. Note