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Processing of color, form, and motion in macaque area V2

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Abstract

We investigated the representation of color in cortical area V2 of macaque monkeys, and the association of color with other stimulus attributes. We measured the selectivity of individual V2 neurons for color, motion, and form. Most neurons in V2 were orientation selective, about half of them were selective for color, and a minority of cells (about 20%) were selective for size or direction. We correlated these physiological measurements with the anatomical location of the cells with respect to the cytochrome oxidase (CO) compartments of area V2. There was a tendency for color-selective cells to be found more frequently in the thin stripes, but color-selective cells also occurred frequently in thick stripes and inter-stripes. We found no difference in the degree of color selectivity between the different CO compartments. Furthermore, there was no negative correlation between color selectivity and selectivity for other stimulus attributes. We found many cells capable of encoding information along more than one stimulus dimension, regardless of their location with respect to the CO compartments. We suggest that area V2 plays an important role in integrating information about color, motion, and form. By this integration of stimulus attributes a cue-invariant representation of the visual world might be achieved.

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

Introduction

Our visual system is confronted with an abundance of information varying along many different stimulus dimensions. At early levels of visual processing, splitting this information into separate parallel streams that project to different brain areas can help to reduce this huge computational problem, and saves processing resources and time. However, it is reasonable to assume that at some higher level information from different processing streams has to be combined again (Albright, 1992; Sary et al., 1993; Komatsu & Ideura, 1993). This requires that a representation of the complete multidimensional stimulus space is reassembled at some cortical level. We investigated the hypothesis that extrastriate cortical area V2 plays an important role in the integration of visual information from different stimulus attributes.

At the earliest stages of processing in the visual system, information is processed in two anatomically and functionally segregated streams (Leventhal et al., 1981; Perry et al., 1984; Kaplan & Shapley, 1986). At the level of the lateral geniculate nucleus (LGN), neurons in the magnocellular layers have high sensitivity for luminance contrast, are practically color-blind, and prefer low spatial and high temporal frequencies. Neurons in the parvocellular layers, on the other hand, have lower sensitivity to luminance defined stimuli, respond well to stimuli solely defined by color, and prefer lower temporal and higher spatial frequencies (for a review see Livingstone & Hubel, 1987). It has been proposed that this segregation continues in cortical area V1 and beyond, with information processed in separate streams for the analysis of form, color, and motion (Zeki, 1978; Livingstone & Hubel, 1984; DeYoe & Van Essen, 1985; Hubel & Livingstone, 1987). In area V2 in particular, the streams for the processing of motion, color, and form are assumed to correspond to the thick, thin, and inter-stripe regions, respectively, as defined by CO staining (DeYoe & Van Essen, 1985; Hubel & Livingstone, 1987). The target areas of the motion stream are MT, which is known to be of great importance for the analysis of visual motion (Newsome et al., 1985; Britten et al., 1992), and areas in the posterior parietal cortex. The target areas for the processing of color and form are V4, which contains neurons selective for wavelength (Zeki, 1978; Schein & Desimone, 1990) and form (Desimone & Schein, 1987), and areas in the infero-temporal cortex.

The empirical evidence for separate visual processing streams at cortical levels is less compelling. The major ascending projections of the retinothalamocortical magnocellular and parvocellular pathways suggest that they are separate and parallel (Hubel & Wiesel, 1972; Lund, 1973; Lund & Boothe, 1975).

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However, anatomical and lesion studies also have shown that there is a great degree of connectivity between the pathways as early as in area V1 (Lund & Boothe, 1975; Blasdel et al., 1985; Fitzpatrick et al., 1985; Lachica et al., 1992; Yoshioka et al., 1994; Nealey & Maunsell, 1994), and to an even larger degree in area V2 (Rockland, 1985; Levitt et al., 1994*b*). While there is good evidence that there is a motion stream that includes area MT and predominantly receives magnocellular input (Maunsell et al., 1990; Gegenfurtner et al., 1994*a*), area V4 receives about equally strong magnocellular and parvocellular inputs (Ferrera et al., 1994), and neurons there show a larger variety of physiological properties (Zeki, 1978; Desimone & Schein, 1987; Schein & Desimone, 1990; Cheng et al., 1994).

There is some recent evidence that area V2 might play an important role in the integration of information about different stimulus attributes. The bulk of excitatory lateral connections within area V2 are between CO compartments of *different* types that do represent the *same* region of the visual field (Levitt et al., 1994*b*). These lateral connections in V2 could therefore form the anatomical basis for the integration of visual information about different stimulus attributes. Furthermore, previous quantitative physiological studies have shown that the segregation into different processing streams in area V2 is at best incomplete (Peterhans & von der Heydt, 1993; Levitt et al., 1994*a*), as far as the basic spatiotemporal properties of cells and the representation of contours are concerned. However, these studies did not investigate the color properties of cells in great detail.

Knowledge about color properties is particularly important, since the technique of presenting stimuli at isoluminance is widely used in psychophysics as a means of isolating functional neural pathways (for a review see Shapley, 1990). While this technique presumably works very well for the retinogeniculate parvocellular and magnocellular streams, it is unclear what happens at the cortical level. Many perceptual phenomena are apparently impaired at isoluminance (for a review see Livingstone & Hubel, 1987). However, most quantitative psychophysical experiments seem to indicate that there is little impairment of perception at isoluminance, once the difference in sensitivity to luminance and isoluminance has been accounted for (DeValois & Switkes, 1983; Switkes et al., 1988; Webster et al., 1990; Krauskopf & Farell, 1991; Gegenfurtner & Kiper, 1992; Derrington & Henning, 1993; Würger & Landy, 1993; Metha et al., 1994; Hawken et al., 1994; Stromeyer et al., 1995; Gegenfurtner & Hawken, 1995). We therefore characterized the response properties of single cortical neurons in area V2 to color, form, and motion. A segregation into separate functional streams, which might or might not correspond to the anatomical division into CO compartments, should be apparent in the association between selectivities to color, form, and motion in each individual neuron.

Materials and methods

Preparation and maintenance

These experiments were performed on eight young adult *Macaca fascicularis* monkeys. Animals were initially premedicated with atropine (0.25 mg), and acepromazine maleate (PromAce: 0.05 mg/kg). After induction of anesthesia with intramuscular injections of ketamine (Vetalar:10–30 mg/kg), surgery was continued under halothane and then, after cannulation of the saphenous veins, under intravenous anesthesia with Sufentanil citrate as described below.

After cannulation of the trachea, the animal's head was fixed in a stereotaxic frame. The ear bars' tips were coated with a local anesthetic (lidocaine jelly) to alleviate pain at the stereotaxic pressure points. A small craniotomy was made over the lunate sulcus, and after making a small slit in the dura, a tungsten-in-glass microelectrode (Merrill & Ainsworth, 1972) was positioned approximately 1 mm behind the lip of the sulcus; the hole was then covered with warm agar. Action potentials were conventionally amplified and displayed; standard pulses triggered by each impulse were stored by a personal computer (resolution 250 μs) and were also fed to an audiomonitor.

On completion of surgery, animals were paralyzed to minimize eye movements. Paralysis was maintained with an infusion of vecuronium bromide (Norcuron: 0.1 mg/kg/h) in lactated Ringer's solution with dextrose (5.4 ml/h). Animals were artificially ventilated with room air or with a 49:49:2 mixture of N_2O, O_2, and CO_2. Peak expired CO_2 was maintained near 4.0% by adjusting the respirator stroke volume or the CO_2 content in the gas mixture. Rectal temperature was kept near 37°C with a thermostatically controlled heating pad. Anesthesia was maintained by continuous infusion of Sufentanil citrate. The dosage of Sufentanil citrate was between 4 and 8 microgram/kg/h, and was adjusted according to each animal's tolerance of the drug. This was accomplished before paralysis by testing the animal's reaction to noxious stimuli (pinching of the paw) and making sure that no directed motor responses could be elicited that way. After paralysis, electroencephalogram (EEG) desynchronization and alterations in cardiac rhythm following a noxious stimulus were taken as signs to increase the level of anesthesia. The EKG, EEG, and rectal temperature were monitored continuously to ensure the adequacy of anesthesia and the soundness of the animal's physiological condition. Animals also received daily injections of a broad-spectrum antibiotic (Bicillin: 300,000 units), as well as dexamethasone (Decadron: 0.5 mg/kg) to prevent cerebral edema.

The pupils were dilated and accommodation paralyzed with topical atropine, and the corneas protected with gas- permeable contact lenses; supplementary lenses were chosen that maximized the spatial resolution of the first recorded units. Lenses were removed periodically for cleaning and the eyes rinsed with saline. At the beginning of the experiment, and at regular intervals thereafter, the foveas were located and plotted using a reversible ophthalmoscope.

Anatomical methods

At the conclusion of the recording session, all animals were overdosed with 60 mg/kg sodium pentobarbital, or until complete flattening of the EEG was observed, and perfused through the heart with 4% paraformaldehyde following exsanguination with heparinized saline. The tissue blocks containing the penetrations were allowed to equilibrate in 30% sucrose. Frozen sections were cut at 40 μm in the coronal plane, and adjacent series of sections were stained for CO (Wong-Riley, 1979), NADPH diaphorase, which we have found to coincide with CO in V2 as well as V1 (Sandell, 1986; method 1), with cresyl violet, and for Cat-301. Sections processed for CO or NADPH diaphorase histochemistry were reacted free floating in the dark, with gentle agitation, at 37°C. Sections processed for Cat-301 immunocyto-

chemistry were treated free floating with 1% bovine serum albumin in phosphate-buffered saline (PBS) for 30 min to block nonspecific binding, then incubated overnight at room temperature in the antibody diluted 1:5 in PBS containing 0.03% Triton-X 100. The sections were then incubated for 2 h in biotinylated horse-anti-mouse IgG (Vector Labs, Burlingame, CA, at a dilution of 1:250), and labeled with the avidin-biotin-peroxidase complex method (Vector ABC Elite Kit) with diaminobenzidine as the chromogen.

Track reconstruction

Sections containing electrode tracks were drawn at low power using an Olympus BHS microscope equipped with a camera lucida. Adjacent sections were aligned precisely using blood vessels and the section outlines as fiducial marks. The laminar locations of the recorded units were assigned on the basis of distance from recorded gray/white matter transitions and from electrolytic lesions made during the recording sessions. Separate corrections for shrinkage were calculated for portions of V2 at the pial surface and within the lunate where necessary. If insufficient data were present to permit assignment to a layer, only designations of "superficial" and "deep" were used for the extremes of the penetration; units whose location could not be specified were omitted from laminar analyses.

The identification of thick and thin CO stripes can be quite difficult in macaques. To increase the certainty with which our assignments were made, we examined each dark stripe in two, or if possible, three adjacent CO-stained sections. NADPH diaphorase reactivity exactly coincided with CO, but was more robust in some animals; these sections were used if the CO was extremely weak or variable. The nearest sets of Cat-301 stained sections were used to assist in thick stripe identification. As described by DeYoe et al. (1990) and illustrated in Fig. 1, Cat-301 immunoreactive neurons are more numerous and darkly stained in the thick stripes, although they are clearly present in the thin stripes as well. Examination of a single Cat-301 reacted section does not provide an adequate basis for stripe compartment identification. In cases where a CO stripe could not be identified unambiguously, units located within that stripe were eliminated from the compartmental analysis.

Characterization of receptive fields

Receptive fields were initially mapped by hand on a tangent screen using black and white or colored geometric targets. When a single neuron's activity was isolated, we established the neuron's dominant eye, and occluded the other for quantitative experiments. Generally there was little difference between left and right eye. Very few neurons responded to binocular stimulation only. While it is possible that we missed some neurons that are tuned near or far for disparity, only few neurons have been reported in area V2 that do not at all respond at zero disparity (Poggio & Fischer, 1977). We first mapped the location and size of the neuron's minimum response field (Barlow et al., 1967), and then determined selectivity for the orientation, direction of motion, and size (particularly endstopping) of stimuli. After this initial qualitative characterization, we positioned the receptive field on the face of a display CRT, and quantitative experiments proceeded under control of a personal computer.

Each experiment consisted of several (generally 4–10) blocks of trials. Within each block, all stimuli were presented for the

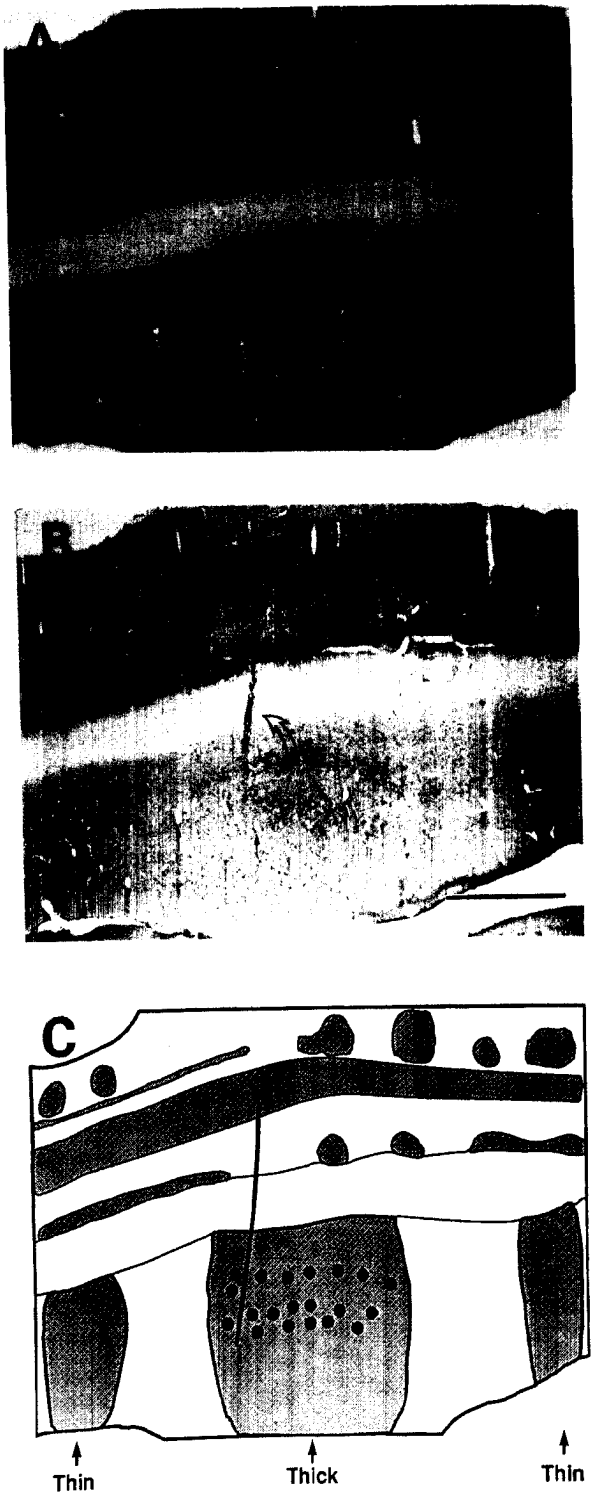

Fig. 1. Representative penetration passing through the V1/V2 border region dorsally, and through a thick stripe in V2. A: CO-stained section showing the electrode track (curved arrow) in a CO-dark region that appears to be thicker than the two flanking dark stripes. B: Adjacent section stained for Cat-301. Cat-301 immunoreactive cells are most abundant in the center stripe, but are also present in the right-hand stripe. Comparison with the nearest Cat-301 sections in the series confirmed a greater density in the middle stripe. Small arrows mark the same blood vessels in the two sections. Scale bar = 1 mm. C: Composite reconstruction of the electrode track relative to the CO and Cat-301 patterns. The consistent presence of dense Cat-301 staining confirms that the units encountered were located within a thick stripe.

same amount of time, generally 4 s. There were few units that showed signs of adaptation; for these we chose shorter durations. To minimize effects of response variability, stimuli were presented in a random order within each experimental block, and the results of several repeated blocks (typically between 4 and 8) averaged. We also always measured responses to a uniform grey field of the same mean luminance as our other stimuli to measure the cell's spontaneous firing rate. Responses were compiled into average histograms synchronized to each temporal cycle of the stimulus. These histograms were then Fourier analyzed to calculate responses at d.c. and at the fundamental stimulus frequency (F1). For complex cells, which respond with an unmodulated elevation in discharge rate, we used the d.c. response (mean firing rate) as the response measure; for simple cells we used the F1 response.

Visual stimulation

Stimuli were displayed on a BARCO CCID 7351B color television monitor driven by an AT Truevision Vista Graphics board. At a viewing distance of 174 cm the screen subtended 12.5 deg × 9 deg of visual angle. Drifting sinusoidal grating stimuli were modulated around an average white point with CIE (Commission Internationale de l'Eclairage) *xy* coordinates of (0.31, 0.32) with an average luminance of 37.5 cd/m^2. To measure the color properties of cells, we used periodic square-wave gratings consisting of colored bars on a black background. The square-wave gratings were of optimal spatial frequency, temporal frequency, size, and orientation. The colored bars all were of equal luminance (37.5 cd/m^2) and distributed in color space along an ellipse. Fig. 2 shows the distribution of colors in the CIE *xy* chromaticity diagram. The axes of color modulations, indicated by the dashed lines in Fig. 2, were chosen to isolate the second stage color-opponent processes (MacLeod & Boynton, 1979). For stimuli in the red and green directions, this resulted in a 5% and 9% change of contrast in the L- and M-cones, respectively, as compared to a white bar of the same luminance. For stimuli in the blue and yellow directions only S-cone excitation was different compared to the white bar (60% S-cone contrast). At the given luminance level of 37.5 cd/m^2, these were the most saturated colors that could be achieved on our monitor.

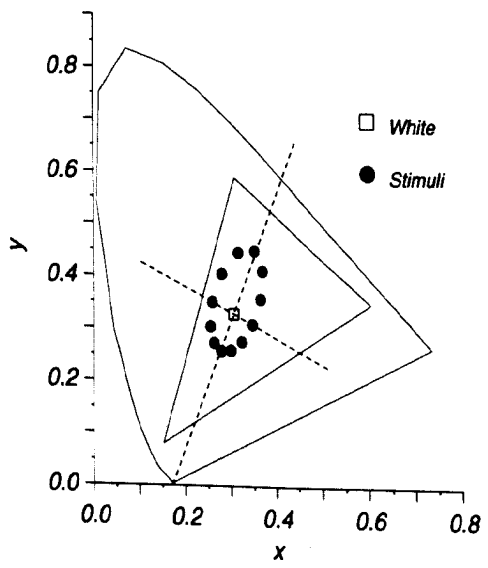

Fig. 2. C.I.E. *xy* chromaticity diagram illustrating the color stimuli used in our experiments. At the center is a neutral white. Stimuli are chosen along the two axes indicated by the dashed lines, which correspond to the axes in the chromaticity diagram introduced by MacLeod and Boynton (1979). Stimuli were chosen symmetrically around the white point in a way that cone contrasts in both directions were of equal magnitude and opposite sign. The triangle indicates the C.I.E. coordinates of the phosphors of our monitor. Since the mean luminance of our stimuli was higher than the maximum luminance of the red and the blue phosphors, the range of colors was even more restricted.

Results

Description of basic experiments

We recorded from 140 single neurons in area V2 of eight macaque monkeys. Of these cells, we were able to assign 119 unambiguously to one of the CO compartments; 90% of the units had receptive fields centered within 5 deg of the fovea, the remaining were within 10 deg. For each neuron we measured the tuning and sensitivity to otherwise optimal stimuli of different orientations, directions, sizes, and colors.

Fig. 3A shows responses of a cell (378l012) from a thick stripe to black and white sinusoidal gratings moving at different orientations. Gratings were of optimal spatial and temporal frequency and size. This cell responded very briskly to gratings oriented at an angle of approximately 60 deg (upward and to the right), and did not give any response at the orthogonal orientations or the opposite direction. The dashed horizontal line shows the response baseline of the cell. Standard errors of the response are shown, but for this cell they were smaller than the symbols in most cases. We fitted a smooth function through the data points (shown by the solid curve) and defined a *direction index*

$$DI = 1 - \frac{\text{Response in opposite direction} - \text{Baseline}}{\text{Response in optimum direction} - \text{Baseline}}$$

and an *orientation index*

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

Cells with a $DI > 0.7$ were classified as directionally selective, and cells with an $ORI > 0.7$ were classified as oriented. These criteria require at least a threefold increase in firing at the optimum for a cell to be classified as directionally selective or orientation selective. For the cell in Fig. 3A the values of *DI* and *ORI* are both larger than 1, indicating that the response was slightly inhibited in the opposite direction and at the orthogonal orientation. In further experiments, we found that it was slightly endstopped, responded well to high temporal frequencies (peak = 10 Hz), had a steep contrast response function, and responded well to isoluminant blue-yellow gratings.

Fig. 3B shows responses of a cell (372r006) from an interstripe region to black and white sinusoidal gratings of different sizes. In our experiments, we restricted ourselves to square stimuli, and size refers to the width or height of the stimuli. All other parameters were set to optimize the cell's response. *Endstopping* was defined as

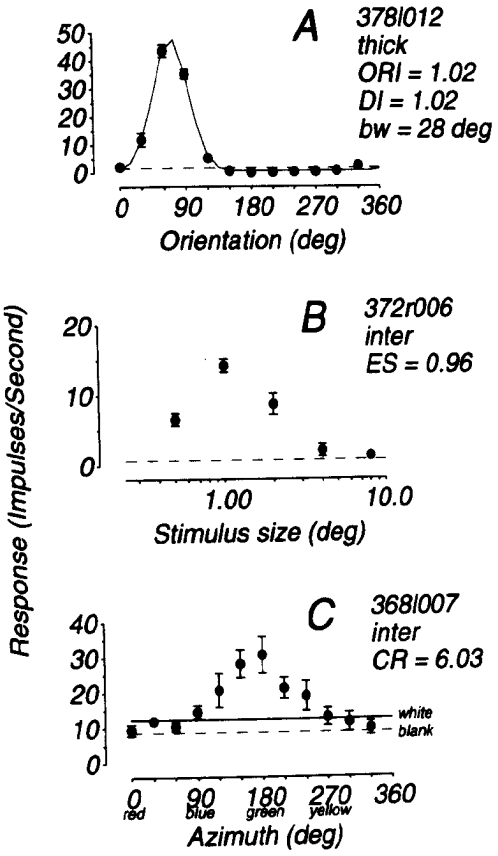

Fig. 3. Response properties of three representative V2 cells. A: Responses of a cell (378l012) from a thick stripe to black/white sinusoidal gratings of different orientations. The dashed horizontal line represents the response baseline. We fitted a smooth function to the data points and defined a *direction index* $DI = 1 -$ (response in opposite direction − baseline)/(response in optimum direction − baseline) and an *orientation index* $ORI = 1 -$ (response in orthogonal orientation − baseline)/(response in optimum orientation − baseline). Cells with a $DI > 0.7$ were classified as directionally selective, cells with an $ORI > 0.7$ were classified as oriented. B: Responses of a cell (372r006) from an inter-stripe region to sinusoidal grating patches of different sizes. *Endstopping* was defined as $ES = 1 -$ (response to largest stimulus − baseline)/(response to optimum stimulus − baseline). Cells with an $ES > 0.5$ were classified as being endstopped. C: Responses to bars of different color for a cell (368l007) from an inter-stripe region. Stimuli were alternating black and colored bars. The solid horizontal line shows the response to a white bar of the same luminance (37.5 cd/m^2) as the colored bars. We defined *color responsivity* as $CR =$ (best response to coloured bar − baseline)/(response to white bar − baseline). Cells with a $CR > 1.4$ were classified as color selective.

$$ES = 1 - \frac{\text{Response to largest stimulus} - \text{Baseline}}{\text{Response to optimum stimulus} - \text{Baseline}}$$

Cells with an $ES > 0.5$ were classified as being endstopped. This cell was almost completely inhibited by large stimuli ($ES = 0.96$). In other experiments, we found that it was also very tightly tuned for spatial frequency ($bw = 0.5$ octaves) and orientation ($bw =$ 17 deg). Contrast sensitivity was poor. However, it was also highly color selective: the response to a red bar was more than twice as high as that to a white bar of the same luminance.

For another cell from an inter-stripe region (368l007) responses to bars of different colors are given in Fig. 3C. Stimuli in this experiment were square-wave gratings made of alternating black and colored bars. Orientation, spatial and temporal frequency, and size were set to the cell's preferred values. The solid horizontal line shows the response to a white bar of the same luminance (37.5 cd/m^2) as the colored bars. We defined *color responsivity* as

$$CR = \frac{\text{Best response to colored bar} - \text{Baseline}}{\text{Response to white bar} - \text{Baseline}}$$

Cells with a $CR > 1.4$ were classified as color selective. For this cell, we found that the response to a green bar was six times as high as the response to the white bar (after subtracting the baseline). It gave hardly any response to the white bar.

We ran several other experiments to investigate the chromatic properties of cells in more detail, but we found that CR was an index providing a reliable indication of color-opponent inputs to a cell. In experiments with chromatic sinusoidal gratings (see Derrington et al., 1984), we found that color opponency was often overestimated due to slight variations in cells' isoluminant planes in combination with highly nonlinear contrast response curves of V2 neurons. Many cells showed large variations in the responses to isoluminant gratings with different colors, but when thoroughly tested showed a complete response null at a luminance ratio not far from photometric isoluminance. In the experiment with colored bars on a black background all stimuli have a high luminance contrast, which in the absence of color opponency would saturate the cell irrespective of small deviations from photometric luminance. Only if the cell indeed receives significant color-opponent inputs will CR be larger than 1. Along the same line of reasoning, any luminance artifacts introduced by chromatic aberration should be negligible compared to the luminance contrast of the stimuli. Besides that, since we used stimuli at the cells' preferred spatial frequency in these experiments, and since the preferred spatial frequencies of most of the cells we tested were rather low (<2 cycles/deg for 85% of the cells), we are confident that chromatic aberration did not significantly contribute to our results. Notice that our measure of color selectivity CR is similar to the white index WI defined by Burkhalter and Van Essen (1986). However, they used a color index CI to classify cells as being color selective, which relates the best and the worst response to chromatic stimuli. For basically all cells we encountered (and for almost all cells in the Burkhalter & Van Essen study), the values for CI were larger than values for WI. Their criterion of $CI > 0.7$ leads to approximately the same classification as our criterion $CR > 1.4$ (equivalent to $WI > 0.3$), together with the constraint of assigning a CI of 1 to all cells for which the best chromatic response was not statistically significantly different from the response to luminance. Notice also that the saturation of the colors we could produce on our TV monitor was lower than for the narrow-band stimuli used by Burkhalter and Van Essen and in many other studies.

Distribution of response properties

Fig. 4 shows the distribution of response properties of the neurons in our sample. Fig. 4A shows our classification given a strict set of criteria ($DI > 0.9$, $ORI > 1.0$, $CR > 2.0$, $ES > 0.7$), Fig. 4B uses medium criteria ($DI > 0.7$, $ORI > 0.7$, $CR > 1.4$, $ES > 0.5$) that are roughly comparable to other published clas-

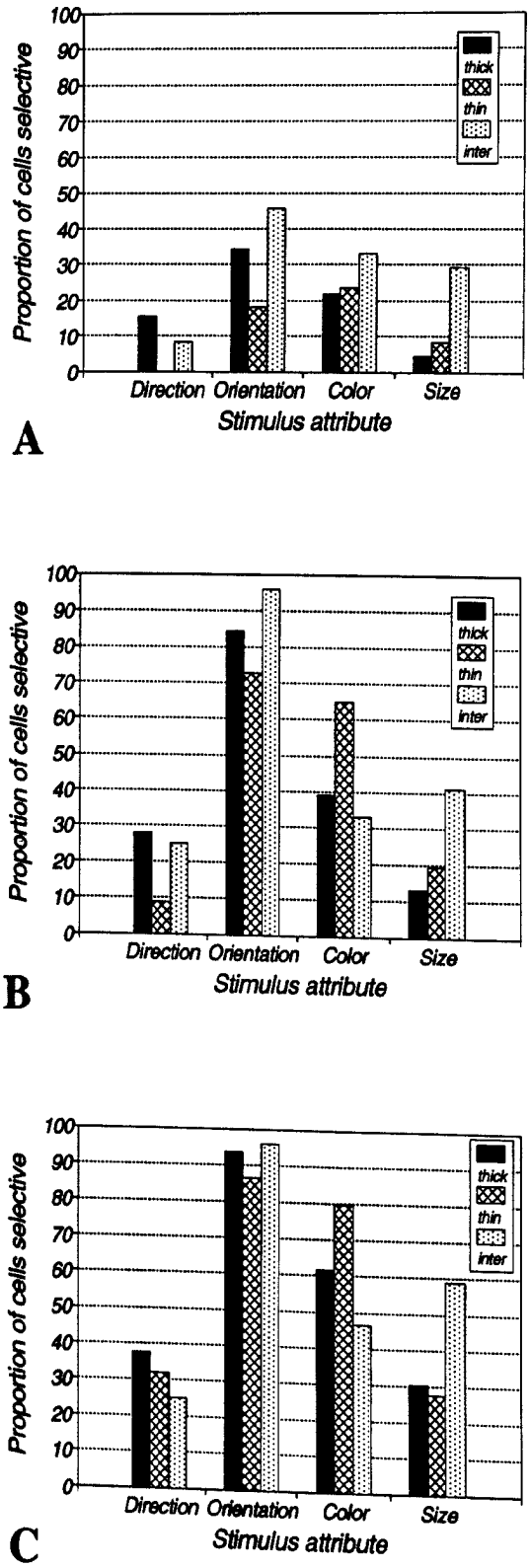

Fig. 4. Proportion of cells in the three different CO compartments (indicated by different fill patterns) being selectively responsive to direction ($N = 100$; 32 thick, 44 thin, 24 inter), orientation (100;32,44,24), size (72;26,34,15), or color (76;23,36,17). Different criteria were used to classify cells as being selective for each attribute. A: Strict set of criteria: $DI > 0.9$, $ORI > 1.0$, $CR > 2.0$, $ES > 0.7$. B: Medium set of criteria: $DI > 0.7$, $ORI > 0.7$, $CR > 1.4$, $ES > 0.5$. C: Weak set of criteria: $DI > 0.5$, $ORI > 0.5$, $CR > 1.25$, $ES > 0.3$.

sifications, and Fig. 4C uses a weaker set of criteria ($DI > 0.5$, $ORI > 0.5$, $CR > 1.25$, $ES > 0.3$). We will first compare the medium classification (Fig. 4B) with other published data, and then look at possible effects of using different criteria.

In good agreement with other quantitative experiments (for an overview see Felleman & Van Essen, 1987) we found that 82 of 100 V2 cells (82%) were selective for orientation. This result was independent of whether we used the orientation index or orientation bandwidth to classify cells. A high proportion of cells (36 out of 72; 50%) was strongly selective for the color of the stimulus, even with the rather conservative criterion we had chosen. A minority of cells was directionally selective (19 out of 100; 19%) or endstopped (17 out of 76; 22%). The proportions of neurons selective for each of color, direction, orientation, and endstopping agree quite well with previous investigators (Baizer et al., 1977; DeYoe & Van Essen, 1985; Burkhalter & Van Essen, 1986; Felleman & Van Essen, 1987; Hubel & Livingstone, 1987; Peterhans & von der Heydt, 1993; Levitt et al., 1994*a*). Cells with these properties did occur more frequently in the CO compartment associated with the corresponding stimulus attribute. Cells showing endstopping were found far more frequently in the inter-stripe regions (41%) than in the thick (13%) or thin (19%) stripes. Color- selective cells did occur more frequently in thin stripes (65%). But it is noteworthy that about a third of the cells in the thick stripes (39%) and inter-stripes (33%) were selectively responsive to color. Finally, 12 of 44 cells (27%) in the thin stripes were not selective for orientation, which is more than in the other compartments. This confirms previous findings that there is some anatomical segregation of physiological properties of cells in V2.

Any comparison of response properties across CO compartments is potentially dependent on the criterion employed. However, a comparison of Figs. 4A–4C shows that the basic pattern of results changes little for the three different sets of criteria. Most notably, even for the strictest criterion ($CR > 2.0$) there are still between 20% and 30% color-selective cells in all three CO compartments. The predominance of endstopped cells in the inter-stripes and of unoriented cells in the thin stripes is also not affected by different criteria. Our results on directional selectivity show that the most directionally selective cells were in the thick and inter-stripes, but when using a weaker criterion ($DI > 0.5$) we found roughly equal proportions in all three types of CO compartments, indicating a proportion of weakly directionally selective cells in the thin stripes.

Even though any observed segregation was along the lines we had expected based on previous published data, the degree of segregation fell short of our expectations. When rigorously tested with statistical methods (χ^2-test), we found that the difference between the three CO compartments (using the medium criteria) were not quite significant, as was the case for selectivity for direction ($P = 0.08$), orientation ($P = 0.06$), and for size ($P = 0.09$), or were just marginally significant, as was the case for color ($P = 0.03$). Since all four indices for selectivity were continuously distributed introducing an artificial criterion might effect the observed degree of segregation. We therefore ran an analysis of variance on the indices themselves, which does not inflict any artificially imposed criteria. The results were similar to the results of the above χ^2-tests. We found no significant difference in mean selectivity for direction ($P = 0.23$), orientation ($P = 0.10$), color ($P = 0.34$), or size ($P = 0.09$). Color, directionality, orientation selectivity, and endstopping

were represented in all three types of CO compartments. There is good evidence of some degree of segregation, but there was no absolute segregation of selective sensitivity to color, form, and motion information into different processing streams.

We also studied the laminar distribution of cells selective for each stimulus attribute. Table 1 shows the proportion of cells selective for color, size, orientation, and direction in different layers. There is no difference between different layers, except for fewer endstopped cells in layer 4. This could be due to sampling error, since our sample of layer 4 cells was rather small. A combined analysis of laminar distribution and CO compartments has the disadvantage of small numbers of cells. We did find, however, that most directionally selective cells in the thick stripes came from the deep layers (six of nine). Unoriented cells were encountered in all layers of the thin stripes, six in superficial layers, one in layer 4, and five in deep layers. Color cells were about evenly distributed across laminae of the thin stripes, eight of 13 (62%) in the superficial layers, three of five (60%) in layer 4, and 11 of 16 (69%) in the deep layers. Endstopped cells occurred in approximately equal proportions in superficial and deep layers of all three CO compartments.

Association between different stimulus attributes

Even though the correlation of certain response properties with the anatomical location is an interesting issue, the more fundamental question is how much integration and correlation there is between the response properties themselves. If, for example, form and color were completely segregated, we would not expect to find any oriented color cells or any endstopped color cells. Our data did not comply with this prediction. No systematic relationship between color and orientation selectivity, endstopping, or directionality was visible.

Fig. 5A shows a scatterplot of orientation indices and color responsivities for 106 V2 cells. For 66 of these cells we ran both experiments. The large filled symbols indicate median values for both indices and show that there are small differences between different CO compartments. Cells in the thin stripes are on average more color selective and less orientation selective. As mentioned above, none of these differences is statistically significant. The ranges of the distributions for all three CO compartments completely overlap. There is no correlation between selectivity for color and orientation. Fig. 5B shows a similar scatterplot for color and directional selectivity. Once again, there are small differences on average, but the ranges overlap and there is no correlation. However, it should be noted that the upper right quadrant of this graph is rather empty. Even though there are cells that combine selectivity to color and motion, they are not the cells with the most distinguished selectivity for both attributes. Fig. 5C shows the association between color and endstopping. Figs. 5A–5C also indicate that all four indices are distributed continuously. Therefore, any criterion to classify cells as being selectively responsive to a certain attribute is rather arbitrary.

Nevertheless, we used our previous (medium) set of criteria (Fig. 4B) and computed a statistical measure for the degree of association between each pair of stimulus attributes. We used Fisher's exact test for probabilities (see Hays, 1981, pp. 552–555) to test the hypothesis that there is an association between different stimulus attributes. Fig. 6 illustrates the association between selectivities to the different stimulus attributes. Table 2 shows fourfold tables of the occurrences of neurons being selective for a certain attribute. The probability of obtaining this particular table, or one that is even more indicative of association given the same marginals, under the null hypothesis of no association, is indicated in the rightmost column. None of the nine values is statistically significant at the 0.05 level. Therefore, we cannot reject the null hypothesis of no association.

Fig. 6 illustrates these results. Each group of bars represents cells that are selective for the attribute indicated on the x axis. The bars indicated by the arrows show the proportion of cells selective to that particular attribute in the whole sample. For example, in the group of bars indicated by color, the individual bars from left to right show the proportions of cells sensitive to another attribute that were also selective to color. Thus, we can see that about 27% of directional cells, 43% of oriented cells, and 56% of endstopped cells were also sensitive to color, while the proportion of color cells in the whole population was 50%. If attribute segregation was complete in area V2 (the segregation hypothesis), only few of the bars (other than the whole sample bars) should be different from zero. For example, there should not be any cells responsive to size and color at the same time. This is not the case. On the contrary, if the representation of stimulus attributes were totally independent (the independence hypothesis), all of the bars within each block should have identical heights, equal to that of the population bar. The above statistical analysis showed that our data are not inconsistent with the independence hypothesis. This would mean that the probability with which a given cell responded to color, for example, did not depend on whether the cell was also responsive for motion or form.

Table 1. *Laminar distribution of cell properties*[a]

Attribute	Superficial	Middle	Deep	Total	*N* (sup; middle; deep)
Direction	17	13	10	19	100 (42; 15; 43)
Orientation	79	87	84	82	100 (42; 15; 43)
Color	52	55	47	50	72 (27; 11; 34)
Endstopping	29	8	22	22	76 (31; 13; 32)

[a]Numbers are for all cells on which quantitative experiments were run. Shown is the percentage of cells in the superficial, middle, and deep layers, that were selective for each attribute. To the right is the percentage of cells being selective for the whole population, and the number of cells tested. In parenthesis is the distribution across layers (sup; middle; deep).

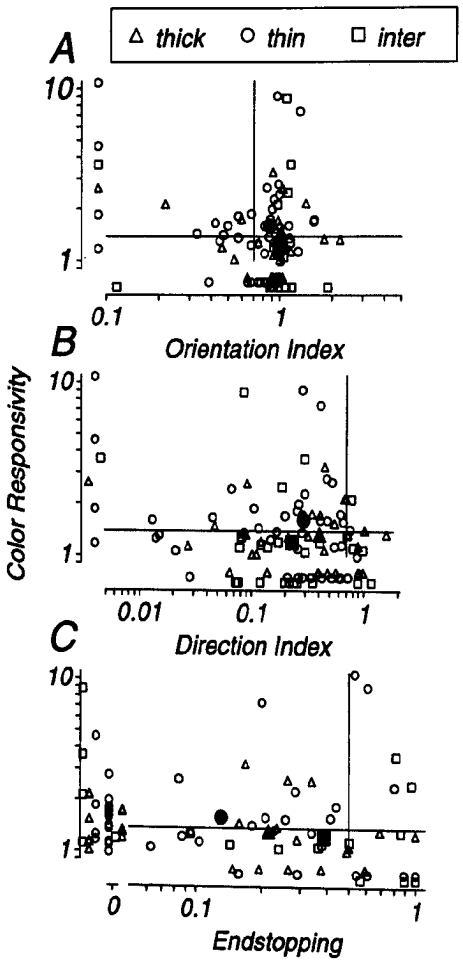

Fig. 5. Association between different response properties. A: Scatterplot of orientation indices and color responsivities for 100 V2 cells (32 thick, 44 thin, 24 inter). Different symbols indicate cells from different CO compartments (triangles: thick stripes, circles: thin stripes, squares: inter-stripes). For 66 cells (22 thick, 30 thin, 14 inter), we ran both experiments. For the cells below the *y* axis and to the left of the *x* axis, we only ran the orientation tuning or color tuning, respectively. The large filled symbols indicate median values for the three groups of cells. B: Scatterplot of direction indices and color responsivities for 100 V2 cells. Symbols are as in (A). C: Scatterplot of endstopping and color responsivities for 76 V2 cells (23 thick, 34 thin, 20 inter). Symbols are as in (A).

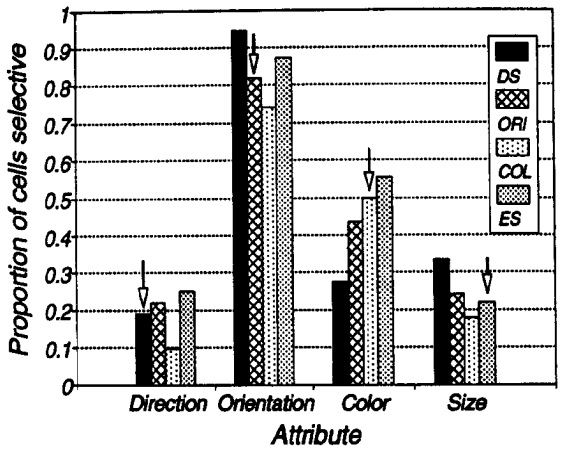

Fig. 6. Association between selectivities to different stimulus attributes. For each attribute (indicated on the *x* axis), we show the proportion of cells being selectively responsive to that attribute in the populations of directionally selective cells (*DS*), orientation-selective cells (*ORI*), color-selective cells (*COL*), and endstopped cells (*ES*). The columns indicated by the arrow show selectivity for the reference attribute in the whole population of cells. If color, form, and motion were statistically independent, each group should contain four bars of equal height. If stimulus attributes were completely segregated, some of the bars should be 0.

Discussion

Our results clearly show that for all stimulus attributes selectivity of cells is distributed continuously, and that there are many cells in V2 that are selective to more than a single stimulus attribute. Classifying cells in general, and classifying them based on one response property in particular, is therefore not appropriate.

There was a tendency toward more color selectivity in the thin stripes, but generally there was color selectivity in all CO compartments. The fact that statistical tests did not show significant differences in selectivities between different CO compartments might be explained by our relatively small sample size (119 cells), since the overall trends were in the directions where we expected differences. However, it should be clear that segregation was by no means absolute. Knowing the responses of a single cell does not allow one to classify that cell as belonging

Table 2. *Incidence of combinations of different attributes*[a]

Attribute (A *vs.* B)	A and B	A and not B	not A and B	not A and not B	*P*
Color *vs.* direction	3	28	8	27	0.098
Color *vs.* orientation	23	8	30	5	0.12
Color *vs.* endstopping	5	23	4	25	0.25
Direction *vs.* endstopping	4	8	12	49	0.16
Orientation *vs.* endstopping	14	44	2	13	0.20

[a]For each pair of attributes (A and B), we show the number of cells selective for A and B, A and not B, not A and B, not A and not B. The rightmost column indicates the probability of obtaining such a fourway table (or one even more indicative of association) under the hypothesis that there is no association between stimulus attributes A and B, according to Fisher's exact test for probabilities. None of the entries was statistically significant ($\alpha = 0.05$).

to a particular processing stream or CO compartment. To an even lesser degree does knowing the selectivity of a cell along one stimulus dimension allow predictions of its other properties. What might be possible is to assign a whole group of neighboring cells (for example, from one penetration) to a certain CO compartment with high probability.

Even though we did not find a significant association between any two stimulus attributes, our data gave no clear evidence for the existence of highly directional color cells. The cells we found to be selective for color and direction of motion at the same time were either just marginally responsive to color or just marginally directional. It seems, therefore, that color selectivity in combination with directional selectivity, which can be observed psychophysically (Derrington & Henning, 1993; Metha et al., 1994; Stromeyer et al., 1995; Gegenfurtner & Hawken, 1995), is formed in another area of cortex. There is some preliminary evidence that area V3, which also receives input from area V2 (see Felleman & Van Essen, 1991), might have that specific integration function (Gegenfurtner et al., 1994*b*). We found earlier (Gegenfurtner et al., 1994*a*) that there are hardly any color-selective cells in area MT. It is therefore plausible that the most directionally selective cells from the thick stripes of area V2 project to area MT (DeYoe & Van Essen, 1985), where most cells are directionally selective and insensitive to color (Gegenfurtner et al., 1994*a*).

Comparison to other studies

Our results are remarkably similar to other quantitative studies of response properties of neurons in area V2. Peterhans and von der Heydt (1993) also found a continuous distribution of neuronal selectivities for all attributes, and no clear segregation of selectivity for orientation, direction, and endstopping into different CO compartments. Their experiments were done on awake behaving monkeys (*Macaqua mulatta*). Using criteria similar to ours, they observed 35% weakly oriented or unoriented cells in the thin stripes (including cells they failed to drive), compared to 28% in our smaller sample. Overall they found 20% (78 of 390) V2 cells falling into that category, compared to 18% (18 of 100) in our sample. In accordance with our results, they found more directionally selective cells in the thick stripes (30% compared to 28% in our study) and inter-stripes (34% compared to 25% in our study) than in the thin stripes (21% compared to 9% in our study). The larger percentage of directionally selective cells in the thin stripes in their study was probably due to their lower criterion ($DI > 0.5$) for classifying cells as directionally selective than we used ($DI > 0.7$). Using their lower criterion (Fig. 4C), we found about equal proportions of approximately 25%–35% directionally selective cells in all compartments. Similar to our results, they found more endstopped neurons in the inter-stripes (30% compared to our 41%) than in the thin stripes (22% compared to our 19%) and thick stripes (20% compared to our 13%). Peterhans and von der Heydt (1993) did not investigate chromatic properties of cells.

Levitt et al. (1994*a*) used experimental conditions similar to ours to investigate basic spatio-temporal response properties of cells across different CO compartments in V2. They used sine-wave gratings and the paradigm introduced by Derrington et al. (1984) to determine color properties of cells. Their data also indicated no strict segregation into different processing streams, even though their data tended more strongly towards segregation than the data of Peterhans and von der Heydt (1993) or our study. They did find more unoriented cells in the thin stripes (50%) and more directionally selective cells in the thick stripes (50%). Their proportion of color-selective cells was lower than the 50% we found, which was probably due to the insufficient sensitivity of their color measurements. In fact, the systematic deviations in their experiments of V2 cells' responses to chromatic stimuli from the linear model used by Derrington et al. (1984) in the LGN was one of the motivations for the present study.

Furthermore, the overall number of cells we found selective for orientation, direction, size, and color are within the range of values reported earlier by other investigators in single-unit recordings (Baizer et al., 1977; Zeki, 1978; Burkhalter & Van Essen, 1986; Hubel & Livingstone, 1987). Of these studies, Burkhalter and Van Essen also looked at polyfunctional neurons, i.e. neurons being selective for more than one stimulus attribute. In agreement with our results, they found that color selectivity was independent of selectivity to direction and orientation in V2 cells.

By far the most extensive study of V2 has been the work of Hubel and Livingstone (1987). However, it is difficult to compare their results directly to ours. They mostly used receptive-field geometry to classify cells into unoriented, complex unoriented, oriented complex, disparity tuned, and endstopped cells. They recorded from macaques and squirrel monkeys. In the following, we will concentrate on their data from macaques. They reported 76% (299 of 394) to be selective for orientation, which is similar to our finding (82%). They found 24% of cells to be endstopped, which is close to what we found (22%). However, in their study only 8% (30 of 394 cells) were directionally selective compared to 19% in our study. Unfortunately, Hubel and Livingstone did not test color properties of oriented cells. They found 75% of all unoriented cells to be color selective, compared to 62% in our experiment. Given that we found 43% of all oriented cells to be color selective, the negative correlation between color and orientation they proposed might actually be relatively low. For our small sample, it did not reach statistical significance. More recently, and using methods more similar to Hubel and Livingstone (1987) than to ours, Roe and Ts'o (1993) also reported evidence for oriented color cells in area V2 of macaques. Whether these cells fall into separate subcompartments within the CO stripes of V2, as suggested by Roe and Ts'o (1993), is unclear.

One conclusion from these comparisons is that the actual data between the various experiments vary to a much lesser degree than the interpretations by the various experimenters. Our results show that there do seem to be differences in the emphasis that cells in the different CO compartments put on the various stimulus dimensions. However, the results also make clear that there is no absolute segregation and that all attributes are processed in all compartments.

Isoluminance in extrastriate cortex

Independently of the issue of segregated functional streams in different CO compartments, our data show clearly that neurons in all three CO compartments are color selective, and that color is represented in combination with other stimulus attributes. This fact has a very strong implication for experiments which try to use color as a means of isolating neural pathways. There

are good reasons to assume that isoluminant stimuli indeed mostly stimulate parvocellular LGN neurons (Shapley, 1990), even though some magnocellular neurons might show a frequency-doubled response to isoluminant stimuli (Schiller & Colby, 1983; Derrington et al., 1984). But given the large extent of mixing of parvocellular and magnocellular signals in V1 and V2, it is not surprising to see a lesser segregation of color processing at the level of V2. Our finding that many cells selective for color share other response properties, useful for analysis of form or motion, is consistent with quantitative psychophysical experiments, indicating that the primate color system is capable of supporting analysis of form and motion (DeValois & Switkes, 1983; Switkes et al., 1988; Webster et al., 1990; Krauskopf & Farell, 1991; Gegenfurtner & Kiper, 1992; Derrington & Henning, 1993; Würger & Landy, 1993; Metha et al., 1994; Hawken et al., 1994; Stromeyer et al., 1995; Gegenfurtner & Hawken, 1995). What is typically found in quantitative psychophysical experimentation with isoluminant stimuli is a reduced response of the color system, when its performance is compared to performance for high-contrast luminance stimuli (Livingstone & Hubel, 1987).

There are two major reasons which could explain this reduced sensitivity. First, because the spectral sensitivities of L- and M-cones largely overlap, the input contrast to the visual system at the level of the cones is vastly reduced for isoluminant stimuli (Shapley, 1990; Gegenfurtner & Kiper, 1992). When stimuli are used that are equated for cone contrast, psychophysical performance at isoluminance was shown to equal or even exceed that for luminance in many psychophysical tasks (Chaparro et al., 1993; Derrington & Henning, 1993; Metha et al., 1994; Stromeyer et al., 1995; Gegenfurtner & Hawken, 1995). A second reason might lie in the continuing integration of signals along the various stages of processing in visual cortex. In the LGN many neurons respond exclusively to isoluminant stimulation (Derrington et al., 1984), which has the advantage of decorrelating the signals from the L- and M-cones (Buchsbaum & Gottschalk, 1983). In the cortex fewer neurons show that behavior (Schiller et al., 1991; Gegenfurtner et al., 1994*a*). Since there is little input to the visual system that is exactly isoluminant, and the magnitude of such input is naturally lower, it would be wasteful for the visual system to allocate much resources to process these stimuli. For the visual system, it seems to be more important to detect borders defined by luminance and color, rather than isoluminant boundaries. Our data show that there are many cells selective for orientation and color, which can code these. Given these constraints, it is not surprising that in many cases performance at isoluminance equals that for luminance when the difference in sensitivities is taken into account (DeValois & Switkes, 1983; Switkes et al., 1988; Webster et al., 1990; Krauskopf & Farell, 1991; Gegenfurtner & Kiper, 1992; Würger & Landy, 1993). What is quite clear from our data is that isoluminant stimulation does not isolate different processing streams at the level of extrastriate area V2.

Conclusions

In summary, we found evidence for both segregation and integration of color, form, and motion in V2. Thin stripes did tend to have a higher proportion of color cells or unoriented cells. To the same degree there were more endstopped cells in the interstripe regions. Directionally selective cells were more more frequently encountered in thick stripes and inter-stripes than in thin stripes. This indicates that the emphasis in the three different CO compartments of V2 is different. However, our results also show that this does not imply a complete functional segregation between color, form, or motion. Each cell can combine selectivity to more than one attribute, and this seems to happen frequently in V2. Rather than having three pathways that exclusively process one aspect of the stimulus, we think that the anatomical segregation in V2 corresponds to three pathways that each can code information about all stimulus attributes. V2 is known to play an important role in integrating information across space (von der Heydt & Peterhans, 1989; Peterhans & von der Heydt, 1989, 1993; Merigan et al., 1993). Based on our results and the anatomical results by Levitt et al. (1994*b*), we suggest that it also integrates information about different stimulus attributes and thus lays the groundwork for a cue-invariant representation of the visual world, which has been found at higher levels of visual processing in several recent studies (Albright, 1992; Sary et al., 1993; Komatsu & Ideura, 1993).

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References

Albright, T.D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science* **255**, 1141-1143.

Baizer, J.S., Robinson, D.L. & Dow, B.M. (1977). Visual responses of area 18 neurons in awake, behaving monkey. *Journal of Neurophysiology* **40**, 1024-1037.

Barlow, H.B., Blakemore, C. & Pettigrew, J.D. (1967). The neural mechanism of binocular depth discrimination. *Journal of Physiology* **193**, 327-342.

Blasdel, G.G., Lund, J.S. & Fitzpatrick, D. (1985). Intrinsic connections of macaque striate cortex: Axonal projections of cells outside lamina 4C. *Journal of Neuroscience* **5**, 3350-3369.

Britten, K.H., Shadlen, M.N., Newsome, W.T. & Movshon, J.A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *Journal of Neuroscience* **12**, 4745-4765.

Buchsbaum, G. & Gottschalk, A. (1983). Trichromacy, opponent colours coding and optimum colour information transmission in the retina. *Proceedings of the Royal Society B* (London) **220**, 80-113.

Burkhalter, A. & Van Essen, D.C. (1986). Processing of color, form and disparity information in visual areas VP and V2 of ventral extrastriate cortex in the macaque monkey. *Journal of Neuroscience* **6**, 2327-2351.

Chaparro, A., Stromeyer, C.F., III, Huang, E.P., Kronauer, R.E. & Eskew, R.T. (1993). Colour is what the eye sees best. *Nature* **361**, 348-350.

Cheng, K., Hasegawa, T., Saleem, K.S. & Tanaka, K. (1994). Comparison of neuronal selectivity for stimulus speed, length, and contrast in the prestriate cortical areas V4 and MT of the macaque monkey. *Journal of Neurophysiology* **71**, 2269-2280.

Derrington, A.M. & Henning, G.B. (1993). Detecting and discriminating the direction of motion of luminance and colour gratings. *Vision Research* **33**, 799-811.

Derrington, A.M., Krauskopf, J. & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology* **357**, 241-265.

DESIMONE, R. & SCHEIN, S.J. (1987). Visual properties of neurons in area V4 of the macaque: Sensitivity to stimulus form. *Journal of Neurophysiology* **57**, 835-868.

DE VALOIS, K.K. & SWITKES, E. (1983). Simultaneous masking interactions between chromatic and luminance gratings. *Journal of the Optical Society of America* **73**, 11-18.

DEYOE, E.A. & VAN ESSEN, D.C. (1985). Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. *Nature* **317**, 58-61.

DEYOE, E.A., HOCKFIELD, S., GARREN, H. & VAN ESSEN, D.C. (1990). Antibody labeling of functional subdivisions in visual cortex: Cat-301 immunoreactivity in striate and extrastriate cortex of the macaque monkey. *Visual Neuroscience* **5**, 67-81.

FELLEMAN, D.J. & VAN ESSEN, D.C. (1987). Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. *Journal of Neurophysiology* **57**, 889-920.

FELLEMAN, D.J. & VAN ESSEN, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex* **1**, 1-47.

FERRERA, V.P., NEALEY, T.A. & MAUNSELL, J.H.R. (1994). Responses in macaque visual area V4 following inactivation of the parvocellular and magnocellular LGN pathways. *Journal of Neuroscience* **14**, 2080-2088.

FITZPATRICK, D., LUND, J.S. & BLASDEL, G.G. (1985). Intrinsic connections of macaque striate cortex: Afferent and efferent connections of lamina 4C. *Journal of Neuroscience* **5**, 3329-3349.

GEGENFURTNER, K.R. & KIPER, D.C. (1992). Contrast detection in luminance and chromatic noise. *Journal of the Optical Society of America A* **9**, 1880-1888.

GEGENFURTNER, K.R., KIPER, D.C., BEUSMANS, J., CARANDINI, M., ZAIDI, Q. & MOVSHON, J.A. (1994*a*). Chromatic properties of neurons in macaque MT. *Visual Neuroscience* **11**, 455-466.

GEGENFURTNER, K.R., KIPER, D.C. & LEVITT, J.B. (1994*b*). Analysis of color and motion in macaque area V3. *Society for Neuroscience Abstracts* **20**, 1741.

GEGENFURTNER, K.R. & HAWKEN, M.H. (1995). Temporal and chromatic properties of motion mechanisms. *Vision Research* **35**, 1547-1563.

HAWKEN, M.J., GEGENFURTNER, K.R. & TANG, C. (1994). Contrast dependence of colour and luminance motion mechanisms in human vision. *Nature* **367**, 268-270.

HAYS, W.L. (1981). *Statistics* (third edition). New York: CBS College Publishing.

HUBEL, D.H. & LIVINGSTONE, M.S. (1987). Segregation of form, color, and stereopsis in primate area 18. *Journal of Neuroscience* **7**, 3378-3415.

HUBEL, D.H. & WIESEL, T.N. (1972). Laminar and columnar distribution of geniculo-cortical fibers in the macaque monkey. *Journal of Comparative Neurology* **158**, 421-450.

KAPLAN, E. & SHAPLEY, R.M. (1986). The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proceedings of the National Academy of Sciences of the U.S.A.* **83**, 2755-2757.

KOMATSU, H. & IDEURA, Y. (1993). Relationships between color, shape, and pattern selectivities of neurons in the inferior temporal cortex of the macaque. *Journal of Neurophysiology* **70**, 677-694.

KRAUSKOPF, J. & FARELL, B. (1991). Vernier acuity: Effects of chromatic content, blur and contrast. *Vision Research* **31**, 735-749.

LACHICA, E.A., BECK, P.D. & CASAGRANDE, V.A. (1992). Parallel pathways in macaque monkey striate cortex: Anatomically defined columns in layer III. *Proceedings of the National Academy of Sciences of the U.S.A.* **89**, 3566-3570.

LEVENTHAL, A.G., RODIECK, R.W. & DREHER, B. (1981). Retinal ganglion cell classes in the old-world monkey: Morphology and central projections. *Science* **213**, 1139-1142.

LEVITT, J.B., KIPER, D.C. & MOVSHON, J.A. (1994*a*). Receptive fields and functional architecture of macaque V2. *Journal of Neurophysiology* **71**, 2517-2542.

LEVITT, J.B., YOSHIOKA, T. & LUND, J.S. (1994*b*). Intrinsic cortical connections in macaque area V2: Evidence for interaction between different functional streams. *Journal of Comparative Neurology* **342**, 551-570.

LIVINGSTONE, M.S. & HUBEL, D.H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience* **4**, 309-356.

LIVINGSTONE, M.S. & HUBEL, D.H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience* **7**, 3416-3468.

LUND, J.S. (1973). Organization of neurons in the visual cortex, area 17, of the monkey (*Macaca mulatta*). *Journal of Comparative Neurology* **147**, 455-475.

LUND, J.S. & BOOTHE, R.G. (1975). Interlaminar connections and pyramidal neuron organization in the visual cortex, area 17, of the macaque monkey. *Journal of Comparative Neurology* **159**, 305-334.

MACLEOD, D.I.A. & BOYNTON, R.M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America* **69**, 1183-1186.

MAUNSELL, J.H.R., NEALEY, T.A. & DEPRIEST, D.D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. *Journal of Neuroscience* **10**, 3323-3334.

METHA, A.B., VINGRYS, A.J. & BADCOCK, D.R. (1994). Detection and discrimination of moving stimuli: The effects of color, luminance, and eccentricity. *Journal of the Optical Society of America A* **11**, 1697-1709.

MERIGAN, W.H., NEALEY, T.A. & MAUNSELL, J.H.R. (1993). Visual effects of lesions of cortical area V2 in macaques. *Journal of Neuroscience* **13**, 3180-3191.

MERRILL, E.G. & AINSWORTH, A. (1972). Glass-coated platinum-plated tungsten microelectrode. *Medical and Biological Engineering* **10**, 495-504.

NEALEY, T.A. & MAUNSELL, J.H.R. (1994). Magnocellular and parvocellular contributions to the responses of neurons in macaque striate cortex. *Journal of Neuroscience* **14**, 2069-2079.

NEWSOME, W.T., WURTZ, R.H., DÜRSTELER, M.R. & MIKAMI, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *Journal of Neuroscience* **5**, 825-840.

PERRY, V.H., OEHLER, R. & COWEY, A. (1984). Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. *Neuroscience* **12**, 1101-1123.

PETERHANS, E. & VON DER HEYDT, R. (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *Journal of Neuroscience* **9**, 1749-1763.

PETERHANS, E. & VON DER HEYDT, R. (1993). Functional organization of area V2 in the alert macaque. *European Journal of Neuroscience* **5**, 509-524.

POGGIO, G.F. & FISCHER, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *Journal of Neurophysiology* **40**, 1392-1405.

ROCKLAND, K.S. (1985). A reticular pattern of intrinsic connections in primate area V2 (area 18). *Journal of Comparative Neurology* **235**, 467-478.

ROE, A.W. & TS'O, D.Y. (1993). Visual field representation within primate V2 and its relationship to the functionally distinct stripes. *Investigative Ophthalmology and Visual Science* (Suppl.) **34**, 812.

SANDELL, J.H. (1986). NADPH diaphorase histochemistry in the macaque striate cortex. *Journal of Comparative Neurology* **251**, 388-397.

SARY, G., VOGELS, R. & ORBAN, G.A. (1993). Cue-invariant shape selectivity of macaque inferior temporal neurons. *Science* **260**, 995-997.

SCHEIN, S.J. & DESIMONE, R. (1990). Spectral properties of V4 neurons in the macaque. *Journal of Neuroscience* **10**, 3369-3389.

SCHILLER, P.H. & COLBY, C.L. (1983). The responses of single cells in the lateral geniculate nucleus of the rhesus monkey to color and luminance contrast. *Vision Research* **23**, 1631-1641.

SCHILLER, P.H., LOGOTHETIS, N.K. & CHARLES, E.R. (1991). Parallel pathways in the visual system: Their role in perception at isoluminance. *Neuropsychologia* **29**, 433-441.

SHAPLEY, R. (1990). Visual sensitivity and parallel retinocortical channels. *Annual Review of Psychology* **41**, 635-658.

STROMEYER, C.F., III, KRONAUER, R.E., RYU, A., CHAPARRO, A. & ESKEW, R.T. (1995). Contributions of human long-wave and middle-wave cones to motion detection. *Journal of Physiology* **485.1**, 221-243.

SWITKES, E., BRADLEY, A. & DE VALOIS, K.K. (1988). Contrast dependence and mechanisms of masking interactions among chromatic & luminance gratings. *Journal of the Optical Society of America A* **7**, 1149-1162.

VON DER HEYDT, R. & PETERHANS, E. (1989). Mechanisms of contour

perception in monkey visual cortex. I. Lines of pattern discontinuity. *Journal of Neuroscience* **9**, 1731–1748.

WEBSTER, M.A., DE VALOIS, K.K. & SWITKES, E. (1990). Orientation and spatial-frequency discrimination for luminance and chromatic gratings. *Journal of the Optical Society of America A* **7**, 1034–1049.

WONG-RILEY, M. (1979). Changes in the visual system of monocularly sutured and enucleated cat demonstrated with cytochrome oxidase histochemistry. *Brain Research* **171**, 11–28.

WÜRGER, S.M. & LANDY, M.S. (1993). Role of chromatic and luminance contrast in inferring structure from motion. *Journal of the Optical Society of America A* **10**, 1363–1372.

YOSHIOKA, T., LEVITT, J.B. & LUND, J.S. (1994). Independence and merger of thalamocortical channels within macaque monkey primary visual cortex: Anatomy of interlaminar projections. *Visual Neuroscience* **11**, 467–489.

ZEKI, S.M. (1978). Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *Journal of Physiology* **277**, 273–290.