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Chromatic properties of neurons in macaque MT

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Abstract

We have studied the responses of MT neurons to moving gratings, spatially modulated in luminance and chromaticity. Most MT neurons responded briskly and with high contrast sensitivity to targets whose luminance was modulated, with or without added chromatic contrast. When luminance modulation was removed and only chromatic stimulation was used, the responses of all MT neurons were attenuated. Most were completely unresponsive to stimulation with targets whose modulation fell within a "null" plane in color space; these null planes varied from neuron to neuron, but all lay close to the plane of constant photometric luminance. For about a third of the neurons, there was no color direction in which responses were completely abolished; almost all of these neurons had a definite minimum response for chromatic modulation near the isoluminant plane. MT neurons that responded to isoluminant targets did so inconsistently and with poor contrast sensitivity, so that only intensely modulated targets were effective. Whereas the best thresholds of MT neurons for luminance targets are close to behavioral contrast threshold, the thresholds for isoluminant targets lie considerably above behavioral contrast threshold. Therefore, although some MT neurons do give responses to isoluminant targets, they are unlikely to be the source of the chromatic motion signals revealed behaviorally.

Keywords: Isoluminance, Motion, Color, Macaque, MT

Introduction

The role of chromatic signals in visual motion processing is much debated. Recent anatomical and physiological results led to the proposal that color and motion are processed by two distinct and independent pathways within the visual system (Zeki, 1978; Hubel & Livingstone, 1987; Livingstone & Hubel, 1984). One pathway originates in the magnocellular layers of the LGN and projects *via* layers 4Cα and 4B in V1 to the middle-temporal area (MT), both directly from V1 and *via* the thick stripes in area V2. Cells along that pathway have high contrast sensitivity, are strongly directional, and are insensitive to color. The other pathway preferentially receives signals from the parvocellular layers of the LGN. It projects to layer 4Cβ in V1, and from there *via* the cytochrome oxidase rich blobs and the thin stripes in V2 to area V4. Cells in this pathway have a low-luminance contrast sensitivity and are often unoriented; they, however, respond well to chromatically defined stimuli. It seems therefore that the anatomically defined pathways are also functionally separate, with the MT pathway being specialized for the processing of motion information, and the V4 pathway for color information. If the two pathways were indeed functionally completely separate, the magno-pathway would be able to convey information about motion only, and would be blind to the color of stimuli. The parvo-pathway would signal the color of stimuli only, unable to determine the direction of motion. Accordingly, the perception of motion would be impossible in the absence of luminance information.

Some early psychophysical results seemed to support this notion (Ramachandran & Gregory, 1978; Livingstone & Hubel, 1987). However, recent investigations into the role of luminance and color have shown that many aspects of motion perception are preserved at isoluminance (Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Lindsey & Teller, 1990) and that subjects can indeed identify the direction of moving isoluminant stimuli.

These results have led several investigators to study the responses of neurons in extrastriate visual area MT to isoluminant stimuli. MT is a small area on the posterior bank of the superior temporal sulcus (Zeki, 1969). In macaques, whose visual system resembles the human visual system (De Valois et al., 1974), area MT is thought to be of special importance in visual motion processing. Neurons in area MT of macaques have been shown to be involved in the analysis of visual motion

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(Zeki, 1974; Albright, 1984; Movshon et al., 1985; Newsome et al., 1991) and the generation of signals guiding pursuit eye movements (Newsome et al., 1985; Movshon et al., 1991*a*).

Physiological studies (Saito et al., 1989; Charles & Logothetis, 1989; Dobkins & Albright, 1990, 1991*a*,*b*) have shown that some MT neurons can respond and retain their direction selectivity at isoluminance. Saito et al. (1989) used drifting bars and measured the response of cells as a function of the bar/background luminance ratio and the drift direction. They observed that in about half of the cells the response was attenuated considerably at a luminance ratio close to unity (the human photometric isoluminance condition).

We have measured the chromatic properties of MT neurons and their sensitivity to targets modulated in luminance and chromaticity. Our goal was to find out how MT cells combine the input from the different classes of cones and whether the sensitivity to chromatic modulations of individual neurons in MT can reach the sensitivity found in psychophysical tasks. Our results show that while some MT neurons do respond at isoluminance (and the pathway is therefore not "color-blind"), they do so in a way that makes them unlikely candidates for the source of chromatic motion signals evident from visual behavior. We have briefly reported some of these results elsewhere (Movshon et al., 1991*b*).

Methods

Preparation and maintenance

These experiments were performed on five young adult *Macaca fascicularis* monkeys weighing between 3 and 4 kg. Animals were initially premedicated with atropine (0.25 mg) and acepromazine maleate (PromAce: 0.05 mg/kg, Aveco Inc., Fort Dodge, IA) or diazepam (Valium:0.5 mg/kg, Steris Labs Inc., Phoenix, AZ). After induction of anesthesia with intramuscular injections of ketamine (Vetalar:10–30 mg/kg, Parke-Davis, Morris Plains, NJ), cannulae were inserted in the saphenous veins and surgery was continued under intravenous anesthesia with Sufentanil citrate (Jansen Pharmaceutica, Piscataway, NJ) as described below.

After cannulation of the trachea, the animal's head was fixed in a stereotaxic frame. A small craniotomy was made over the intraparietal and superior temporal sulci, and after making a small slit in the dura, a tungsten-in-glass microelectrode (Merrill & Ainsworth, 1972) was positioned approximately 3 mm behind the intraparietal sulcus; the hole was then covered with warm agar. Electrode penetrations were directed to the lower bank of the superior temporal sulcus. Action potentials were conventionally amplified and displayed; standard pulses triggered by each impulse were stored by a PDP11 computer 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, Organon Inc., West Orange, NJ) 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 μg/kg/h, and was adjusted according to each animal's tolerance of the drug. 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, Wyeth Inc., Pittsburgh, PA), as well as dexamethasone (Decadron:0.5 mg/kg, Mark Sharp Inc., West Point, PA) to prevent cerebral edema.

The pupils were dilated and accommodation paralyzed with topical atropine, and the corneas protected with gas-permeable +2 diopter contact lenses; supplementary lenses were chosen that permitted the best spatial resolution of recorded units. Lenses were removed periodically for cleaning and the eyes rinsed with saline. At the beginning of the experiment, and before beginning each day's recording, the foveas were located and plotted using a reversible ophthalmoscope.

Track reconstruction and histology

During recording, small electrolytic lesions were produced at locations of interest along the electrode track by passing d.c. current (1–2 μA for 2–5 s, tip negative) through the electrode tip. At the end of the experiment, the animals were sacrificed with an overdose of Nembutal, and perfused through the heart with 2 l of 0.1 M phosphate-buffered saline, followed by 2 l of a solution of 10% formalin. Blocks containing the region of interest were stored overnight in the cold in a postfix solution of 4% paraformaldehyde plus 30% sucrose, after which 40-μm coronal sections were cut on a freezing microtome. Sections were stained for cell bodies with the Nissl stain cresyl violet and every tenth section was stained for myelinated fibers by the method of Gallyas (1979). Tracks were reconstructed and identified by their distinctive pattern of lesions in the cresyl-violet-stained sections. The boundaries of MT were located in the myelin-stained sections.

Visual stimuli

The stimuli were displayed on a Conrac 7211 13-in. color television monitor driven by an Adage 3006 frame buffer controller, controlled in turn by a PDP 11 computer. The frame buffer controller generated images on the monitor by reading through the picture memory in a raster scan and interpreting the numbers in each location as a color defined in a 256-element color lookup table. The intensity of each of the three CRT primaries was controlled by a 10-bit digital-to-analog converter. The frame rate of the display was 120 Hz. Our stimuli were sine-wave gratings modulated around the neutral white point. All of these stimuli had a space- and time-averaged mean luminance of 36 cd/m^2.

We use the color space introduced by Krauskopf et al. (1982) to describe our stimuli (Fig. 1). At the origin is an equal-energy white point with C.I.E. *xy* coordinates of (0.323,0.302). There are two chromatic axes, L − M and S − (L + M). These two axes define a plane of constant luminance, which is essentially the same as the chromaticity diagram proposed by MacLeod and Boynton (1979), the L − M axis corresponding to their *r* coordinate and the S − (L + M) axis to their *b* coordinate. Along the third axis, L + M, luminance is varied. The spectral sensitivities of the long- (L), middle- (M) and short- (S) wavelength-

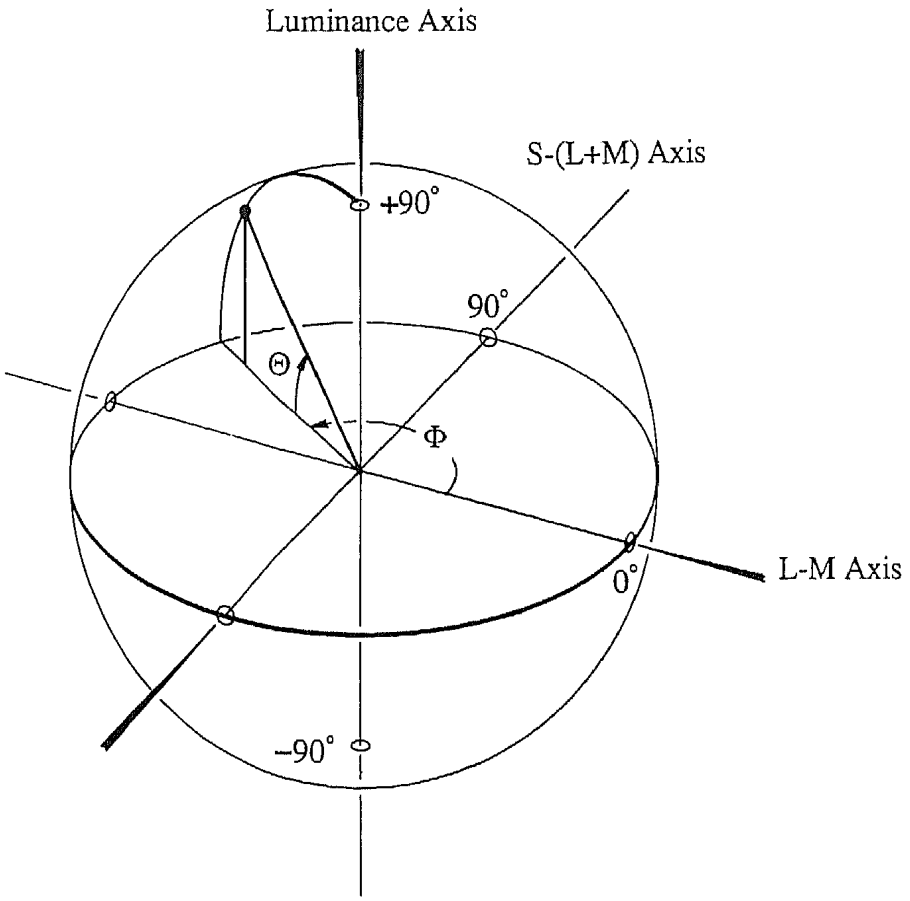

Fig. 1. Color space used to describe the stimuli. The origin is a neutral white. Along the L – M axis, excitation of the L- and M-cones covaries so as to leave their sum constant. Along the S – (L + M) axis only the excitation of the S-cones changes. Along the luminance axis, the excitation of all three cone types is varied in proportion to their excitation at the white point. Φ denotes the azimuth of a stimulus vector, and Θ its elevation out of the isoluminance plane.

sensitive cones on which this space is based are those derived by Smith and Pokorny (1975). By convention we scale the L- and the M-cones so that their sum results in the human photopic sensitivity function $V(\lambda)$. This is achieved by weighting the L-cone wavelength sensitivity twice as much as the M-cone sensitivity (see Boynton, 1979, p. 153).

The rationale for using this particular space is the assumption that the signals at an early stage in the visual system are processed by three independent mechanisms, as found in psychophysical and physiological experiments (Krauskopf et al., 1982; Derrington et al., 1984). The luminance mechanism, L + M, simply sums the weighted input from the L- and the M-cones. The L – M mechanism takes a weighted difference between the L- and the M-cones. The S – (L + M) mechanism takes the difference between the S-cones and the sum of L- and M-cones. The three axes of the cardinal-direction-space are chosen so that changes along each one of them only affect one of the mechanisms and leave the other two constant. This results in the following set of rules: Changes along the L – M axis are achieved by covarying the excitations of the L- and M-cones so as to keep luminance (L + M) constant. The excitation of the S- (short-wavelength-sensitive) cones is constant along this axis. Along the S – (L + M) axis only the S-cone excitation varies and the excitation of the L- and M-cones is constant. Along the luminance axis, the excitations of all three classes of cones vary in proportion to their values at the white point. Note that even though the S-cones do not directly contribute to the luminance mechanism, their excitation is changed by modulation along this axis, too, so that the S – (L + M) mechanism remains unperturbed.

We will frequently describe stimuli by their polar coordinates in this space. The *azimuth* of a stimulus is defined as the angle formed by its projection on the isoluminant plane and the L – M axis. An azimuth of 0 deg, for example, denotes a stimulus modulated along the L – M axis, and an azimuth of 90 deg denotes a stimulus modulated along the S – (L + M) axis. The *elevation* is given by the angle the stimulus forms with its projection on the isoluminant plane. An elevation of 90 deg or −90 deg therefore describes a luminance stimulus, and an elevation of 0 deg describes a stimulus lying in the isoluminant plane.

The scaling of all three axes relative to each other in this space is arbitrary. We chose to scale the axes so that the largest excursion possible on our equipment corresponds to a contrast of 1. Expressed in C.I.E. *xy* coordinates, unit contrast modulation along the L – M axis varied from (0.393,0.267) to (0.236,0.345). This corresponds to a contrast of 18.5% for the M-cones and 9.1% for the L-cones, whereas the excitation of the S-cones is constant along this axis. Unit contrast modulation along the S – (L + M) axis varied from (0.434,0.498) to (0.276,0.220). This corresponds to a contrast of 89% for the S-cones, whereas the contrasts for the L- and M-cones are zero. For a unit contrast luminance modulation, the contrast for all three cone types was 100%. The fact that the cone contrasts are smaller along the L – M axis results directly from the constraint of isoluminance. For a symmetric modulation around an equal-energy white point, the maximum physically realizable cone contrasts are approximately 15% and 34% for the L- and M-cones, respectively. It is not possible to achieve this full modulation on CRT monitors, because the phosphors impose constraints

on the maximum achievable, and our most intense chromatic stimuli reached only about 60% of the physical limits when modulating the L- and M-cones at isoluminance. Moreover, because we wished to use equal modulations in all different color directions, we typically used only 75% of unit modulation. This resulted in cone contrasts of 6.8% and 13.9% for the L- and M-cones along the L − M axis, respectively, and in 66.7% S-cone contrast along the S − (L + M) axis.

For our purposes the directions in which particular classes of cones are silenced are also of special importance. The direction along which the L- and S-cones are silenced and only the M-cones are excited was given by an azimuth of −5 deg and an elevation of −5 deg. An elevation of 9 deg with an azimuth of 7 deg describes the direction along which the L-cones only were modulated. Because intermediate angles do depend on the relative scaling of the three axes, and because we chose to scale our axes relative to the maximal excursions on our equipment, note that these numbers are valid only in the context of this paper.

For ease of expression we will denote the L − M axis as the "red-green" axis, and the S − (L + M) axis as the "blue-yellow" axis. This is slightly misleading because the appearance of stimuli along the S − (L + M) axis is neither blue nor yellow. The stimuli look purplish-blue and greenish-yellow. Stimuli along the L − M axis do appear reddish and greenish, but even at the ends of the axes stimuli do not appear very saturated.

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. We first mapped the location and size of the neuron's minimum response field, 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 using sinusoidal grating stimuli of optimal size proceeded under control of the same PDP 11 computer that controlled the Adage display processor.

Each experiment consisted of several (generally 4–10) blocks of trials. Within each block, all stimuli were presented for the same amount of time (generally 4 s). To minimize effects of response variability, stimuli were presented in a random order within each experimental block, and the results of several repeated blocks averaged. We also measured responses to a uniform grey field of the same mean luminance as our other stimuli to measure the cell's spontaneous firing rate.

Quantitative data from 127 neurons were obtained. Twenty-two of the neurons had their receptive fields centered within 1 deg of the fovea and 75% were within 3.6 deg of the fovea. The average eccentricity was 2.9 deg. First, we quantitatively determined each cell's tuning for orientation and direction of movement, spatial frequency, temporal frequency, and contrast response for luminance gratings. As expected for area MT, the great majority of these were completely direction-selective, and had large visual receptive fields of a generally "complex" character. Sizes typically varied between 2 deg × 2 deg for the most central fields and 4 deg × 4 deg for fields within 4 deg of the fovea. After completion of these basic measures, we proceeded with the experiments that are the subject of this paper.

Behavioral measurements

To allow a comparison of the neuronal responses to psychophysical data, we measured behavioral thresholds for an adult pigtail macaque (*Macaca nemestrina*).

The target was a foveally viewed sinusoidal grating with a spatial frequency of 1 cycle/deg, vignetted by a two-dimensional Gaussian with a standard deviation of 1 deg visual angle and a duration of 500 ms. Mean luminance and mean chromaticity were the same as in the physiology experiments. Targets were foveally presented for a relatively long duration to obtain conditions under which psychophysical performance at isoluminance is optimal (Stromeyer et al., 1990; Gegenfurtner & Hawken, 1992; Derrington & Henning, 1993).

The monkey, who was seated in a testing cage, was trained by standard operant techniques to identify the direction of motion of the sine-wave gratings moving at a variety of temporal frequencies (1–8 Hz) matching those used in the physiology experiments. The details of the experimental procedure have been described elsewhere (Williams et al., 1981; Kiorpes, 1992; Kiorpes et al., 1993). Briefly, the animal controlled stimulus presentations by placing his face in a face mask mounted on the testing cage. He viewed the display with his natural pupils and gave responses by pulling one of two bars mounted inside the cage. The animal had restricted access to water outside of the testing room and correct responses during testing were rewarded by 0.25 ml of diluted (40%) apple juice; incorrect responses were followed by a tone and a time-out. The duration of the tone and time-out were under the experimenter's control and were adapted to optimize the animal's performance.

This experiment used the method of constant stimuli. For each temporal frequency, five stimulus contrasts were chosen to span the performance range from chance to 100% correct. The stimuli were presented in a randomized block design. Each block contained a presentation of each stimulus presented in pseudorandom order. Fifty trials per stimulus condition were collected. The threshold for a grating with a temporal frequency of 1 Hz was obtained first. After performance had stabilized and threshold had not improved on several consecutive days of testing, we repeated the same procedure with a temporal frequency of 8 Hz.

We used a maximum-likelihood method based on probit analysis (Finney, 1971) to fit the integral of a Gaussian to each set of data. This analysis yielded estimates of thresholds and standard errors of the estimate for each conditions. Threshold is defined as the 75% correct point.

Results

Chromatic preferences

After determining each cell's optimal orientation, spatial frequency, temporal frequency, and size, using luminance stimuli we measured the cell's chromatic properties. If cells combine the input from the different cone classes linearly, the responses to all colors can be predicted from measurements in just a few directions of color space. This approach was successfully used

by Derrington et al. (1984) to characterize the chromatic properties of LGN neurons, and by Lennie et al. (1990) for neurons in V1. We therefore tested 47 cells using stimuli similar to the ones used by the above investigators; gratings at four different azimuths at elevations of 0 (isoluminant) and 45 (later on 20) deg and a luminance grating. The contrast was set to 75% of unit contrast, which was the largest contrast achievable in all color directions. This was done for the cell's preferred spatial frequency as well as for a spatial frequency towards the lower end of its tuning curve. Psychophysically the spatial-frequency sensitivity is low-pass for isoluminant gratings and bandpass for luminance (Mullen, 1985), and a similar behavior is often exhibited by cortical neurons (Lennie et al., 1990). Therefore we explored the possibility that the best response to isoluminant gratings might be at a lower spatial frequency than for luminance.

All 47 cells gave brisk responses to stimuli with a luminance component (elevation > 0 deg) irrespective of the azimuth of the stimulus. In all cases, it was the luminance component of the stimulus that determined the response, and at an elevation of 20 deg (25% luminance contrast) the response for most cells was already saturated. In the same experiment, none of the responses at photometric isoluminance (elevation = 0 deg) showed any systematic tuning. Responses to isoluminant stimuli in this experiment were hardly above the baseline response. This response pattern is consistent with cells responding best to an elevation of 90 deg (luminance) and having their response null plane in the isoluminant plane. However, we frequently observed that the cell's response to an isoluminant grating would be especially poor after presentation of a high-contrast luminance grating. Therefore we changed the experiment and excluded stimuli with luminance contrast from the stimulus set. For 17 different cells, we measured the response to eight directions in the isoluminant plane. The responses were still rather small, but for 13 out of the 17 cells tested this way the maximum response at photometric isoluminance was at least twice as large as the response baseline. We used the results of this experiment to extract the cell's optimal azimuth. The linear model of Derrington et al. (1984) provided a good fit for these 13 cells. For the remaining cells, we simply defined the optimal azimuth to be the color direction where each cell gave its best response. Fig. 2 shows a histogram of the preferred azimuths obtained in this experiment. The distribution is centered around the red–green axis. None of the observed cells responded best to blue–yellow modulations. This is the case even though the cone contrasts in the blue–yellow direction were significantly higher (66.7%) than the contrasts in the red–green direction (13.9% for the M-cones, 6.8% for the L-cones). There was very little if any S-cone input to these cells.

In all subsequent experiments, we used the cell's optimal azimuth if there was a clear maximum response, and an azimuth of 0 deg (red–green) otherwise.

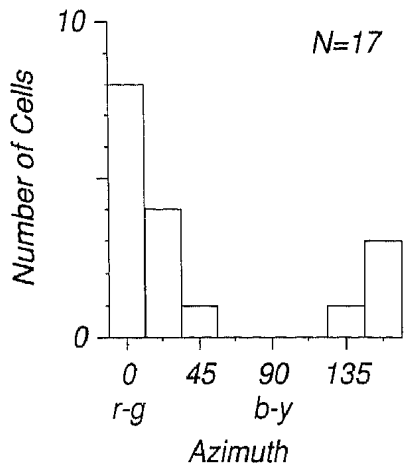

Fig. 2. Distribution of preferred azimuths for 17 MT cells. For each cell, we tested eight different color directions in the isoluminant plane. The preferred azimuth was defined as the color direction in which the cell gave the largest response. An azimuth of 0 deg corresponds to a preference for red–green gratings, and an azimuth of 90 deg to a preference for blue–yellow gratings.

Distribution of null plane elevations

After determining its chromatic preferences, we tried to see for any given cell whether the response could be nulled at isoluminance. Given the results of the above experiments, we expected most cells to have a null response close to photometric isoluminance. If a unit linearly sums the inputs from the L- and the M-cones, it should be possible for an increase in L-cone excitation to be balanced by a decrease in M-cone excitation, so that the net input to the unit does not change and its response stays constant (see Shapley, 1990). The ratio of the excitations for the L- and M-cones at which this "silent substitution" occurs will then tell us how the cell weights the different cone types. This response null will always occur in a direction between the +L and the −M direction. In particular, a cell that sums L- and M-cone excitations in the same ratio as the photometric standard will have a null in the isoluminant plane. A cell that takes the difference between L- and M-cone inputs, on the other hand, requires that an increase in L-cone input be balanced by an increase in M-cone input for the net input (L − M) to stay constant. The null for such a cell will occur between the +L and +M direction. A cell taking the exact difference of L- and M-cone input will null in the luminance direction.

In our experiment, we varied the elevation of the modulation around the photometric isoluminant plane. All of the stimuli had a constant chromatic component of 75% of unit contrast. To that we added small amounts of luminance contrast. For each of these colored stimuli, we included a stimulus having exactly the same amount of luminance contrast, but no chromatic component. Fig. 3 illustrates the scheme. The vertical arrows represent luminance stimuli of increasing contrasts, up to 25% (corresponding to the chromatic stimulus with an elevation of 20 deg). The arrows tilted towards the positive diagonal represent colored gratings in which the red bars of the grating were brighter than the green bars. Similarly, arrows tilted towards the negative diagonal represent grating stimuli with bright green and dark red bars. All colored gratings have the same chromatic contrast, and for each colored grating there was one black-white grating whose luminance contrast matched the luminance contrast component of the colored grating. The spatial frequency of the gratings was near or slightly below the optimal frequency for luminance gratings.

Depending on how a given cell combines the input from the different cone types, its response will vary for these stimuli. Cells that add input from the L- and the M-cones according to photometric luminance will respond to the luminance component

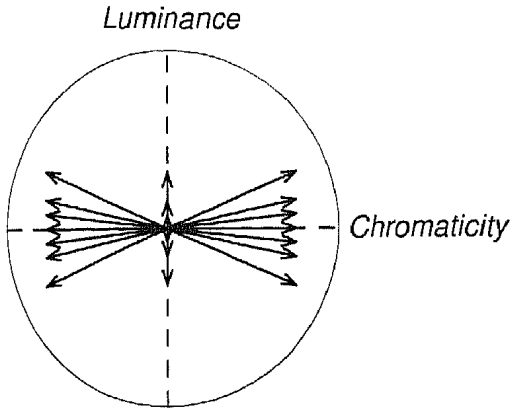

Fig. 3. Schema to illustrate the stimuli used in the elevation experiment. The circle shows a vertical section through the color space in Fig. 1. On the horizontal axis the luminance of the stimuli is constant and the chromatic contrast varies. On the vertical axis luminance is varied. The almost horizontal arrows through the origin represent stimuli with the same chromatic contrast and various amounts of luminance contrast. The vertical arrows through the origin represent low contrast luminance stimuli. Each stimulus with chromatic and luminance contrast has a corresponding stimulus with the same luminance contrast and no chromatic contrast.

of the stimuli only. Responses of these cells do not depend on the chromatic component of the stimulus at all and will therefore be equal for bright-red, bright-white, or bright-green stimuli of the same luminance contrast. Cells that take the difference between L- and M-cone input behave in exactly the opposite way. They will give equal responses to all colored stimuli, irrespective of their luminance contrast. Furthermore, if a cell responds to luminance modulations, but weights its inputs in a way that is different from the human photometric luminance sensitivity curve $V(\lambda)$, then its response curve will be parallel to the luminance response curve, shifted to the right or to the left. This type of cell will give a response at photometric isoluminance, but will be silent for some other elevation instead.

We ran this experiment on 48 cells. The limited luminance contrasts used in this experiment improved the consistency of the responses. The responses of three cells were erratic and were therefore excluded from subsequent analysis. Fig. 4 shows examples of the types of cells we observed. In each plot the filled symbols show the luminance contrast response, while the open symbols show the response to combinations of luminance and color contrast (see Fig. 3). Most of the cells (37 of 45, 82%) behaved like the unit shown in Fig. 4A or 4B, which had a distinct null at an elevation close to photometric isoluminance. The responses to all stimuli were fully accounted for by the lumi-

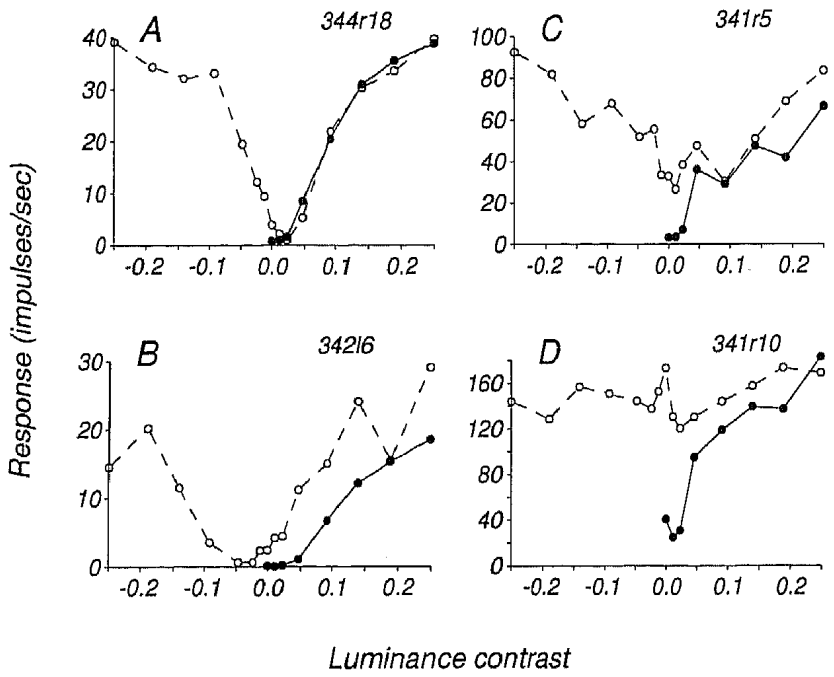

Fig. 4. Typical response patterns observed in the elevation experiment as a function of luminance contrast. The open symbols indicate the response to stimuli having a chromatic component. The closed symbols indicate the responses to purely luminance stimuli. Baseline responses were subtracted. For chromatic stimuli, the contrast of the chromatic component was fixed at 75% of the maximum of our monitor. A: This cell was representative of the most common type. It had a complete null very close to the photometric isoluminant point. The response was fully explained by the luminance component of the stimulus. For this cell the temporal frequency was 7.5 Hz, spatial frequency was 0.4 cycles/deg, and azimuth was 22.5 deg. B: This cell had a null at an elevation close to photometric isoluminance. Its response could also be attributed solely to the luminance component of the stimulus. The preferred temporal frequency for this cell was 7.5 Hz, spatial frequency was 0.4 cycles/deg, and azimuth was 157.5 deg. C: This cell had a minimum response close to isoluminance, but the response did not decrease to baseline. For higher luminance contrasts, the response curves for luminance and color overlapped. Temporal frequency was 7.5 Hz, spatial frequency was 0.4 cycles/deg, and azimuth was 10 deg. D: This cell did not show a minimum response over the range of elevations we used. For this cell the temporal frequency was 3.75 Hz, spatial frequency was 2.3 cycles/deg, and the azimuth was 0 deg. We tested this cell with gratings of different spatial frequencies and the peak spatial frequency for isoluminant gratings was equal to that for luminance.

nance response curve. The unit in Fig. 4A summed its cone inputs according to the photometric luminance sensitivity curve $V(\lambda)$. The chromatic component did not alter its response at all. The unit in Fig. 4B weighted the cone types slightly differently, but also showed a complete null close to photometric isoluminance. Still, because of its high sensitivity, the unit in Fig. 4B gave a response at photometric isoluminance significantly higher than baseline. For 12 of the 37 (32%) cells, the response at photometric isoluminance was higher than twice the baseline firing rate. The unit in Fig. 4C had its minimum response at photometric isoluminance, but even though there was a distinct minimum the response at the minimum was significantly above the response baseline. Of all 45 cells, three (7%) showed this response pattern. Finally, there were five cells (11%) that can be classified as having color-opponent input. Their response did not null or reach a minimum at any elevation between the L- and M-cone isolating directions. One of these five cells (the one shown in Fig. 4D) did not null at all for any of the elevations tested. It exhibited a brisk response that was constant across all elevations and equal to the response at a luminance contrast of 25%.

In the above scheme, the few cells like the one shown in Fig. 4D are the only ones that showed signs of chromatically opponent input. However, because of small (Fig. 4B) deviations of each cell's individual isoluminant point from photometric isoluminance, and because of some cell's (Fig. 4C) residual response at their null, many cells did actually show a significant response to isoluminant gratings. Twenty of the 45 cells (44%) gave a response at a level higher than twice their baseline to isoluminant stimuli. In contrast, only eight cells (18%) gave a significant response at the elevation where they had their response minimum.

We defined a "color-index" to allow us to specify the strength of the responses at isoluminance. Color-index denotes the magnitude of the response at photometric isoluminance divided by the cell's response to a luminance stimulus having the same rms-cone-contrast. Fig. 5 plots a histogram of that measure. Relatively few cells, 13 of 45 (29%), respond better to chromatic modulation than to luminance modulation. The median value for the color-index was 0.330 for our sample. Cells with large color-indices typically had a null significantly different from photometric isoluminance and were relatively insensitive to luminance. However, all of the cells responded well to luminance stimuli, no cell showed a null or a response minimum in the luminance direction. Even though the amplitude of the chromatic modulation is at 75% of what we can obtain on our monitor, only one of the cells (Fig. 4D) reached a response as large as to the stimulus having the maximum luminance contrast of 25%.

Fig. 6 shows the distribution of the elevations where each unit showed its minimum response. The distribution is approximately centered around an elevation of 0 deg and, as described above, most cells showed their minimum response close to an elevation of 0 deg. For reference, the arrows in the graph indicate the directions in which only the L- or the M-cones are stimulated. All the cells with null elevations in between the arrows add inputs from L- and M-cones. This distribution of null elevations is quite similar to what Derrington et al. (1984) and Logothetis et al. (1990) observed for neurons in the magnocellular layers of the LGN. Different fill-patterns in Fig. 6 indicate data from different monkeys. There was no significant difference among the null elevations in the different animals.

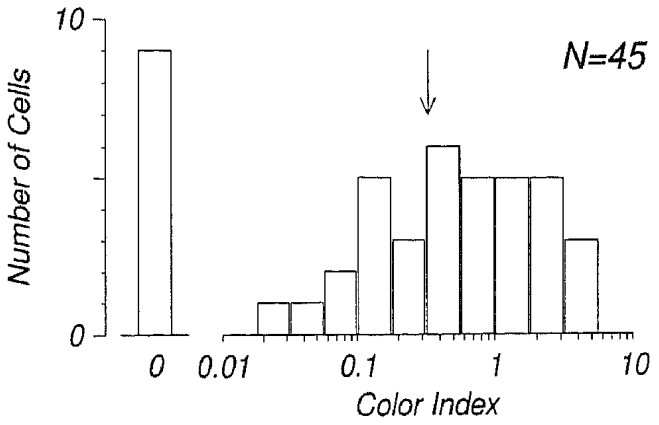

Fig. 5. Distribution of color-indices for the 45 cells from the elevation experiment. The color-index is defined as the magnitude of the response at isoluminance (10.9% rms cone contrast: 6.8% L-cone contrast, 13.9% M-cone contrast, response baseline subtracted) divided by the cell's response to a luminance stimulus with approximately the same rms cone contrast (10%, response baseline subtracted). The median value of the color-index was 0.33 (shown by the arrow), indicating a much smaller response to stimuli defined by color only. Cells with a large color-index typically nulled at elevations significantly away from photometric isoluminance.

Spatial-frequency tuning

It could be that the relatively weak responses to color gratings observed in the preceding experiment were due to the fact that the best spatial frequency for colored gratings is lower than for luminance. For 44 cells, we therefore measured spatial-frequency tuning curves for luminance and isoluminant gratings of optimal orientation and optimal azimuth in the isoluminant plane. We measured responses to drifting gratings whose spatial frequency varied in half-octave steps from 0.1 to 10 or more cycles/deg. We also measured responses to full-field modu-

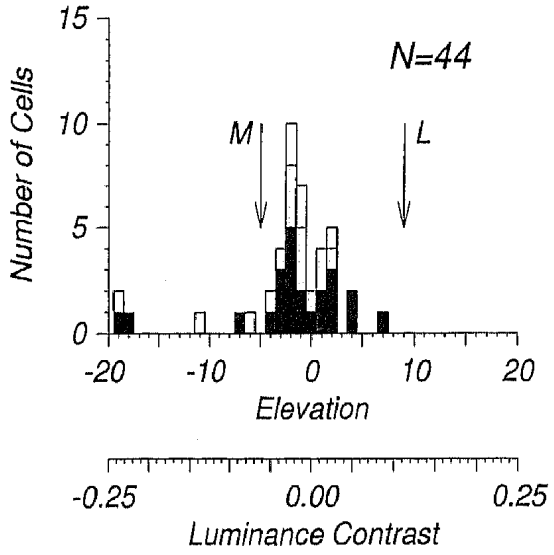

Fig. 6. Distribution of elevations where the cells gave a minimum response. One out of 45 cells did not show a minimum for elevations between −20 deg and 20 deg. Very few cells had their minimum outside the elevations where L- and M-cones are selectively stimulated (indicated by the arrows). Those cells were chromatically opponent. Different shading indicates data from different monkeys. The second abscissa indicates the luminance contrasts of the stimuli.

lation (0 cycle/deg). The contrast of all stimuli was set to be 75% of the maximum modulation in that direction of color space. To each spatial-frequency response function, we fitted a difference-of-exponentials function and derived the optimal spatial frequency and the spatial-frequency bandwidth. The spatial-frequency bandwidth (in octaves) is the ratio between the high and low spatial frequencies where response fell to half of the maximum.

For 24 of these 44 cells, the responses to isoluminant targets were small and erratic, and we could not extract any meaningful tuning parameters. It is interesting to note that none of these cells gave a consistent response even at the highest spatial frequencies, where chromatic aberrations might lead to serious luminance artifacts in the stimulus. For the remaining 20 cells, we compared the spatial tuning curves obtained with isoluminant stimuli to those derived with gratings modulated in luminance. Fig. 7 shows the response curve of a typical cell for luminance and isoluminant stimuli. This cell responded well at photometric isoluminance. Note that there is no sign that the chromatic response peaked at a lower spatial frequency than the luminance response.

Fig. 8 shows the estimates of the peak spatial-frequencies and spatial-frequency bandwidths derived from the curves obtained with purely luminance *vs.* purely chromatic stimuli. These scatter diagrams clearly show that these estimates did not vary in any systematic way between the two conditions. In each graph, the dotted line has a slope of 1, as would be expected if the cells' spatial characteristics were identical with luminance and chromatic stimuli.

Temporal tuning

For a small number of neurons, we also measured a temporal-frequency tuning curve for isoluminant stimuli. Temporal frequency was varied from 0.5 Hz to 30 Hz, all other parameters were set to the cell's optimal values for isoluminant targets. As above, the contrast was set to 75% of unit contrast. As with the spatial-frequency tuning, there was no apparent systematic difference in the tuning to luminance and isoluminant targets. Most noticeably, tuning curves were bandpass even for the isoluminant stimuli, like the one illustrated in Fig. 9.

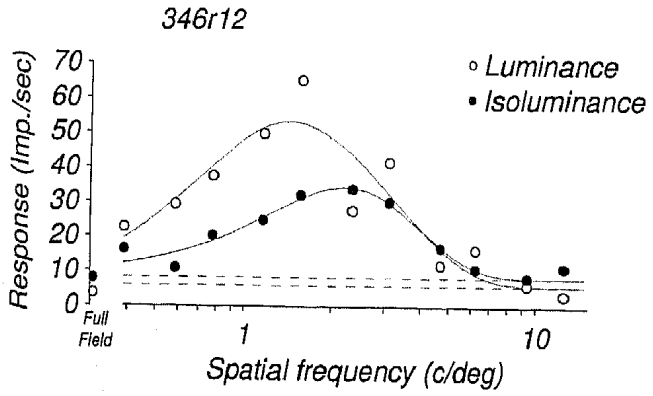

Fig. 7. Example spatial-frequency tuning curve for luminance (open symbols) and isoluminant (filled symbols) gratings. The solid lines show the best fits of a smooth function (difference of exponentials). The dashed lines show the baselines for the two experiments. This cell had a preferred temporal frequency of 3.75 Hz for luminance gratings. It did show a response minimum (with a significant response) at an elevation of −11 deg in the elevation experiment.

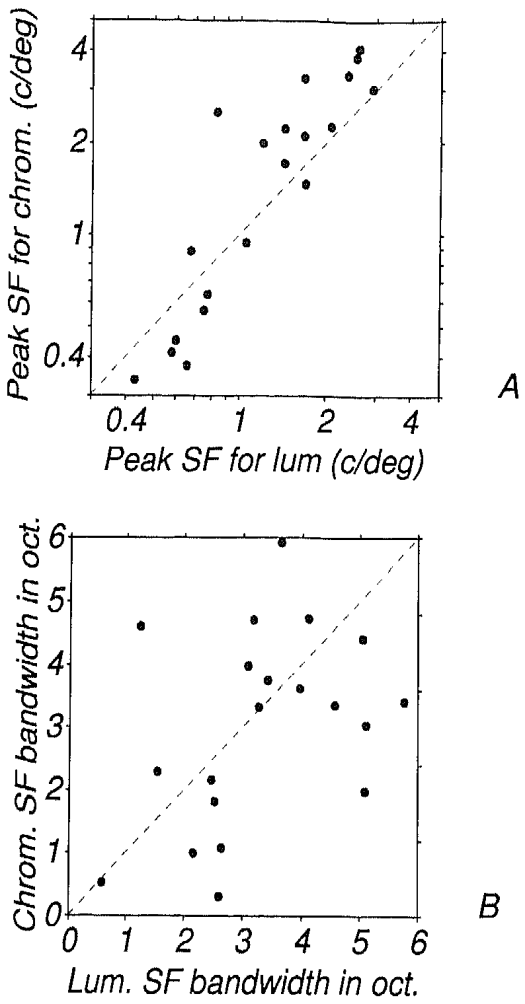

Fig. 8. Scatter diagram showing (A) peak spatial frequency and (B) bandwidth tuning for luminance and chromatic spatial-frequency tuning curves.

Orientation tuning and directional selectivity

For a small number of cells, we also measured a tuning curve in response to variations of orientation and direction of stimulus movement using isoluminant stimuli. Orientation was varied from 0 deg to 360 deg in steps of 22.5 deg. All other parameters were set to the cell's optimal values for isoluminant targets. Contrast was set to 75% of unit contrast. As with the spatio-temporal tuning, there was no apparent systematic difference in the tuning to luminance and isoluminant targets. Directionality was preserved at isoluminance and the preferred orientations for luminance and isoluminance was within measurement error, as illustrated for the unit shown in Fig. 10.

Response to variations in contrast

For cells that gave a significant response to stimuli in the isoluminant plane, we measured contrast-response functions to isoluminant chromatic stimuli. Representative functions are shown in the top of Fig. 11. For comparison, the bottom panel of Fig. 11 shows a sample of typical contrast-response functions obtained with stimuli modulated in luminance. The contrasts in this figure are expressed as the root-mean-square (rms) of the independent modulation of the L- and the M-cones. For luminance stimuli this corresponds to the conventional Michelson contrast. Under the constraint of isoluminance, the largest

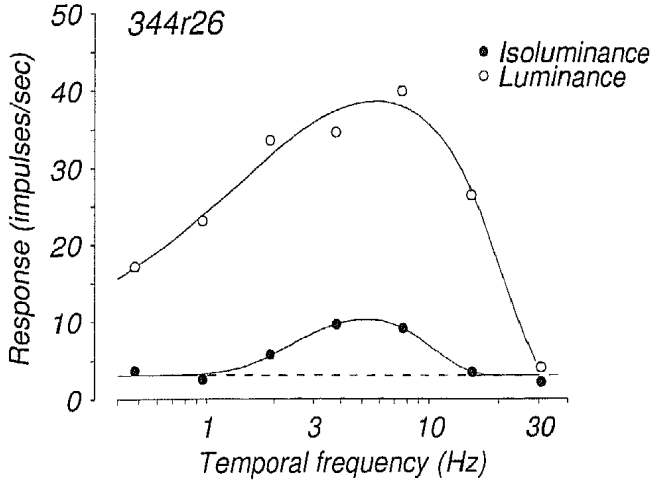

Fig. 9. Example temporal-frequency tuning curve for luminance (open symbols) and isoluminant (filled symbols) gratings. The solid curves show the best fit of a smooth function (difference of exponentials). The dashed line indicates the response baseline. This cell had a preferred spatial frequency of 0.4 cycles/deg for both luminance and isoluminant stimuli. In the elevation experiment it had a complete null at an elevation of 1 deg.

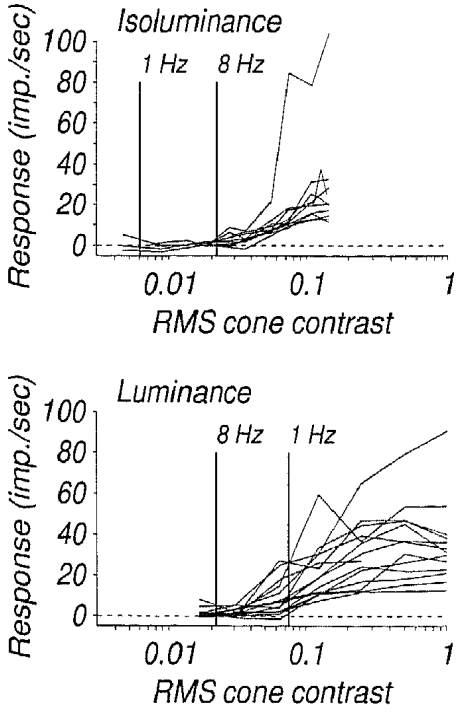

Fig. 11. Typical contrast response curves for (A) isoluminant and (B) luminance stimuli. Typical response curves are shown for luminance. For the isoluminant case, we show only the cases where there was a significant increase in response with contrast. Temporal frequencies used in both cases were chosen to be optimal for each cell and varied from 1.9 Hz to 7.5 Hz with a mean of 5.8 Hz. Average low-frequency cutoff (at half-height) was 1.6 Hz, and the average high-frequency cutoff was 13.3 Hz. Spatial frequencies were also chosen to be optimal for each neuron and varied from 0.4 to 3.1 cycles/deg. There was no difference in the average spatiotemporal tuning parameters for (A) and (B). The vertical lines show contrast thresholds measured in a behavioral experiment for two different temporal frequencies (see text and legend to Fig. 12).

contrast level obtainable is restricted to 14.5% (9.1% L-cone contrast and 18.5% M-cone contrast). It is interesting to see that both sets of response curves begin to rise at about the same level of rms cone contrast.

Behavioral data

To allow us a comparison of the neuronal contrast responses with psychophysical data, we measured behavioral thresholds for an adult pigtail macaque (*Macaca nemestrina*). Psychometric functions were measured in the luminance direction of color space as well as seve
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tions) are also plotted in Fig. 11 as thick vertical lines on top of the contrast-response curves for luminance and isoluminance. In accordance with human psychophysical results (Stromeyer et al., 1990; Gegenfurtner & Hawken, 1992; Derrington & Henning, 1993), we found that in a cone-contrast metric thresholds are lowest for slowly moving, foveally presented isoluminant red–green gratings. Sensitivity is about ten times higher than to luminance gratings of the same temporal frequency. At the higher temporal frequency (8 Hz) thresholds were almost equal for luminance and isoluminance when expressed as rms cone contrast.

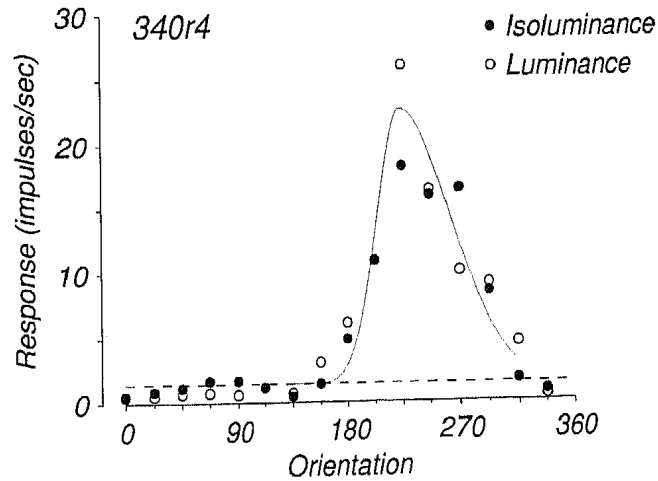

Fig. 10. Example orientation tuning curve for luminance (open symbols) and isoluminant (filled symbols) gratings. The solid curve shows the best fit of a smooth function (asymmetric Gaussian) to the luminance data points. The dashed line indicates the response baseline. This cell showed a response minimum (at about twice the spontaneous firing rate) at an elevation of +2 deg. Its preferred spatial frequency was 1.2 cycles/deg, and its preferred temporal frequency was 7.5 Hz for luminance gratings.

Discussion

Summary

Our results show that the responses of most cells in area MT can be fully explained by summation of their inputs from the L- and M-cones; few cells show any sign of color-opponent input. Because many of the cells have their null elevation slightly

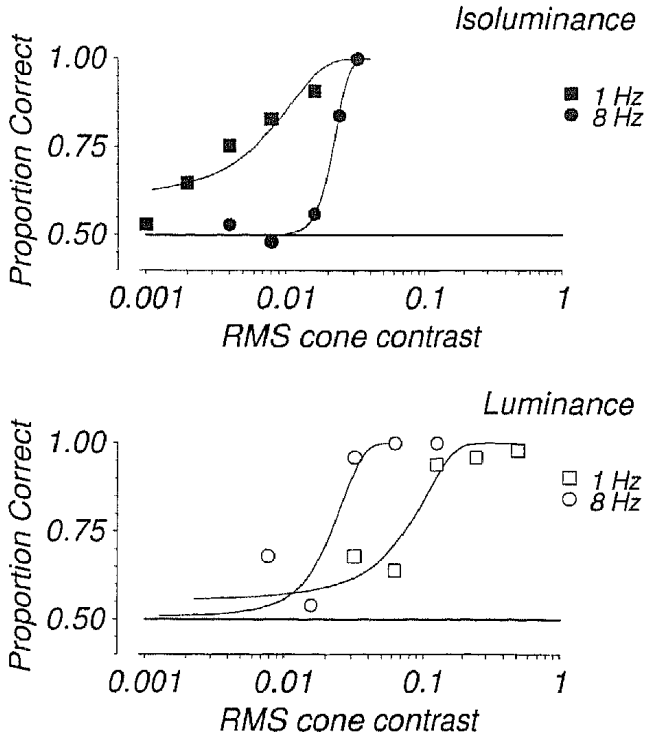

Fig. 12. Psychometric functions for identifying the direction of motion of a foveally presented 1 cycle/deg sinusoidal grating vignetted by a two-dimensional Gaussian window. The subject in this experiment was TJ, an adult pigtail macaque. Circles indicate thresholds for a grating with a temporal frequency of 8 Hz, and squares are for a temporal frequency of 1 Hz. The top graph is for isoluminance, and the bottom graph is for luminance.

tilted away from the photometric isoluminant plane, they do show a weak but significant response at photometric isoluminance. Whereas cells respond to luminance stimuli briskly and with high sensitivity, they respond only to the highest chromatic contrasts obtainable on our display.

Comparison to other studies

Our results are in good qualitative agreement with those of Saito et al. (1989), who measured the responses of MT cells to drifting bars with various degrees of luminance and color contrast. Most neurons in their experiment showed a considerable decrease in response at or near photometric isoluminance (similar to the cells shown in Figs. 4A and 4B), but about half of their cells showed a significant and directional response. The response patterns Saito et al. observed for these cells are similar to those shown in Figs. 4C and 4D. The fact that Saito et al. found these cells in higher proportion than we did is most likely a result of the higher chromatic contrasts they were able to use. Because they used colored bars on a colored background instead of symmetric modulation around a mean-white cone contrasts in their experiment might have been as high as 40%. Saito et al. quantified responsivity of cells by computing a "null-index," the minimum response of a cell to an isoluminant stimulus divided by its maximum response to a grating with both luminance and chromatic contrast. This measure is hard to interpret without knowing the exact cone contrasts used in their experiments, but it seems that, as in our experiments, all cells gave a good response to luminance. There is one result, however, that we could not replicate. Saito et al. (1989) show that adding chromatic contrast improves the response to luminance contrast. We compared responses to a 14% luminance stimulus with and without a chromatic grating added and found no statistically significant difference in the responses of 45 cells ($t = 0.85$, $df = 44$). The fact that for most cells the responses at photometric isoluminance are due to variations in the individual cell's isoluminant point also explains why Saito et al. found good responses for different color combinations (cyan–magenta and blue–yellow). Our results on different color combinations in the isoluminant plane indicate that responses are always best in the L − M direction. This is the case even though along this axis the cone contrasts for the L- and the M-cones are relatively small (about 9.1% and 18.5%, respectively), and along the S − (L + M) axis the contrast in the S-cones is as high as 89%. This agrees well with psychophysical findings that the S-cones contribute little if anything at all to the luminance mechanism (Eisner & MacLeod, 1980; Lee & Stromeyer, 1989; Stockman et al., 1991). Other investigators (Charles & Logothetis, 1989; Dobkins & Albright, 1990, 1991*a*,*b*) also reported significant responses to isoluminant stimuli. The proportions they reported are slightly higher than we found. Once again, this might be due to the higher chromatic contrasts used in their experiments.

Visual pathways

Based on previous studies, it was not clear whether the responses of MT neurons were based exclusively on magnocellular input to MT, or whether there also was some input from the parvocellular pathway (Maunsell et al., 1990). Our results indicate that magnocellular input alone can explain the sensitivity of almost all MT neurons to color. The distribution of null elevations we observe is indeed quite similar to what Derrington et al. (1984) had found in the magnocellular layers of the LGN, and quite different from the distribution in the parvocellular layers. However, in our sample we did find one neuron which behaved as if its response was based on parvocellular input, and Saito et al. (1989) found a slightly higher proportion of cells showing this response pattern. It is quite possible that some cells in MT actually get input from both magno- and parvocellular LGN neurons, and that some of the neurons showing a complete null in our experiments would have responded to isoluminant stimuli with a higher chromatic contrast. This is in good agreement with the finding of Maunsell et al. (1990) that a small portion of MT multiunit responses remain even after a block of the magnocellular LGN.

Lesion studies also indicate severe deficits in the perception of motion of random dots moving at moderate velocities after magnocellular LGN lesions (Schiller et al., 1990, 1991). In these experiments, parvocellular lesions did not have any noticeable effect on the motion of both luminance-defined and isoluminant dots. Magnocellular lesions led to severe deficits for luminance-defined moving random dots. Merigan et al. (1991) also found deficits for the identification of the direction of motion of a 1 cycle/deg Gabor patch moving at moderate to high velocities after magnocellular LGN lesions. However, for slowly moving stimuli (1 deg/s) there was no deficit for identifying the direction of motion.

The fact that most of the cells did have a complete null was quite surprising to us. MT neurons presumably sum inputs of a whole set of LGN neurons. Any significant variation of the individual nulls of these input cells would lead to a significant

residual response of an MT neuron (Logothetis et al., 1990). However, this was not usually evident. Furthermore, we also saw variation in null elevations in cells within one animal, implying that the isoluminant point for an MT cell does not directly depend on factors like the ratio of M- and L-cones.

Comparison to behavioral data

Recent experiments by Britten et al. (1992) support the possibility that the psychophysical performance for detecting moving targets is mediated by cells in area MT. Our results show also that for drifting luminance gratings the threshold for the most sensitive MT neurons is comparable to the threshold levels observed behaviorally in macaque monkeys. It is natural to ask whether cells in MT could also support the perception of moving isoluminant targets. The sensitivity to isoluminant targets in psychophysical tasks is typically thought to be lower than to luminance targets, implying that motion processing is impaired at isoluminance. It is therefore tempting to speculate that the reduced sensitivity of MT cells at isoluminance directly underlies the reduced sensitivity revealed in psychophysical tasks. Fig. 11 compares neuronal contrast-response curves with our psychophysical data obtained under matching conditions. The fast condition (8 Hz) is close to the peak temporal frequency for most MT neurons and significantly below the high-frequency cutoff for all of the cells whose contrast responses are shown in Fig. 11. The slow condition (1 Hz) for most MT neurons is below the low-frequency cutoff for most cells shown in Fig. 11. The response curves of Fig. 11 therefore represent an upper limit on the responses of MT cells to slowly moving targets, and are representative for fast moving targets. Under the 8-Hz condition, the behavioral thresholds fall right onto the rising portion of the contrast-sensitivity curve, both for luminance and at isoluminance. As mentioned above, for slower speeds contrast sensitivity of these cells would be poorer. This matches the behavior observed psychophysically for the luminance condition. Thresholds are higher at 1 Hz than at 8 Hz. However, the reverse holds for isoluminance. The psychophysical threshold for identifying the direction of motion of a 1-Hz grating was significantly lower than that for the 8-Hz grating, and much lower (half a log unit) than the sensitivity of the neurons at their optimal temporal frequency.

If we assume that the pooling and decision rules that relate neuronal performance to behavioral threshold are the same for MT responses to luminance and isoluminance, then this result makes it quite unlikely that perceptual judgements about isoluminant gratings, at least at slow drift rates and for foveally presented targets, are based on the responses of MT cells. The assumption about equal pooling rules can be challenged. There is psychophysical evidence that the integration time of the visual system might be longer at isoluminance (Mullen & Boulton, 1992; Chaparro et al. 1993). However, the cells responding to luminance and isoluminance in MT have the same temporal tuning properties for both types of stimuli. Furthermore, as we have seen the responses of MT neurons to color are due to cells that respond best to luminance stimuli. It has been shown in previous psychophysical studies (Stromeyer et al., 1990; Gegenfurtner & Hawken, 1992) that in a cone contrast metric sensitivity for direction of motion is best to slowly moving isoluminant stimuli presented foveally, and that the motion of most slowly moving stimuli is identified by a chromatically opponent mechanism. Our behavioral data above confirm this result. This is in sharp contrast to the nature of the chromatic response of MT neurons. Interestingly enough, Gegenfurtner and Hawken (1992) also found that fast moving targets might be detected by a single motion mechanism, irrespective of their color. Therefore it seems quite likely that MT is the neural substrate for the detection of motion for fast moving isoluminant targets. However, it does not seem to be the neural substrate for the detection of motion in slowly moving foveally presented isoluminant targets. Color-sensitive cells in other areas of visual cortex might be sensitive to direction of motion, and might mediate the detection of motion for slowly moving isoluminant targets.

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