

# Segmentation by Color Influences Responses of Motion-Sensitive Neurons in the Cortical Middle Temporal Visual Area

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We previously showed that human subjects are better able to discriminate the direction of a motion signal in dynamic noise when the signal is distinguished (segmented) from the noise by color. This finding suggested a hitherto unexplored avenue of interaction between motion and color pathways in the primate visual system. To examine whether chromatic segmentation exerts a similar influence on cortical neurons that contribute to motion direction discrimination, we have now compared the discriminative capacity of single MT neurons and psychophysical observers viewing motion signals with and without chromatic segmentation. All data were obtained from rhesus monkeys trained to discriminate motion direction in dynamic stimuli containing varying proportions of coherently moving (signal) and randomly moving (noise) dots. We obtained psychophysical and neurophysiological data in the same animals, on the same trials, and using the same visual display. Chromatic segmentation of the signal from the noise enhanced both neuronal

and psychophysical sensitivity to the motion signal but had a smaller influence on neuronal than on psychophysical sensitivity. Hence the ratio of neuronal to psychophysical thresholds, one measure of the relation between neuronal and psychophysical performance, depended on chromatic segmentation. Increased neuronal sensitivity to chromatically segmented displays stemmed from larger and less noisy responses to motion in the preferred directions of the neurons, suggesting that specialized mechanisms influence responses in the motion pathway when color segments motion signal in visual scenes. These findings lead us to reevaluate potential mechanisms for pooling of MT responses and the role of MT in motion perception.

*Key words:* visual cortex; motion processing; color processing; image segmentation; extrastriate; middle temporal; direction selectivity; direction discrimination; monkey; behavior; psychophysics; neurophysiology

Determining the direction in which a friend moves through a crowd is easier if she wears a distinctively colored hat. The hat allows segmentation on the basis of chromatic structure in the scene, improving detection of the motion of the segmented object. We previously documented this naturalistic interaction between color and motion processing, leading to an important general insight into the nature of cue interactions: scene structure formed on the basis of one cue influences how another cue is processed (Croner and Albright, 1997). Despite the abundant effects of such cue interactions on our everyday behavior, little is known about the neural mechanisms involved.

We explored this interaction using a visual stimulus and experimental paradigm used widely in recent studies of motion processing (Williams and Sekuler, 1984; Newsome and Paré, 1988; Downing and Movshon, 1989; Newsome et al., 1989; Britten et al., 1992, 1993). The stimulus consists of a dynamic array of dots, a variable fraction of which move coherently and constitute a motion signal, while the remaining dots move randomly and consti-

tute motion noise (Fig. 1A). Psychophysical studies of subjects' ability to discriminate signal direction revealed a consistent relationship between motion signal strength and performance (Downing and Movshon, 1989; Britten et al., 1992), enabling the measurement of discrimination thresholds. To investigate how color segmentation influences motion processing, we introduced a simple but critical change: we made the signal and noise dots different colors (Fig. 1B). This manipulation profoundly enhanced human subjects' ability to discriminate signal direction, decreasing thresholds by, on average, a factor of six (Croner and Albright, 1997).

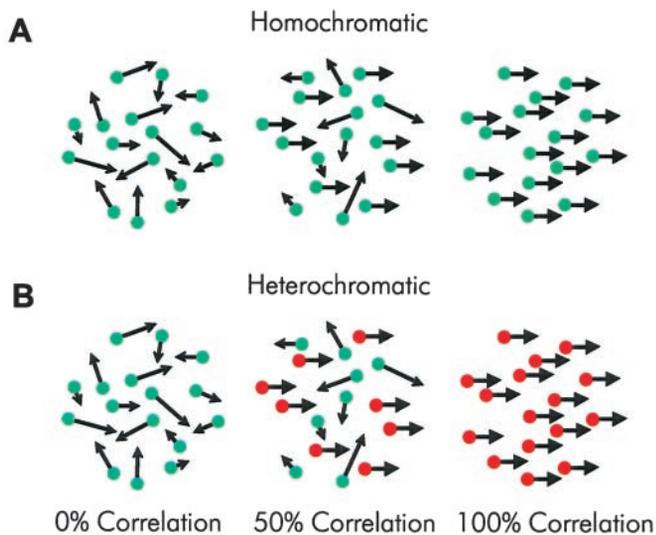
To study the neural basis of this perceptual phenomenon we have now recorded activity of neurons in the middle temporal area (MT) of extrastriate visual cortex in rhesus macaques. MT neurons are highly sensitive to the motion signal in stimuli like those in Figure 1A, in which all the dots are the same color: on average, individual MT neurons discriminate direction as well as the animal does (Newsome et al., 1989; Britten et al., 1992). Such observations have led to the hypothesis that MT neurons convey information used to guide behavioral (psychophysical) choice about motion direction. Because performance of the psychophysical direction discrimination task is greatly improved by chromatic segmentation, we predicted that chromatic cues would elicit a parallel improvement in discrimination performance of MT neurons. This prediction does not contradict the apparent lack of chromatic sensitivity in MT neurons (Dobkins and Albright, 1994; Gegenfurtner et al., 1994), because chromatic cues are used herein to distinguish moving features, not (as in previous studies) to define them.

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**Figure 1.** Schematic diagram of the motion stimuli used in this study. Each stimulus consisted of a sequence of frames of randomly positioned dots appearing on a CRT screen. Dots in each of the six circular apertures of the figure represent dots in six different stimuli. Arrows show the location of each dot in the next step of the motion sequence and so represent velocity (direction and speed). The proportion of dots moving in the same direction at the same speed, expressed as a percentage and termed the “correlation”, describes the strength of the motion signal. At 0% correlation, all of the dots are replotted at random positions, generating a purely stochastic motion display. At 50% correlation, half of the dots (those with larger arrowheads) are replotted at a fixed offset. At 100% correlation, all of the dots are replotted with the same offset. *A*, In the conventional “homochromatic” condition, all of the dots have the same color (*green*). *B*, In the novel “heterochromatic” condition, the dots moving in a correlated manner are a different color (*red*) from those moving randomly (*green*).

Our results reveal that chromatic segmentation enhances the discriminative capacities of MT neurons, but the enhancement is smaller than that observed behaviorally. These findings raise questions about pooling of MT responses and about the role of MT in motion perception.

Some of these results have been briefly reported elsewhere (Croner and Albright, 1996).

## MATERIALS AND METHODS

### *Animal preparation and experimental routine*

Two adult female rhesus macaques (*Macaca mulatta*) served as subjects in these experiments. All protocols were approved by the Salk Institute Animal Care and Use Committee. The monkeys were treated in accordance with United States Department of Agriculture regulations, the United States Public Health Service Policy on Humane Care and Use of Laboratory Animals, and the National Institutes of Health Guide for the Care and Use of Laboratory Animals.

Each monkey was prepared for behavioral training and electrophysiological recording using conventional techniques, which have been described in detail elsewhere (Dobkins and Albright, 1994; Chaudhuri and Albright, 1997). Briefly, surgical procedures were performed under aseptic conditions using either barbiturate or halothane anesthesia. Before training, a scleral search coil for measuring eye position was implanted under the conjunctiva of one eye (Robinson, 1963; Judge et al., 1980), and a stainless steel post for head restraint was fastened to the skull. After several months of training on a direction discrimination task, a stainless steel recording chamber was fastened to the skull over parietal cortex, to allow microelectrode access to area MT via a dorsal approach. Positioning of the recording chamber was guided by cranial magnetic resonance imaging (MRI) scans of each monkey's brain, obtained at the University of California, San Diego MRI facility (Nahm et al., 1994).

After recovery from surgery, the monkeys began training or recording

sessions. During each session, the monkey was seated in a primate chair (Crist Instruments, Damascus, MD) in a quiet, light-tight room. The implanted headpost was bolted to the frame of the primate chair to maintain the head in an upright position and to prevent head movements. Behavioral control was achieved via small (0.1 ml) juice rewards delivered on conclusion of each correctly performed trial. The animal was returned to its home cage after each session.

### *Visual stimuli*

**Apparatus.** Visual stimuli were generated using a programmable digital graphics display controller (Number Nine Computer Corporation, Cambridge, MA; Pepper SGT Plus; 640 × 480 pixels, analog red–green–blue (RGB) output, 8 bits/gun) installed in a personal computer. The computer presented stimuli on a 21" analog RGB monitor (Nanao, Torrance, CA; FlexScan F760i-W; 60 Hz frame rate, noninterlaced) positioned 27 inches in front of the monkeys' eyes. The stimuli were stored as computer files containing sequences of frames for animation. One sequence of 120 frames (2 sec) was created for each motion signal (see Control of motion signal below) used in an experiment with one neuron. Motion in one direction was displayed by running the animation forward, and motion in the opposite direction was displayed by running it backward.

**Control of motion signal.** We used dynamic dot stimuli in which dot positions were manipulated to create a motion signal of variable strength embedded in dynamic noise (e.g., Newsome and Paré, 1988; Britten et al., 1992, 1993) (Fig. 1). Our method of constructing the stimuli is described elsewhere (Croner and Albright, 1997). Briefly, a proportion of the dots was randomly selected to be replotted at a location shifted a given distance in the same direction after a temporal delay of two stimulus frames (the time between the first and second appearances of the dot was 50 msec). The percentage of dots undergoing correlated motion is referred to as the “correlation” and is an expression of the strength of the motion signal. The remaining dots were replotted at random positions after the same temporal delay, yielding dynamic noise.

In the stimuli used in this study, each signal dot was deliberately displaced for three sequential temporal steps, instead of one step as has been the case in previous experiments (e.g., Britten et al., 1992; Croner and Albright, 1997). This was implemented by randomly selecting a proportion of dots in each frame to be initiated as signal dots, with the number of dots selected equivalent to: [(percent correlation) × (number of dots in frame)] – (number of dots appearing in frame as steps one or two of three-step motion sequence). This increased signal dot lifetime from 50 msec (3 frames) to 150 msec (3 × 3 frames). We found that, for peripherally viewed stimuli, these longer dot lifetimes were required to obtain robust and reliable separation of psychophysical thresholds for homochromatic and heterochromatic conditions (see Experimental conditions below), which was essential to our experiment.

**Experimental conditions.** To evaluate the contribution of chromatic segmentation to motion processing, we used two stimulus conditions. In the homochromatic condition, signal and noise dots were the same color, either red or green (Fig. 1*A*). This is the same configuration used by previous researchers (Newsome et al., 1989; Britten et al., 1992) (with the exception that our signal dots had longer lifetimes) and served as our control condition. The percept was of global motion diffusely distributed across the stimulus. Our second condition was the heterochromatic condition, in which signal and noise dots were different colors—either signal was red and noise was green, or vice versa (Fig. 1*B*). This novel stimulus configuration served as our experimental condition, in which motion signal and noise were segmented on the basis of color. The percept was of motion carried by distinctly colored signal dots among irrelevant noise dots. For a given correlation level, the heterochromatic and homochromatic stimuli presented during an experiment were identical except for the indicated differences between the colors of the signal and noise dots.

**Stimulus parameters.** Illumination, chromaticity, and luminance were measured with a spectroradiometer (Photo Research, Chatsworth, CA; PR-650). Ambient illumination in the experimental room was ~2 lux. Each stimulus appeared against a dark gray background of luminance <0.1 cd/m<sup>2</sup>. The red and green dots of the experimental stimuli appeared within a circular region on this background and were produced by modulation of the red or green phosphors of the monitor, respectively. The C.I.E. chromaticity coordinates of these phosphors were: red (R), (0.622, 0.339); green (G), (0.286, 0.600). The luminance of red dots was 10 cd/m<sup>2</sup>.

Green dot luminance was selected to be isoluminant with the red dots (so that heterochromatic signal and noise dots were distinguishable

solely on the basis of their chromatic properties), as determined separately for each animal. To establish the point of perceptual isoluminance, we began by using the “heterochromatic fusion nystagmus” (HFN) procedure described by Chaudhuri and Albright (1992). However, when we used the HFN-determined green dot luminance in random dot stimuli placed away from the fovea, we found that the monkeys’ ability to discriminate direction in heterochromatic stimuli depended on the color of the signal dots, suggesting that one color was perceived to be brighter than the other. Most likely, the isoluminant point for the small, nonfoveal dots in experimental stimuli differed from that measured with HFN. We therefore developed a second method to determine behavioral isoluminance for red and green dots presented more peripherally. This method involved measures of behavioral direction discrimination performance elicited by a heterochromatic random dot stimulus. The stimulus correlation level and red dot luminance were held constant while the green dot luminance was varied until both red and green signal stimuli elicited the same performance. We repeated this measure for stimuli at various locations in the visual field, and used the green dot luminances so obtained in experimental stimuli at those locations. Although our main goal in determining these luminances was to equate behavioral performance, we also found that these luminances equated neuronal performance. We evaluated this by selecting a subset of experiments during which we had collected sufficient trials to reliably measure both behavioral and MT neuronal discrimination thresholds (see Data analysis below) for both red and green signal heterochromatic stimuli. During all experiments in which behavioral performance was the same for both heterochromatic stimuli, neuronal discrimination thresholds for the two stimuli were statistically indistinguishable. Thus, equating behavioral performance also equated MT neuronal discriminability, justifying pooling of neuronal responses to the red and green signal heterochromatic stimuli. In addition, neuronal discrimination thresholds for red and green homochromatic stimuli were statistically indistinguishable, as expected.

Because the spatial and temporal characteristics of low-level visual processes vary with retinal eccentricity, we expected that it might be necessary to modify parameters of nonfoveal stimuli to show the same behavioral heterochromatic discrimination enhancement that we had found with foveal stimuli (Croner and Albright, 1997). In modifying the stimuli, our goal was to settle on stimulus parameters for which simply changing signal dot color improved behavioral direction discrimination. For instance, we described above that longer signal dot lifetimes were required to obtain a segmentation effect on behavioral discrimination of direction in nonfoveal stimuli. In addition, we found that changes in the dot size and density were necessary to demonstrate the segmentation effect nonfoveally. Because perceived color of eccentrically viewed patches depends on stimulus size (Abramov et al., 1991), we increased the dot size to be at least as large as the center regions of parasol ganglion cell receptive fields at the same eccentricity (Croner and Kaplan, 1995). We also found that decreasing the dot density enhanced the separation between heterochromatic and homochromatic thresholds for peripherally viewed stimuli. We selected a combination of these two stimulus parameters that yielded robust and reliable separation of psychophysical homochromatic and heterochromatic thresholds for each monkey and used those values for all experiments. The parameters used for the first monkey were:  $0.2^\circ$  dot diameter,  $37 \text{ dots} \cdot \text{deg}^{-2} \cdot \text{sec}^{-1}$ . The parameters used for the second monkey were:  $0.2^\circ$  dot diameter,  $37 \text{ dots} \cdot \text{deg}^{-2} \cdot \text{sec}^{-1}$  for stimuli centered within  $5^\circ$  eccentricity;  $0.25^\circ$  dot diameter,  $18.6 \text{ dots} \cdot \text{deg}^{-2} \cdot \text{sec}^{-1}$  for stimuli centered beyond  $5^\circ$  eccentricity.

To measure neuronal direction discrimination, we collected responses over many trials of each correlation level tested for a given neuron (see Data collection). For each such trial we used the same stimulus bitmap so that all the trials had exactly the same sequence of dot positions. We did this to allow analysis of spike timing relative to the dot sequence; these data will be presented elsewhere. As shown by Britten et al. (1993, 1996), the absence of within stimulus variation does not affect the type of analyses used in the current study.

To prevent animals from learning to discriminate specific dot sequences, the particular bitmap chosen for a given correlation level varied across experiments. Several (4–6) different bitmaps were generated for each correlation level of each possible stimulus composition (determined by motion signal axis, signal speed, and stimulus aperture size; see Data collection below), resulting in  $\sim 200$  bitmaps for each correlation level. During experiments, a particular composition was first chosen, and then one of the 4–6 bitmaps of this composition was chosen for each correlation level. During physiological experiments, the required composition

changed depending on the neuron studied; we imposed a similar variation during training. This variation in the bitmaps used made it unlikely that monkeys learned to distinguish the dot sequences in particular bitmaps.

Using one of several possible bitmaps for each correlation level of a given stimulus composition introduced the possibility that, because of nonuniform distribution of velocities within the noise dot population of particular bitmaps, performance for a particular correlation level might depend on the bitmap used. To examine this, we executed ANOVAs evaluating whether either psychophysical or neuronal performances (proportion of correct trials; see Data analysis below) depended on bitmap identity for any particular correlation level. For the bitmaps used in this study, we found no significant dependence of performance on bitmap. This indicates that performance variation swamped any variation caused by possible small differences in signal strength across bitmaps for a given correlation level, rendering small deviations from the intended signal strength in particular bitmaps irrelevant.

### Electrophysiological recording

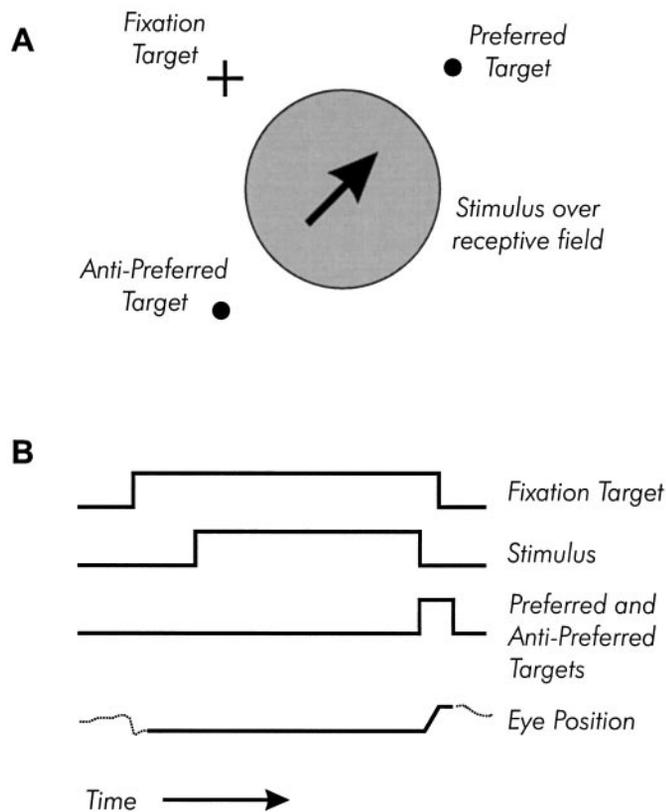
Neuronal activity was recorded extracellularly with parylene-coated tungsten microelectrodes (Frederick Haer & Company, Bowdoinham, ME) with exposed tips of  $10 \mu\text{m}$  or less. An electrode, a sterilized stainless-steel guide tube, and a hydraulic microdrive assembly were attached to the implanted recording chamber by way of an x-y stage (David Kopf Instruments, Tujunga, CA). The guide tube was positioned so that its tip extended 1 or 2 mm below the dura. The electrode was lowered through the guide tube with the hydraulic microdrive until the electrode tip was in area MT. Recorded neuronal activity was amplified (Bak Electronics, Rockville, MD), filtered (Krohn-Hite, Avon, MA), and directed to a digital oscilloscope (Nicolet, Madison, WI), an audio monitor, and either a manual electronic window discriminator (Bak Electronics) or a spike-sorting system (Alpha Omega Engineering, Nazareth, Israel). The activity of single neurons was isolated, and digital pulses were sent to the computer to signal spike times. Eye positions were recorded with a scleral search coil system (CNC Engineering, Seattle, WA) and sent to the computer as x- and y-position voltages. Data acquisition and control of events during training and recording sessions were achieved using a personal computer and software developed for this purpose at the Laboratory of Neuropsychology, National Institute of Mental Health (CORTEX, version 4.3).

As an electrode was lowered, regions of neural activity and silence were correlated with cortical tissue and sulci visible on the structural MRI scans of the monkey’s brain. This allowed us to determine when the electrode entered the posterior bank of the superior temporal sulcus (STS), where MT is located. When activity of a single neuron was isolated, we first assessed whether the neuron responded to any of a variety of moving or stationary bright bars or spots. If so, we attempted to map the receptive field and measure sensitivity to direction of motion (see below). We used the estimated electrode position relative to the STS, receptive field sizes, and proportion of directionally selective neurons as criteria to establish when the electrode tip was in MT.

### Data collection

**Receptive field mapping.** The animal fixated a target while a high contrast white bar ( $27 \text{ cd/m}^2$  on a  $<0.1 \text{ cd/m}^2$  background) was moved on the display to determine the minimum response field of the neuron. The length, width, orientation, speed, and position of the bar were controlled by the experimenter using a computer mouse and keyboard command system.

**Direction and speed tuning.** We next quantified the velocity tuning of the neuron. The fixation target was positioned so that ocular fixation would center the receptive field of the neuron at the center of the video display. The monkey was rewarded for successfully maintaining fixation throughout each trial. The fixation window allowed eye movements up to  $0.7^\circ$  from the fixation target, but in practice eye position was much closer to the target. For each trial, a 100% correlated random dot stimulus (white dots of  $27 \text{ cd/m}^2$  on a  $<0.1 \text{ cd/m}^2$  background) was shown for 1 sec in a  $4.6^\circ$  diameter circular aperture centered over the receptive field. Stimulus motion had one of eight possible directions (the four cardinal directions and the four intermediate directions) and two possible speeds ( $5$  or  $10^\circ/\text{sec}$ ). Each direction–speed combination was presented for a minimum of four and a maximum of eight trials, randomly interleaved. Response was measured as the number of action potentials during stimulus presentation. Average responses were evaluated to determine the preferred speed. For this speed, the direction evoking maximal response was referred to as the “preferred direction”, and the opposite



**Figure 2.** Diagram of the psychophysical paradigm used in this study. *A*, Example spatial configuration of the fixation target, stimulus aperture, and targets for direction choice. The stimulus aperture diameter was matched to the receptive field diameter of the neuron under study, and the fixation target was positioned separately for each neuron to center the receptive field on the stimulus aperture, which was at the center of the video display. Signal motion during each trial was in either the preferred or antipreferred direction of the neuron; the targets for direction choice were positioned according to the preferred direction of the neuron. *B*, Diagram of the temporal sequence of events during one trial. A trial was initiated with the onset of the fixation target (*Fixation Target*). Five hundred milliseconds after fixation was achieved (*Eye Position*), the motion stimulus was presented for 2 sec (*Stimulus*). When the stimulus was extinguished, the *Preferred* and *Anti-Preferred Targets* appeared and remained on until the monkey indicated its direction choice by making a saccadic eye movement to one of them.

direction was referred to as the “antipreferred direction.” If the response distributions for the preferred and antipreferred directions were entirely nonoverlapping, we initiated our experiment to quantify direction discrimination thresholds for this neuron. This criterion is identical to that used by Britten et al. (1992) and ensured that each neuron was directional enough, in principle, to yield a measure of its direction discrimination thresholds.

**Direction discrimination thresholds.** The goal of this experiment, which was the main source of data presented here, was to measure simultaneously both behavioral and neuronal thresholds for discriminating opposite directions of motion. This was achieved by collecting neuronal responses while the monkeys performed a two-alternative direction discrimination task. Our procedure for determining thresholds was the same as that used by Britten et al. (1992) with the exception that, whereas Britten et al. measured thresholds for one stimulus condition (similar to our homochromatic condition), we obtained thresholds for the heterochromatic as well as homochromatic condition.

Monkeys were trained to perform a two-alternative direction discrimination task (Britten et al., 1992). Figure 2 diagrams the spatial configuration of the display (Fig. 2*A*) and the sequence of events (Fig. 2*B*) during a trial. A trial was initiated with the onset of a 0.15° diameter fixation target. Five hundred milliseconds after the monkey established fixation, the experimental stimulus was presented for 2 sec in the recep-

tive field of the neuron. The stimulus was either a homochromatic or heterochromatic random dot pattern of a particular correlation level moving in the preferred or antipreferred direction of the neuron. The diameter of the stimulus aperture was matched to that of the receptive field of the neuron, and the speed of motion was the preferred speed (of the two tested) of the neuron. The monkey was required to maintain fixation within 0.7° of the target during the 2 sec stimulus. If the monkey broke fixation, the trial was terminated, the data for that trial was discarded, and either the trial was reinitiated, or a trial of a different stimulus condition was begun. If the monkey successfully maintained fixation, the random dot stimulus was extinguished, and two targets appeared at positions corresponding to the two possible directions of stimulus motion. The monkey reported the perceived direction of motion by making a saccadic eye movement to the corresponding target. Correct decisions were rewarded with a drop of juice; incorrect decisions were followed by a time-out of up to 6 sec.

We obtained data for determining discrimination thresholds over a single block of trials for each neuron. For each trial, neuronal response was measured as the number of action potentials fired during presentation of the random dot stimulus. A block consisted of a series of randomly interleaved homochromatic and heterochromatic trials, with motion of several different stimulus correlations moving in the preferred and antipreferred directions of the neuron presented in random order. For a given correlation level within such a block, we presented an equal number of trials with the different possible dot color combinations (homochromatic, red or green; heterochromatic, red signal and green noise, or vice versa), randomly interleaved. We used four or five correlation values spaced by a factor of two (rarely, four) for each neuron and chose the particular range of values to span the psychophysical threshold. Each block consisted of at least eight trials of each combination of motion direction, stimulus correlation, and stimulus condition (homochromatic or heterochromatic). We continued recording from any one neuron as long as neuronal isolation was maintained and the monkey performed the direction discrimination task. Typically, a successful experiment with one neuron lasted between 1 and 3 hr.

#### Data analysis

**Psychophysical thresholds.** For each block of trials, direction judgments for both preferred and antipreferred directions of motion were pooled to give one data point for each correlation level of the homochromatic or heterochromatic condition. The data were plotted separately for the two conditions as the proportion of correct responses against percent correlation. We used a maximum-likelihood method to fit these psychometric data with the sigmoidal Quick function (Quick, 1974):

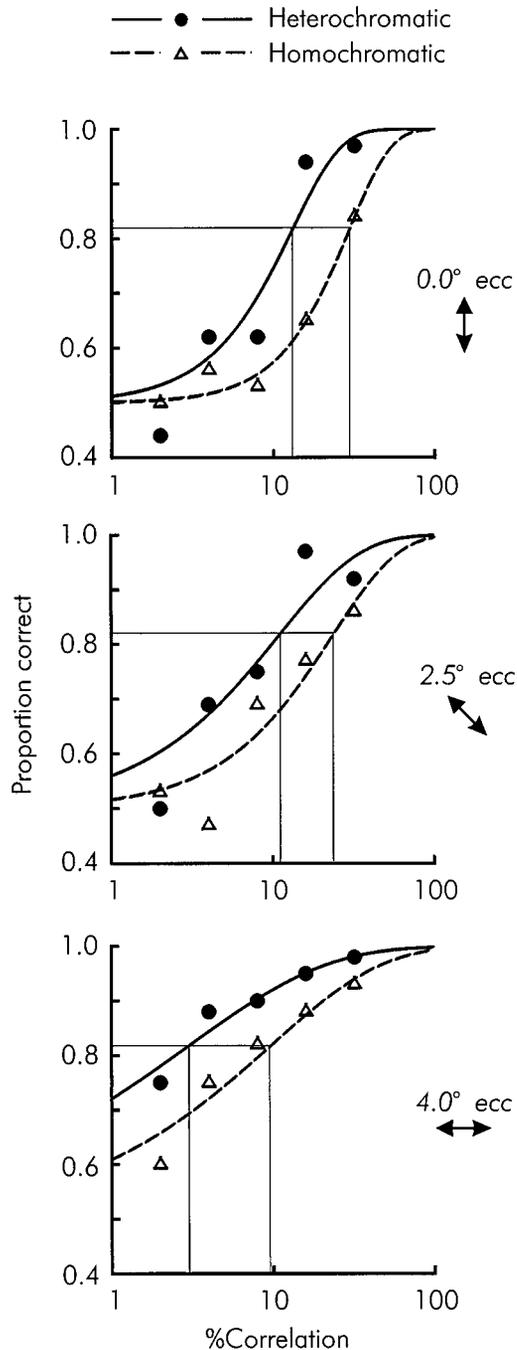
$$p = 1 - 0.5e^{-(c/\alpha)\beta}$$

where  $p$  is the proportion of correct responses,  $c$  is the correlation level of the stimulus,  $\alpha$  is the stimulus correlation at which threshold performance (82% correct) is achieved, and  $\beta$  is the slope of the curve in the region midway between chance (50% correct) and perfect (100% correct) performance. The goodness of fit was evaluated using a  $\chi^2$  criterion ( $p < 0.05$ ). Examples of psychometric functions obtained over three separate blocks appear in Figure 3.

For the psychometric functions obtained in each block, we performed a statistical test based on that used by Britten et al. (1992) to evaluate whether the thresholds fitted to the homochromatic and heterochromatic conditions were significantly different. For this test, we fit Quick functions to the data from both conditions, comparing  $\chi^2$  from a fit that determined threshold and slope parameters independently for the two conditions with  $\chi^2$  from a fit that was constrained to generate the same threshold for the two conditions. If the difference in  $\chi^2$  exceeded the criterion value ( $\chi^2$  distribution;  $df = 1$ ;  $p < 0.05$ ), we concluded that the two conditions had significantly different thresholds.

**Neuronal thresholds.** Following Britten et al. (1992), we used receiver operating characteristic (ROC) analysis (Green and Swets, 1966) of neuronal responses obtained during one block of trials to determine neuronal thresholds for direction discrimination. The unique characteristic of our analysis is that, whereas Britten et al. (1992) computed one neurometric threshold per neuron, we determined two thresholds: homochromatic and heterochromatic. ROC analysis has been described elsewhere (e.g., Britten et al., 1992); we describe it only briefly here.

The goal of the analysis was to calculate a measure of the ability of a neuron to discriminate between its preferred and antipreferred directions of motion. We calculated the performance of a hypothetical ideal



**Figure 3.** Example psychometric functions. Each plot shows data obtained in a single block of randomly interleaved homochromatic and heterochromatic trials. The *inset* to the *right* of each plot gives the retinal eccentricity of the stimulus and the axis of signal direction used in each block. The data are plotted as the proportion of correct direction decisions against the stimulus correlation level (homochromatic, *white triangles*; heterochromatic, *black circles*), and are fit with Quick functions (see Materials and Methods) (homochromatic, *dashed lines*; heterochromatic, *solid lines*). In each plot, a *thin horizontal line* is drawn through threshold performance (0.82). Where this line intersects each psychometric function, a *thin vertical line* is drawn to intersect the *x*-axis at the threshold correlation of the function. The homochromatic and heterochromatic psychophysical thresholds, respectively, were 29.7 and 13.2% (32–37 trials per point) (*top*), 23.5 and 10.9% (32–37 trials per point) (*middle*), and 9.5 and 2.9% (40–44 trials per point) (*bottom*).

observer judging stimulus direction by monitoring the responses of a neuron to its preferred and antipreferred directions. In principle, the fidelity of the direction judgment depends on the degree of overlap between the distributions (relative to their widths) of the responses of the neuron to the two directions; decreased overlap (more separation between the distributions) would result in improved discriminability. By measuring the area of an ROC curve constructed from these response distributions, we generated a nonparametric measure of the ideal observer's performance. We computed performance for each stimulus correlation level of both the homochromatic and heterochromatic conditions, and plotted "neurometric" functions (the proportion of correct judgments as a function of %correlation) for each condition. Examples of response distributions and the resulting neurometric functions for three neurons appear in Figure 5. We fitted the homochromatic and heterochromatic neurometric data of each neuron with Quick functions and evaluated whether heterochromatic and homochromatic thresholds were significantly different, as described above for psychometric functions.

**Confidence intervals for thresholds and threshold ratios.** To provide additional tests of significance of threshold and threshold ratios (see Figs. 4, 6, 9), we determined confidence intervals for thresholds and for threshold ratios. We used the method of "constant  $\chi^2$  boundaries as confidence limits" (Press et al., 1988), locating 95% confidence boundaries within a two-dimensional space defined by either threshold and slope (for fits of a single Quick function) or threshold ratio and slope ratio (for fits of two Quick functions simultaneously). We then weighted each individual value in the distributions by the inverse of its confidence interval magnitude and calculated the weighted mean and SE of each distribution. For all distributions so evaluated, the results were qualitatively the same as those from standard statistical tests using unweighted values. In Results, we present the unweighted parameters of these distributions to allow comparison with previous studies (e.g., Britten et al., 1992) and because the unweighted values are the best estimates of true thresholds and threshold ratios.

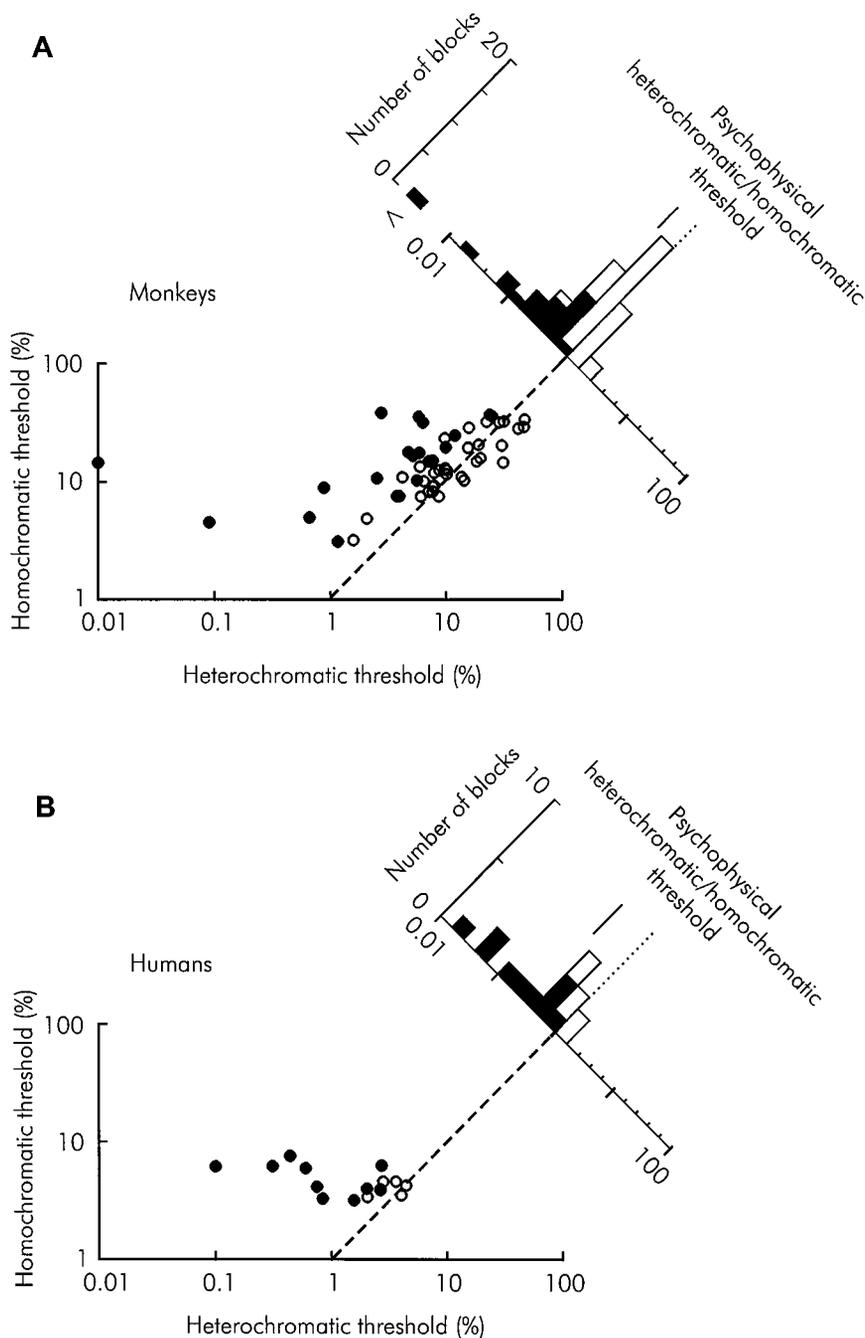
#### Neuronal database

Our results are based on quantitative analysis of 75 MT neurons. These neurons were culled from a total of 572 neurons studied during these experiments. Approximately 40% (229) were excluded from the study because they did not meet our criterion for direction selectivity to 100% correlated random dot stimuli. An additional 268 were excluded because their data were poorly fit by the Quick function and thus did not yield reliable discrimination thresholds. This stemmed from two possible causes: either the neuron was lost before sufficient trials were collected, or the discriminabilities of the neuron were too variable to yield a statistically significant fit of the Quick function. For the remaining 75 neurons, we were able to obtain statistically significant fits for one or both of the homochromatic and heterochromatic conditions; 50 yielded good fits for both conditions. The neurons had receptive fields ranging from 0.5 to 14.6° eccentricity (mean, 5.6°; SD, 2.5°).

## RESULTS

### Psychophysical data

We previously demonstrated a robust perceptual effect of color segmentation on direction discrimination performance by human subjects (Croner and Albright, 1997). Figure 3 shows that a similar effect could be measured in monkeys viewing stimuli positioned and modified as necessary for testing neuronal responses. Three pairs of psychometric functions obtained from one monkey performing the direction discrimination task are shown. Each pair was obtained in a single block of randomly interleaved homochromatic and heterochromatic trials, such as would be used to test neuronal discriminability. These data show that the monkey was able to discriminate direction of stimuli centered at different locations in the visual field and moving along various axes and that performance increased with stimulus correlation as expected. Thin straight lines indicate thresholds for direction discrimination performance. Heterochromatic thresholds were lower than the corresponding homochromatic thresholds, and this difference was statistically significant ( $\chi^2$ ;  $p < 0.05$ ; see Materials and Methods) for all three examples.



**Figure 4.** Comparison of behavioral performance for the homochromatic and heterochromatic conditions. The *bottom panels* in *A* and *B* show scatterplots of the absolute thresholds obtained in single blocks of trials. The *black symbols* signify blocks in which the two thresholds were significantly different from each other, evaluated as described in the Materials and Methods; the *broken lines* illustrate where points would fall if the thresholds were identical. The *top right panels* in *A* and *B* show frequency distributions of the ratios of heterochromatic to homochromatic thresholds obtained in single blocks of trials, formed by summing across the scatterplots within diagonally oriented bins. *Dotted lines* indicate unity, and *solid line* segments are aligned with the geometric means. Ratios less than unity indicate that behavioral performance was better (threshold was lower) for the heterochromatic condition. The *black bars* show the threshold ratios for blocks in which the two behavioral thresholds were significantly different from each other. *A*, Thresholds and threshold ratios obtained during our neurophysiological experiments and are the 54 cases for which we obtained good fits of the Quick function to behavioral data for both the homochromatic and heterochromatic conditions. The impact of the outlier (threshold ratio < 0.01) on the threshold ratio distribution was minimal: omitting this datum did not significantly affect the geometric mean of the distribution, nor did it affect the significant difference of the geometric mean from 1.0. *B*, Thresholds and threshold ratios obtained from humans. Shown are 16 cases obtained from block-by-block analysis of data from previously published experiments (Crone and Albright, 1997).

In the majority of blocks during which we also measured neuronal responses, behavioral discrimination was better for the heterochromatic condition, but this difference was not always statistically significant. Of the experiments in which we successfully fit Quick functions to behavioral data for both conditions, 37% revealed a statistically significant decrease of discrimination threshold with color segmentation. These findings are summarized in the top right panel of Figure 4*A*, which displays a histogram of the ratio of heterochromatic to homochromatic behavioral thresholds. Ratios less than one are from experiments in which the heterochromatic threshold was less than the homochromatic threshold, indicating that color segmentation improved performance. Ratios greater than 1 indicate that performance was worse for the heterochromatic case. For all cases in which heterochromatic and homochromatic thresholds were signifi-

cantly different (black bars), color segmentation improved behavioral performance. The geometric mean of the distribution for significantly different thresholds is 0.19. The geometric mean of the entire distribution is 0.50 (significantly different from 1.0; *t* test; *p* < 0.001) (threshold geometric means were homochromatic, 14.55%; heterochromatic, 7.26%), indicating that color segmentation afforded a twofold decrease in behavioral threshold on average. The bottom panel of Figure 4*A* displays a scatterplot of the thresholds contributing to the ratio histogram; the black symbols signify blocks for which the two thresholds were significantly different.

How do these threshold ratios compare with human performance? In our psychophysical studies with human subjects (Crone and Albright, 1997), we averaged out noise across experimental sessions by pooling each subject's responses over many

blocks of trials. To allow direct comparison with monkey psychophysical results, we reanalyzed our human data on a block-by-block basis. Figure 4*B* shows the results. The top right panel shows a histogram of the threshold ratios. The counts are lower than in Figure 4*A*, mainly because human subjects performed fewer trials per block than did the monkeys; we were thus able to obtain statistically significant fits of Quick functions for both conditions on only a minority of the blocks for human subjects. The scatterplot of thresholds shown in the bottom panel reveals that the range of homochromatic thresholds was smaller and distributed around a lower value than for monkeys. Both these differences can be attributed to the fact that the human subjects viewed only foveally centered stimuli with one signal speed, giving rise to lower and more consistent thresholds than measured with the more variably located and configured stimuli used with monkeys. Despite these differences in the data for monkeys and humans, the pattern of results is the same for the two species. As for the monkeys, most of the human threshold ratios and all of those involving significantly different thresholds were  $<1$ . The geometric mean of the distribution for significantly different thresholds is 0.16, and of the entire distribution is 0.30 (significantly different from 1.0,  $t$  test;  $p = 0.001$ ). These values are similar to those obtained from monkeys (0.19 and 0.50). Thus, the heterochromatic enhancement measured in humans and monkeys has similar variability when analyzed on a block-by-block basis. In addition, color segmentation improves direction discrimination to approximately the same extent in humans viewing central stimuli and in monkeys viewing stimuli positioned and modified for neurophysiological studies of MT neurons.

### Neurophysiological data

The first question of interest is whether segmentation by color affects the responses of individual MT neurons. Figure 5 shows data obtained from three neurons illustrating the range of responses found. The top panels contain frequency distributions of the number of spikes per trial for two directions of stimulus motion [preferred (*black bars* in each plot) and antipreferred (*white bars* in each plot)], two stimulus conditions [homochromatic (*left column*) and heterochromatic (*right column*)], and the four or five stimulus correlation levels (increasing from *top* to *bottom*) studied for each neuron. As described in Materials and Methods, we used ROC analysis to calculate the best direction discrimination possible for a stimulus of a given correlation and condition (homochromatic or heterochromatic), based on the responses of each neuron. The resulting neurometric performance data for these neurons are shown in the bottom panels of Figure 5. The curves fitted to these data appear on the plots; straight lines illustrate the thresholds for direction discrimination.

Figure 5*A* shows data from a neuron with a statistically significant decrease in threshold for the heterochromatic condition. The discrimination performance of the neuron improved with stimulus correlation because responses to preferred direction stimuli increased with correlation. The response distributions (*top panel*) for heterochromatic stimuli moving in the preferred direction encompassed larger responses than for homochromatic stimuli of the same correlation moving in this direction. The result was better neuronal discriminability for the heterochromatic case, reflected in an upward shift of heterochromatic points in the bottom panel. This upward shift resulted in a 2.5-fold decrease in threshold (homochromatic threshold, 17.6%; heterochromatic threshold, 7.0%;  $\chi^2$ ;  $p < 0.05$ ). Twenty-two percent (11 of 50) of the neurons for which both thresholds could be deter-

mined showed a statistically significant enhancement of neuronal direction discriminability with color segmentation.

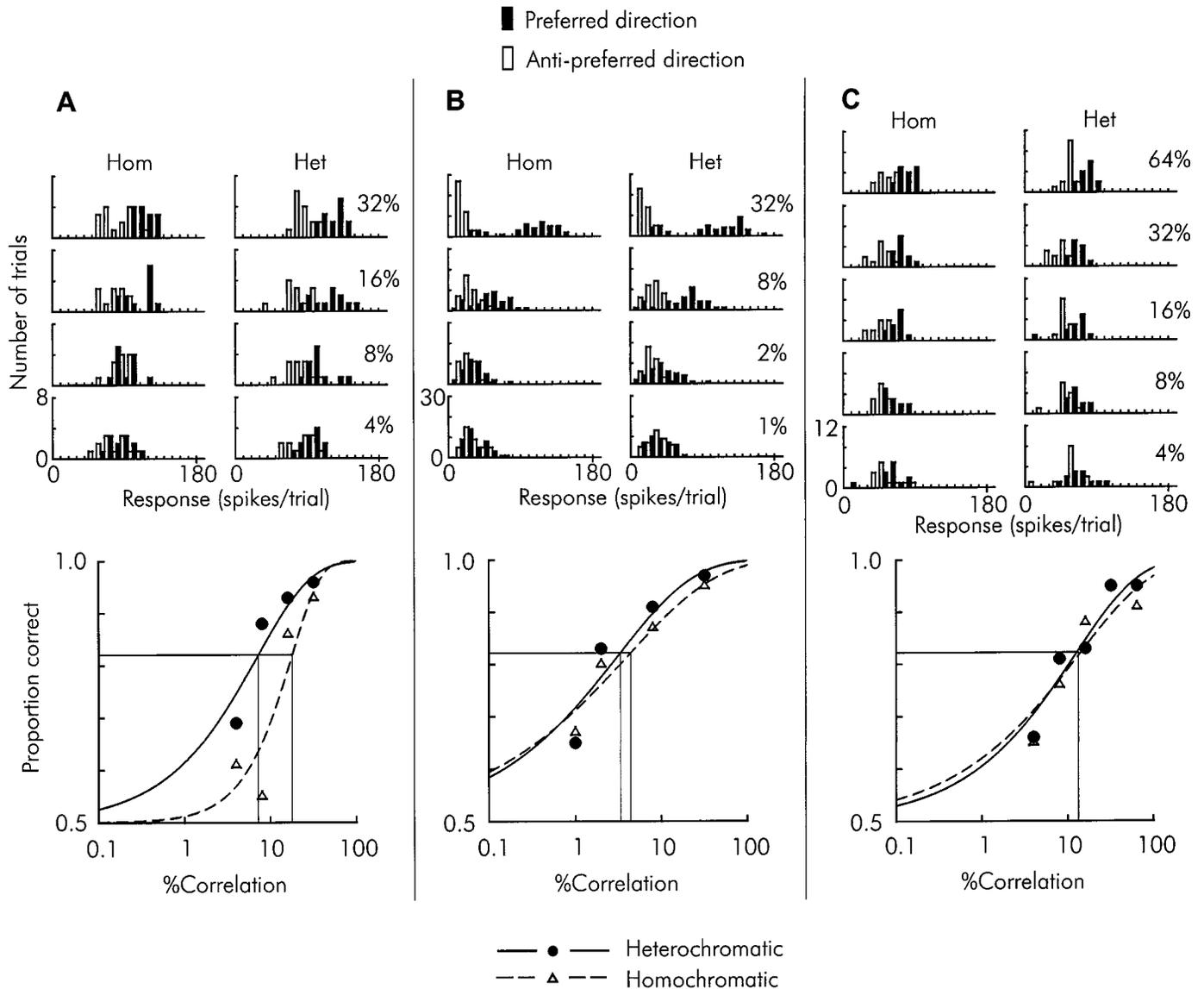
Many of the remaining neurons showed a trend toward better discriminability for the heterochromatic condition. Figure 5*B* illustrates a typical example. Discriminability improved with stimulus correlation because of both increased responses to preferred direction motion and decreased responses to antipreferred direction motion. Responses (*top panel*) to preferred direction motion were slightly larger for heterochromatic than homochromatic stimuli of all but the lowest correlation level, resulting in small upward shifts of the heterochromatic performance data shown in the bottom panel. The fitted curves rendered a slightly decreased heterochromatic threshold that was not significantly different from the homochromatic threshold.

The data in Figure 5*C* are from a neuron that showed no difference in discriminability of direction in heterochromatic and homochromatic stimuli. The response distributions in the top panel demonstrate that increasing stimulus correlation caused larger responses to preferred direction stimuli, but there was no consistent difference in the responses to heterochromatic and homochromatic stimuli. The neurometric curves for the two conditions, shown in the bottom panel, are almost entirely overlapping, and there is no significant difference between their thresholds.

To evaluate the magnitude of color segmentation effects on neuronal direction discriminability, we examined ratios of heterochromatic to homochromatic thresholds. The thresholds and the distribution of their ratios for the 50 neurons for which we obtained good fits of Quick functions for both conditions are plotted in the bottom and the top right panels of Figure 6, respectively. Black symbols and bars signify neurons for which discrimination thresholds for the two conditions were significantly different. As was found for behavioral thresholds, all neurons with significantly different thresholds had ratios less than unity, indicating that neuronal discriminability was always better for the heterochromatic condition in these cases. For this subpopulation of neurons, the geometric mean of the distribution is 0.35. The geometric mean of the entire distribution is 0.74 (significantly different from 1.0,  $t$  test;  $p = 0.001$ ) (threshold geometric means were homochromatic, 20.65%; heterochromatic, 15.27%), reflecting a 1.4-fold enhancement of discriminability accompanying color segmentation. The distribution of neuronal threshold ratios is similar to that for psychophysical thresholds (Fig. 4*A*), suggesting that the enhanced behavioral discrimination performance with color segmentation could be accounted for by MT neurons. We next evaluate this possibility in more detail by directly considering relations between neurometric and psychometric thresholds.

### Comparison of psychometric and neurometric discrimination thresholds

Figure 7 displays examples of psychometric and neurometric functions obtained over the same block of trials. The data in the left column are from a case in which the effect of color segmentation on behavioral and neuronal discriminability were discordant. These data were obtained while we studied the neuron whose responses appear in Figure 5*B*. The behavioral data collected while we recorded from this neuron are plotted at top left of Figure 7, and the neurometric data collected on the same trials are replotted just below to facilitate comparison. There was a large, statistically significant decrease in the perceptual discrimination threshold when signal and noise differed by color, but the



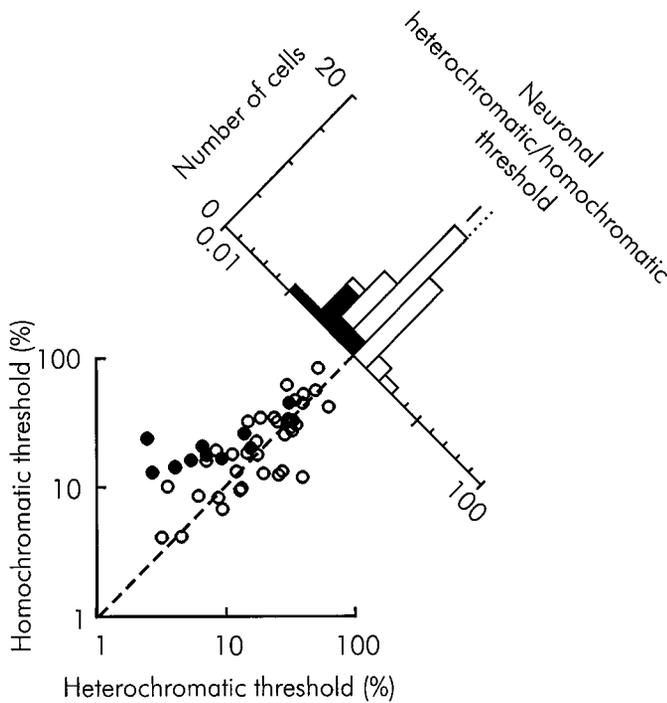
**Figure 5.** Representative neuronal responses to homochromatic and heterochromatic stimuli, and the resulting neurometric functions. The *top panels* show frequency distributions of responses (number of spikes per 2 sec random dot stimulus) to two directions of stimulus motion [preferred (*black bars*) and anti-preferred (*white bars*)], two stimulus conditions [homochromatic, *Hom* (*left column*) and heterochromatic, *Het* (*right column*)], and four or five stimulus correlation levels (increasing from *top* to *bottom*). The *bottom panels* show the resulting neurometric functions; the proportion of correct decisions based on neuronal responses is plotted against stimulus correlation (homochromatic, *white triangles*; heterochromatic, *black circles*), and Quick functions are fitted to the data (homochromatic, *dashed lines*; heterochromatic, *solid lines*). *Thin straight lines* illustrate thresholds, as in Figure 3. *A*, An experiment in which we measured significantly different neuronal thresholds for the homochromatic and heterochromatic conditions. The homochromatic and heterochromatic thresholds, respectively, were 17.6 and 7.0% (24–29 trials per point). *B*, An experiment with a different neuron, whose thresholds for the two conditions were statistically indistinguishable. Neuronal performance was generally better for the heterochromatic condition, and the heterochromatic threshold was slightly lower. The homochromatic and heterochromatic thresholds, respectively, were 4.1 and 3.1% (80–85 trials per point). *C*, An experiment with a neuron that showed no consistent difference in discriminability of the two conditions and with homochromatic and heterochromatic thresholds that were statistically indistinguishable. The homochromatic and heterochromatic thresholds, respectively, were 13.2 and 12.0% (the average threshold of 12.6% is illustrated) (24–29 trials per point).

neuronal threshold decreased only slightly. The neuronal thresholds for both conditions were most similar to the behavioral threshold for the homochromatic condition.

The data in the right column of Figure 7 are from a case in which there was good agreement between the psychometric and neurometric consequences of the chromatic manipulation. A significant decrease in the monkey's behavioral threshold for the heterochromatic condition (top right) was accompanied by a significant decrease in the neuronal threshold (bottom right). Both of the neuronal thresholds were larger than their respective behavioral

thresholds, but the magnitude of the heterochromatic enhancement was approximately the same for behavior and for the neuron.

We also obtained neuronal recordings during blocks of trials when the monkeys' behavioral performance did not show a significant influence of color segmentation. In such cases, neuronal thresholds were sometimes significantly influenced by color segmentation, and sometimes they were not. Thus, we found a range of relations between neuronal and behavioral thresholds for the two conditions. To investigate patterns in these relations, we addressed three questions in further analysis. First we asked



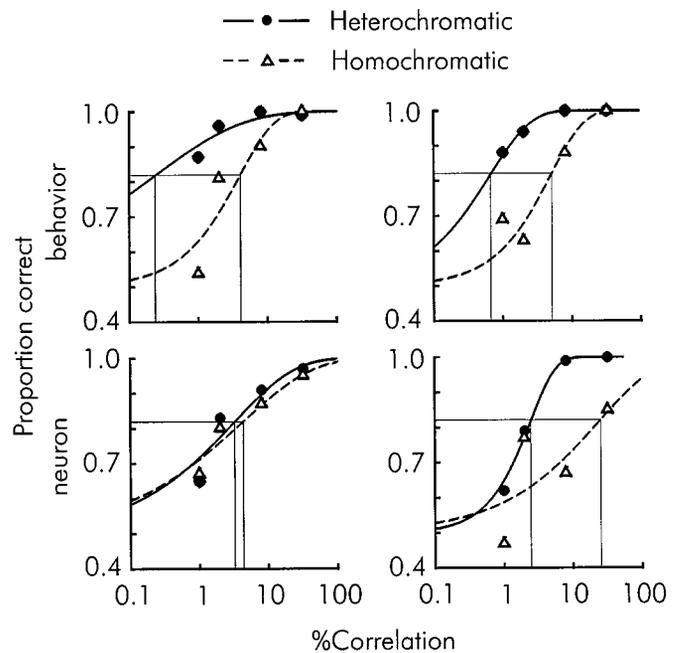
**Figure 6.** Comparison of neuronal performance for the homochromatic and heterochromatic conditions. The *bottom panel* shows a scatterplot of the absolute thresholds obtained in experiments with single neurons. The *black symbols* signify neurons for which the two thresholds were significantly different from each other; the *broken line* illustrates where points would fall if the thresholds were identical. The *top right panel* shows a frequency distribution of the ratios of heterochromatic to homochromatic thresholds, formed by summing across the scatterplot within diagonally oriented bins. The *dotted line* indicates unity, and the *solid line* segment is aligned with the geometric mean. Ratios less than unity indicate that neuronal performance was better (threshold was lower) for the heterochromatic condition. The *black bars* show the threshold ratios for experiments in which the two thresholds were significantly different from each other. The data are from the 50 experiments for which we obtained good fits of the Quick function to neuronal data for both conditions.

whether, on a case-by-case basis, color segmentation affected neuronal and behavioral thresholds in a similar way. We next asked whether the magnitude of neuronal thresholds matched that of simultaneously measured behavioral thresholds. Finally, we asked whether variation in neuronal threshold was correlated with variation in behavioral threshold.

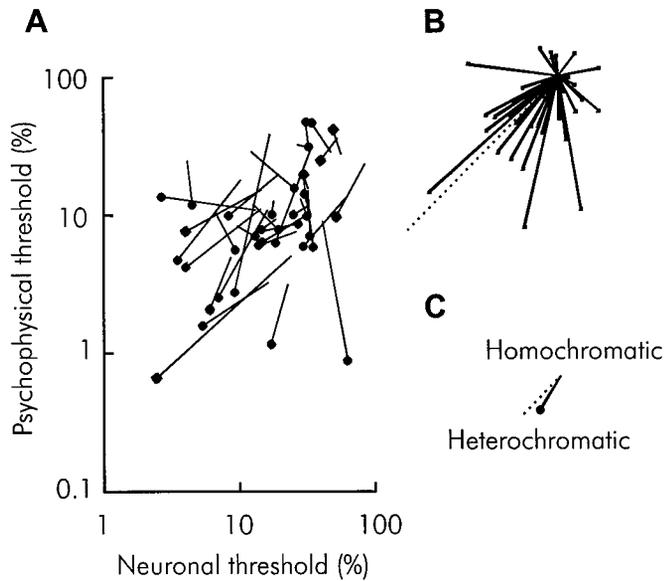
To evaluate whether color segmentation affected neuronal and behavioral performance similarly, we studied the magnitude of neuronal and behavioral threshold enhancements with color segmentation. We found that color segmentation improved both neuronal and behavioral discriminability but had a larger effect on behavioral discriminability. Figure 8 illustrates this by showing the relation between neuronal and behavioral thresholds in detail. Data from the 37 experiments in which we obtained significant fits for all four thresholds (neuronal heterochromatic and homochromatic, behavioral heterochromatic and homochromatic) are plotted in Figure 8A. The plain end of each vector shows the relation between behavioral and neuronal thresholds for the homochromatic condition, and the end with a black dot shows the same relation for the heterochromatic condition during the same experiment. Vectors with a downward component (from homochromatic to heterochromatic) indicate improved behavioral discriminability for the heterochromatic condition. Vectors with a

leftward component indicate improved neuronal discriminability for the heterochromatic condition. The net direction of each vector signifies the relative change in neuronal and behavioral thresholds. The trend from homochromatic to heterochromatic data are clearly down and to the left, indicating that segmentation by color enhanced both behavioral and neuronal direction discrimination. To better view this trend, the vectors are redrawn from the same origin, which represents the homochromatic threshold relation, in Figure 8B, and the average vector is shown separately in Figure 8C. The average vector has logarithmic coordinates (−0.153, −0.266) relative to its origin, signifying that for this set of experiments color segmentation caused neuronal thresholds to decrease to 0.70 of their homochromatic value, and behavioral thresholds to decrease to 0.54 of their homochromatic value on average. This difference between the behavioral and neuronal enhancements afforded by color segmentation was statistically significant (one-tailed paired *t* test; *p* = 0.037). Thus, color segmentation tended to improve behavioral more than neuronal direction discrimination.

We next investigated whether neuronal thresholds matched behavioral thresholds, by studying the ratio of neuronal to behavioral thresholds. Newsome and colleagues found that, when monkeys discriminated direction in homochromatic stimuli, the aver-

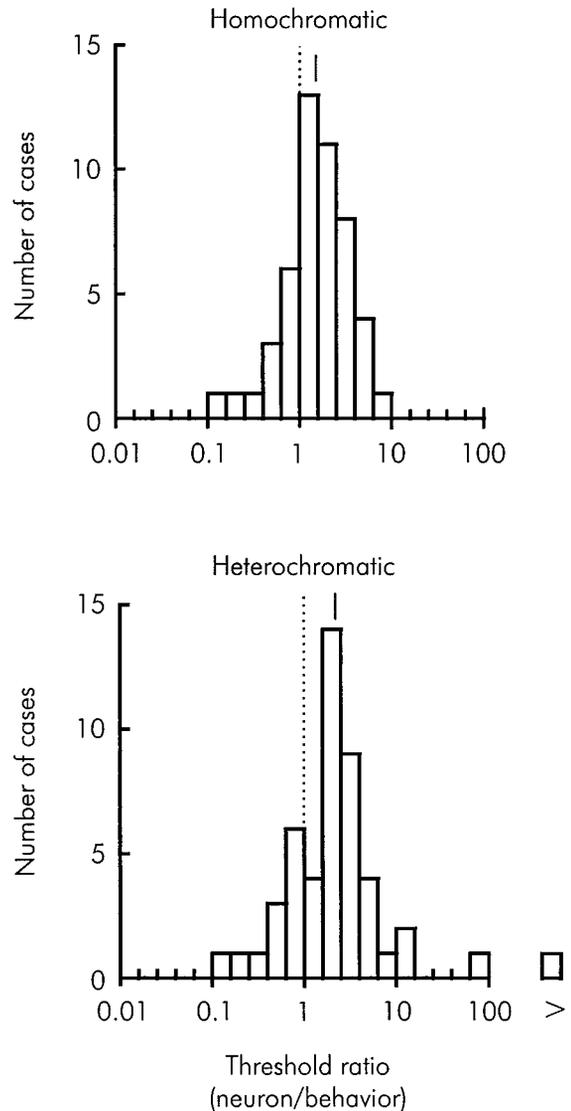


**Figure 7.** Psychometric and neurometric functions obtained in two experiments. The psychometric functions are shown in the *top panels*, and the corresponding neurometric functions obtained at the same time are shown in the *bottom panels*. Homochromatic: *white triangles, dashed lines*; heterochromatic: *black circles, solid lines*. The *left column* shows an experiment in which color segmentation had a large, statistically significant effect on behavioral performance (behavioral thresholds: homochromatic, 3.98%; heterochromatic, 0.23%), but only a small effect on neuronal performance measured at the same time (neuronal thresholds: homochromatic, 4.1%; heterochromatic, 3.1%, not statistically different) (80–85 trials per point). The *right column* shows an experiment in which a large (~10-fold), statistically significant decrease in the behavioral heterochromatic threshold (thresholds: homochromatic, 5.0%; heterochromatic, 0.7%) was accompanied by a large (~10-fold), statistically significant decrease in the neuronal heterochromatic threshold (thresholds: homochromatic, 23.8%; heterochromatic, 2.4%) (16–20 trials per point). (Note: the data in the *left column* are from the same experiment as in Fig. 5B.)



**Figure 8.** Comparison of the change in absolute neuronal and behavioral thresholds afforded by color segmentation. *A*, Vectors show the change in thresholds measured in each experiment. The *plain* end of each vector shows the relation between behavioral and neuronal thresholds for the homochromatic condition, and the end with a *black dot* shows the same relation for the heterochromatic condition. Vectors with a *downward* component (from homochromatic to heterochromatic) indicate enhanced behavioral sensitivity to the heterochromatic condition; vectors with an *upward* component indicate the converse. Vectors with a *leftward* component indicate enhanced neuronal sensitivity to the heterochromatic condition; vectors with a *rightward* component indicate the converse. *B*, The vectors are redrawn from the same origin, which represents the homochromatic thresholds. *C*, The single vector is the average of the vectors shown in *B*. In *B* and *C* the *dotted line* is the 45° diagonal, where vectors would lie if color segmentation influenced behavioral and neuronal thresholds equally.

age neuronal to behavioral threshold ratio was close to one (Newsome et al., 1989; Britten et al., 1992). Because we found that color segmentation decreased behavioral more than neuronal thresholds, we expected to find larger neuronal to behavioral threshold ratios for the heterochromatic condition. Figure 9 shows frequency distributions of the threshold ratios separately for the homochromatic and heterochromatic conditions. Ratios near 1.0 resulted from experiments in which the neuronal and behavioral thresholds were nearly identical, ratios less than 1.0 arose from experiments in which neuronal discriminability was better than behavioral performance, and ratios greater than 1.0 indicate experiments in which behavioral performance exceeded neuronal discriminability. The most noteworthy characteristic of the distributions is that the modal values are near unity, indicating a close relation between neuronal and behavioral thresholds. The heterochromatic distribution is, however, shifted to slightly higher values than the homochromatic distribution. Evaluating the parameters of the distributions, we find that the geometric mean of the homochromatic distribution is 1.5 and is not statistically distinguishable from the value of 1.2 reported by Britten et al. (1992) for the same kind of stimulus condition (one-sample *t* test;  $p = 0.07$ ). By contrast, the geometric mean of the heterochromatic distribution is 2.2 and is significantly greater than both the Britten et al. (1992) homochromatic value (one-tailed one-sample *t* test;  $p = 0.003$ ) and the mean of our own homochromatic distribution (one-tailed paired *t* test;  $p = 0.03$ ). Thus, although (1) we observed the expected ~1:1 ratio of neuronal to behavioral



**Figure 9.** Relative sensitivity of single MT neurons and monkeys. The frequency distributions show the ratio of neuronal threshold to behavioral threshold for the homochromatic (*top*) and heterochromatic (*bottom*) conditions. *Dotted vertical lines* indicate unity, and *solid vertical line* segments are aligned with the geometric means. The ratios are from experiments in which we obtained good fits of the Quick function to both neuronal and behavioral data (homochromatic, 49 experiments; heterochromatic, 48 experiments). The impact of the outlier (threshold ratio > 100) on the heterochromatic distribution was minimal: omitting this datum did not significantly affect the geometric mean of the distribution, nor did it affect the significant difference of the geometric mean from 1.0 or from the geometric mean of the homochromatic distribution.

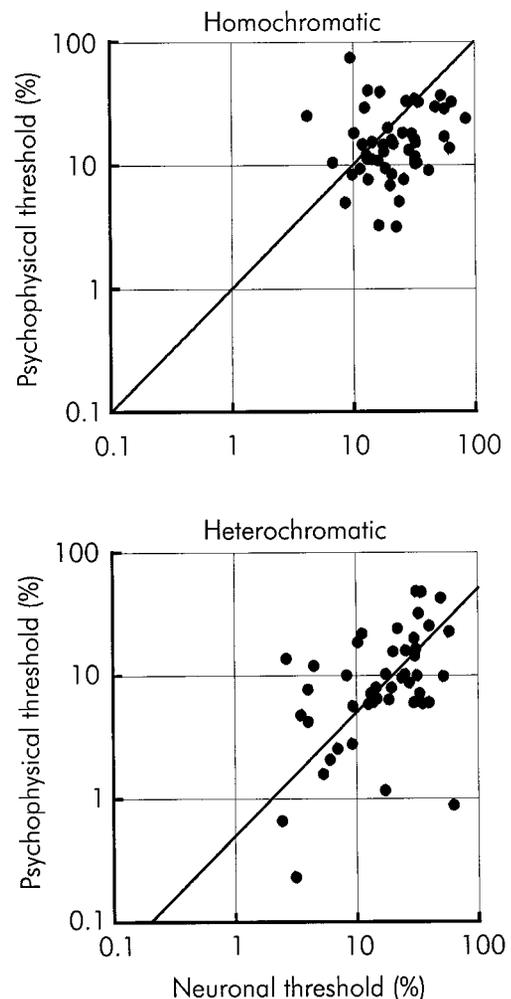
thresholds for homochromatic stimuli, and (2) color segmentation decreased both neuronal and behavioral thresholds, behavioral performance for the heterochromatic condition was, on average, approximately twice as good as predicted from MT responses to the same stimuli.

Finally, we examined whether variation in neuronal thresholds was correlated with variation in behavioral thresholds. Newsome and colleagues also examined this question for their homochromatic condition. They found that, although the ratios of neuronal to behavioral thresholds were distributed near one, neuronal and behavioral thresholds were only weakly correlated on a case-by-case basis. Much of the variability in both thresholds could be

accounted for by monkey identity and by variation in stimulus factors affecting the difficulty of the discrimination, such as the eccentricity, size, and speed of the stimulus (Britten et al., 1992). After accounting for these factors, Britten et al. (1992) found that only an additional 2% of variance in behavioral threshold was accounted for by neuronal threshold. We wished to verify this finding for the homochromatic condition and examine whether it extended to the heterochromatic condition. To our surprise, we found a stronger correlation between neuronal and behavioral performance for the heterochromatic condition, as described below.

Following Britten et al. (1992), we performed a hierarchically structured analysis of covariance to evaluate whether behavioral threshold variability not accounted for by task difficulty and monkey identity was captured by variability in neuronal thresholds. We used data from experiments in which both behavioral and neuronal performances were well fit by the Quick function, for the homochromatic or heterochromatic condition. For the homochromatic condition, we found that stimulus factors (stimulus eccentricity and speed of the motion signal) affecting task difficulty accounted for 39.1% of the variability in behavioral homochromatic thresholds and that neuronal threshold had no significant additional predictive influence on behavioral threshold. This is similar to Britten et al. (1992) and verifies their finding that each MT neuron is a sample from a population whose average threshold matches behavioral performance, which is influenced in a predictable way by task difficulty. Our result for the heterochromatic condition was quite different. The covariance analysis revealed no significant correlation of behavioral threshold with stimulus factors expected to affect task difficulty. Instead, behavioral threshold was significantly correlated with both monkey identity and neuronal threshold, which together accounted for 26.6% of the variability in behavioral heterochromatic thresholds. In other words, using color to segment the motion signal rendered behavioral performance independent of stimulus factors that affect the difficulty of the homochromatic discrimination (within the range of stimuli used). In addition, whatever factor influenced behavioral performance for the heterochromatic condition was reflected in MT neuronal responses.

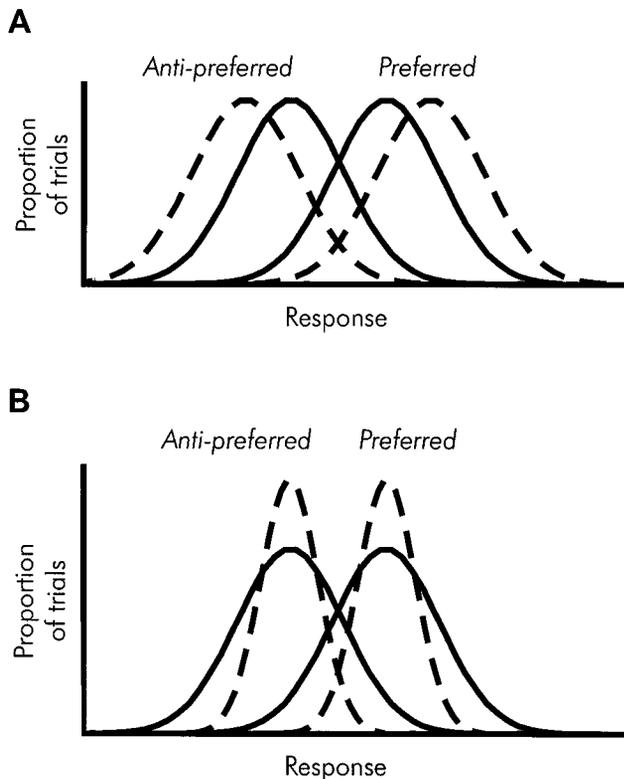
Figure 10 illustrates these findings by showing the relation between neuronal and behavioral thresholds separately for the two conditions. In the plot of homochromatic data (Fig. 10, top), the diagonal line represents equality, where points would lie if behavioral threshold were equal to the simultaneously measured neuronal threshold. As expected, this plot is similar to Figure 10 of Britten et al. (1992), which resulted from the same stimulus condition and task: although the points are distributed around the diagonal, more points lie below than above, indicating that the behavioral threshold was often slightly lower than the simultaneously measured neuronal threshold, and there is no apparent correlation between the two measures. A different pattern was seen for the heterochromatic condition (Fig. 10, bottom). Behavioral thresholds were lower and more variable than for the homochromatic condition. The solid line represents where points would lie if behavioral thresholds were half of neuronal thresholds. The points cluster near this line and are symmetrically distributed around it, consistent with the fact that the average ratio of heterochromatic neuronal to behavioral threshold was approximately two. Another departure from the homochromatic plot is that the heterochromatic neuronal thresholds show wider variation. This variation is correlated with that of behavioral thresholds (Spearman rank-order correlation;  $p = 0.010$ ; correla-



**Figure 10.** Comparison of absolute neuronal and behavioral thresholds. For the homochromatic data (top), the solid diagonal line represents equality, where points would lie if behavioral threshold equaled neuronal threshold. For the heterochromatic data (bottom), the solid diagonal line represents where points would lie if behavioral threshold were exactly half of neuronal threshold (that is, if behavioral discrimination were twice as sensitive as neuronal discrimination).

tion coefficient, 0.368). Lower behavioral thresholds were associated with lower neuronal thresholds.

The covariance analysis described above and illustrated in Figure 10 leads to a provocative conclusion. Although stimulus speed and location predictably influenced homochromatic performance, it appears that segmenting the motion signal by color made the direction decision so much easier that these stimulus factors became largely irrelevant. In short, judgments of direction in heterochromatic stimuli seem to be based on a different decision process. The correlation between heterochromatic neuronal and behavioral thresholds shows that the decision process was reflected in MT responses. One possibility is that differentiating signal dots by color allowed attention to be directed preferentially to signal dots, easing discrimination of their direction. If so, variation in heterochromatic behavioral and neuronal thresholds might reflect variation in the attentional state of the monkey across different experiments. Because attentional state would also be expected to affect how well the monkey performed at the highest correlation levels (asymptotic performance), we asked whether increased behavioral threshold was associated with de-



**Figure 11.** Schematic diagram of response changes that would result in enhanced neuronal discriminability for the heterochromatic condition. Shown are hypothetical frequency distributions of the responses of one neuron to a stochastic motion stimulus of one correlation level, with motion in the preferred or antipreferred direction of the neuron. Hypothetical responses to homochromatic (solid lines) and heterochromatic (dashed lines) stimuli are shown. Improved discriminability based on neuronal responses would result from a change that decreased the overlap of preferred and antipreferred response distributions. *A*, Heterochromatic stimuli could evoke responses that differ in magnitude from responses to homochromatic stimuli. *B*, Heterochromatic stimuli could evoke responses that are less variable than responses to homochromatic stimuli.

creased asymptotic performance. We refit behavioral data with the Quick function, allowing asymptotic performance to vary as a fit parameter. We found that, for heterochromatic experiments with asymptotic performance <100%, there was a significant inverse correlation between threshold and asymptotic performance ( $p < 0.001$ ;  $r^2 = 0.500$ ), consistent with the idea that the monkey was less attentive when heterochromatic threshold was higher. Interestingly, we found no such correlation for homochromatic performance ( $p = 0.857$ ), suggesting that attention may have less influence on performance for this condition.

In summary, color segmentation improved both behavioral and neuronal discriminability but had a smaller effect on neuronal discriminability. The average ratio of neuronal to behavioral threshold was  $\sim 2$  for the heterochromatic condition, indicating less similarity between the thresholds than for the homochromatic condition. Nevertheless, heterochromatic behavioral thresholds were significantly correlated with neuronal thresholds, consistent with a link between MT responses and behavioral discrimination for the heterochromatic condition.

#### Sources of enhanced heterochromatic neuronal discriminability

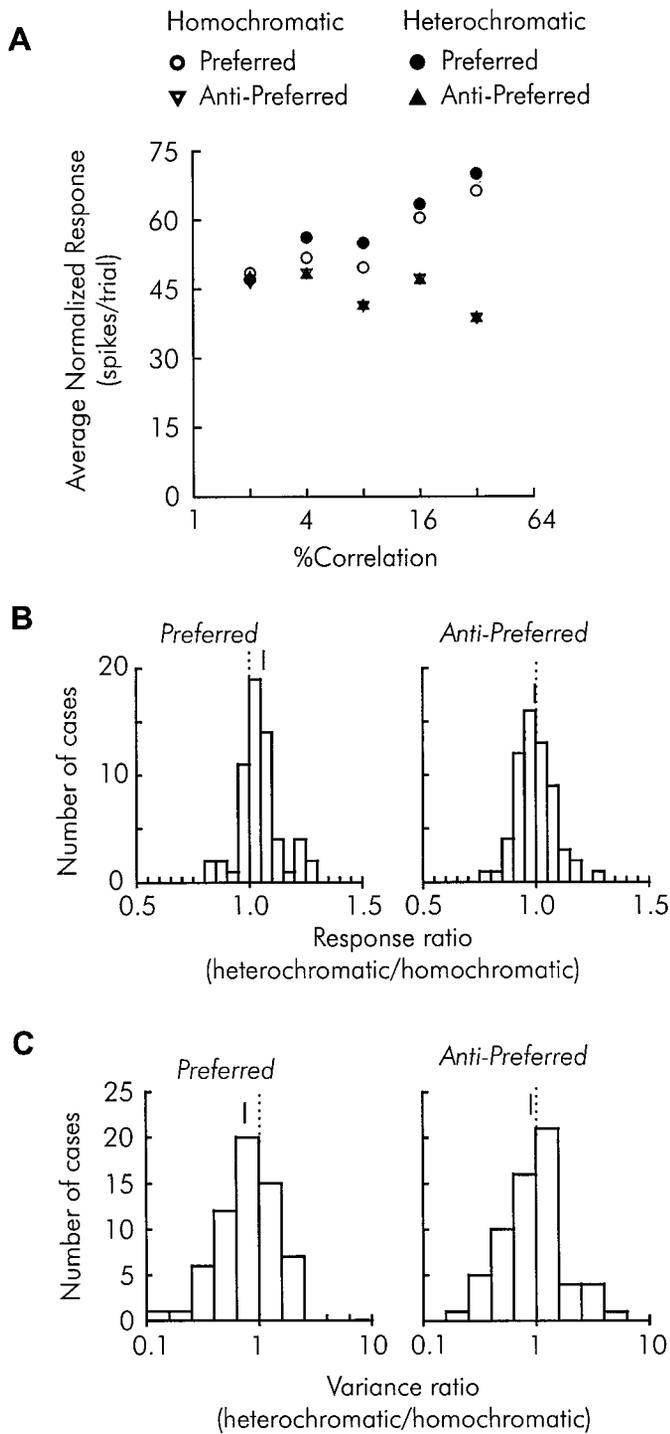
To gain insight into the mechanisms by which color segmentation improved MT neuronal direction discriminability, we considered

what response changes caused neuronal heterochromatic thresholds to decrease. In our neurometric functions (e.g., Fig. 5*A*, bottom panel), a decreased heterochromatic threshold resulted when a neuron had generally higher discrimination performance for the heterochromatic than for the homochromatic condition. Higher neuronal performance for a particular stimulus correlation stemmed from less overlap of the preferred and antipreferred direction response distributions. Decreased overlap could arise from two possible changes in the responses (Fig. 11). First, the magnitude of responses to homochromatic and heterochromatic stimuli could be different, caused by either larger responses to heterochromatic preferred direction motion, smaller responses to heterochromatic antipreferred direction motion, or both (Fig. 11*A*). Second, heterochromatic responses could be less variable and thus have narrower distributions (Fig. 11*B*). Response distributions for either preferred, antipreferred, or both directions could be narrower.

We investigated which of the changes illustrated in Figure 11 were associated with enhanced neuronal discriminability for the heterochromatic condition. We focused our analysis on the neurons whose thresholds were statistically significantly lowered by color segmentation, because these neurons had the most robust differences in their responses to heterochromatic and homochromatic stimuli. Because we wanted to know how responses to each particular stimulus (one stimulus correlation level, one direction) changed with color segmentation, we calculated for each such stimulus the ratio of the heterochromatic to homochromatic response average or variance for each neuron. We performed Spearman rank order correlation tests to evaluate whether these ratios were correlated with stimulus correlation level and found that they were not. We therefore pooled ratios across correlation levels and evaluated the distributions obtained, as described below.

Figure 12*A* shows the general pattern of our results for response magnitude. For illustration, scaled average normalized responses (see figure legend) are plotted against stimulus correlation. Responses to the preferred and antipreferred directions of motion separated as stimulus correlation increased. The separation was larger for heterochromatic than for homochromatic stimuli, caused solely by larger responses to preferred direction heterochromatic stimuli. This can be seen by examining the ratios of the raw average responses of each neuron to heterochromatic and homochromatic stimuli for each stimulus correlation level. Figure 12*B* shows the distributions of these response ratios separately for preferred and antipreferred directions. The mean of the preferred direction distribution is 1.065, significantly different from 1.0 (one-sample  $t$  test;  $p = 0.001$ ). The mean of the antipreferred direction distribution is 0.997, not statistically distinguishable from 1.0 (one-sample  $t$  test;  $p = 0.752$ ). Thus, enhanced heterochromatic discriminability was associated with, on average, 6.5% larger responses to preferred direction stimuli.

Because a 6.5% change in response magnitude is small, we suspected that another response change might also contribute to the heterochromatic enhancement. This was confirmed by our study of response variability. For each neuron, we determined the variance of the total spike count during the two-second stimuli and calculated the ratio of heterochromatic to homochromatic variance for each stimulus correlation and direction. Figure 12*C* shows the distributions of the variance ratios separately for preferred and antipreferred directions. The preferred direction distribution has a geometric mean of 0.78, significantly different from 1.0 (one-sample  $t$  test;  $p = 0.001$ ). The antipreferred direction distribution has a geometric mean of 0.91, not statistically distin-



**Figure 12.** Relative parameters of response distributions for homochromatic and heterochromatic conditions. *A*, To convey the difference between the magnitude of responses to homochromatic and heterochromatic stimuli, average normalized responses to homochromatic (white symbols) and heterochromatic (black symbols) stimuli have been scaled and plotted against stimulus correlation. Preferred direction (circles) and antipreferred direction (triangles) responses are shown. For each neuron, the average responses to preferred and antipreferred directions of homochromatic and heterochromatic stimuli of each stimulus correlation were determined. These averages were normalized by the average response of the neuron to preferred direction heterochromatic stimuli of that correlation level and then averaged across neurons. The processed responses were then multiplied by the average of the heterochromatic responses of all the neurons to a given correlation. *B*, Frequency distributions showing the ratios of raw average heterochromatic to homochromatic responses

guishable from 1.0 (one-sample *t* test;  $p = 0.249$ ). Thus, enhanced heterochromatic discriminability was associated with lower variability (noise) of responses to preferred direction stimuli. Consistent with this, we found that the average ratio of variance to mean, known as the “Fano factor” (attributed to Fano, 1947) and considered a characteristic measure of normalized response noise, was significantly lower for the heterochromatic than for the homochromatic condition (average Fano factors for preferred direction motion: heterochromatic, 1.9; homochromatic, 2.6; paired *t* test;  $p < 0.001$ ).

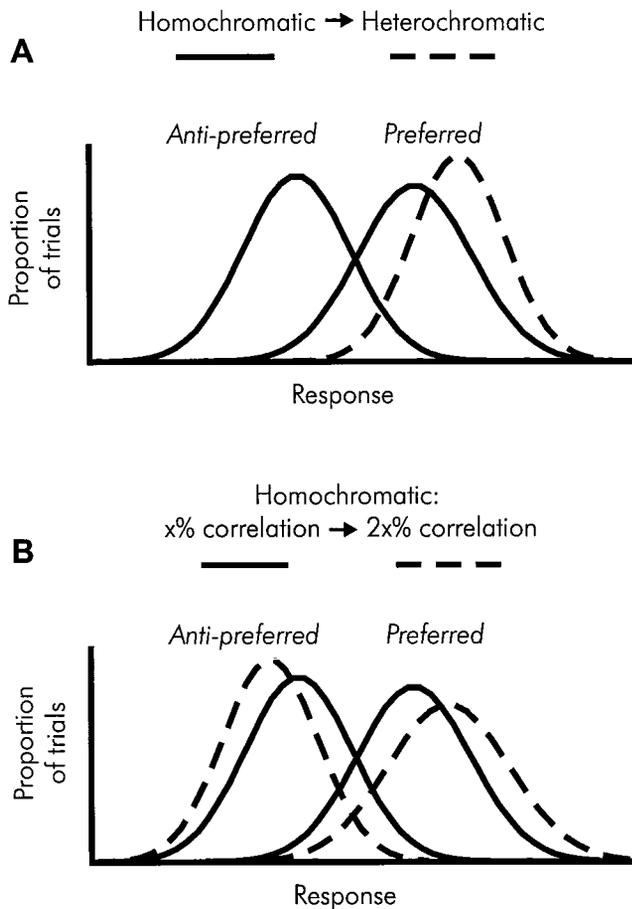
Our findings on the response changes associated with enhanced heterochromatic discriminability are summarized by hypothetical response distributions in Figure 13*A*. The solid lines show distributions of responses to the preferred and antipreferred directions at one stimulus correlation of the homochromatic condition. We have drawn a wider preferred direction distribution to more realistically express the known increase of variance with response magnitude (Dean, 1981; Tolhurst et al., 1981, 1983; Vogels et al., 1989; Snowden et al., 1992). The dashed line shows the distribution of responses to a preferred direction heterochromatic stimulus of the same stimulus correlation. The average response is larger, and the response variance is lower than for the preferred direction homochromatic condition, resulting in less overlap with the antipreferred direction distribution, which is the same for both conditions.

How do the response changes underlying improved heterochromatic discriminability compare with those occurring when the correlation of a homochromatic stimulus is increased? When stimulus correlation increases, improved neuronal discriminability generally stems from larger responses to preferred direction motion and smaller responses to antipreferred direction motion (Britten et al., 1993). This is illustrated with hypothetical response distributions in Figure 13*B*. The solid lines show distributions of the responses of a neuron to a low correlation homochromatic stimulus, and the dashed lines show the responses to a higher correlation. To verify this pattern in our own data, we calculated ratios of average responses to homochromatic stimuli whose correlation levels differed by a factor of two. We used data from the same neurons that we used to determine the response changes underlying heterochromatic enhancement. Within the range of motion signal strengths studied for these neurons, doubling homochromatic correlation gave approximately the same discriminability increase regardless of the starting correlation, justifying the pooling of these values. The mean ratio of responses (higher to lower correlation) for the preferred direction was 1.120 and for the antipreferred was 0.971, both significantly different from 1.0 (one-sample *t* tests;  $p = 0.001$ ). Response variability was as expected from the known relation between firing rate and variability. Thus, our data on the response changes associated with increasing signal strength fit the pattern diagrammed in Figure 13*B*, as expected.

In summary, chromatically segmenting motion signal from

←

for preferred (left) and antipreferred (right) direction motion. Dotted vertical lines indicate unity, and solid vertical line segments are aligned with the means. The means of the two distributions are significantly different (one-sample *t* test;  $p < 0.001$ ). *C*, Frequency distributions showing the ratios of heterochromatic response variance to homochromatic response variance for preferred (left) and antipreferred (right) direction motion. Dotted vertical lines indicate unity, and solid vertical line segments are aligned with the means. The means of the two distributions are significantly different (one-sample *t* test;  $p = 0.044$ ).



**Figure 13.** Schematic diagrams showing the response changes associated with enhanced discriminability by neurons with significantly different homochromatic and heterochromatic thresholds. *A*, Hypothetical frequency distributions of the responses of a neuron to homochromatic stimuli (solid lines) and to heterochromatic (dashed lines) preferred direction stimuli of one stimulus correlation. *B*, Hypothetical frequency distributions of the responses of a neuron to homochromatic stimuli of a low stimulus correlation (solid lines) and to homochromatic stimuli of twice that correlation (dashed lines).

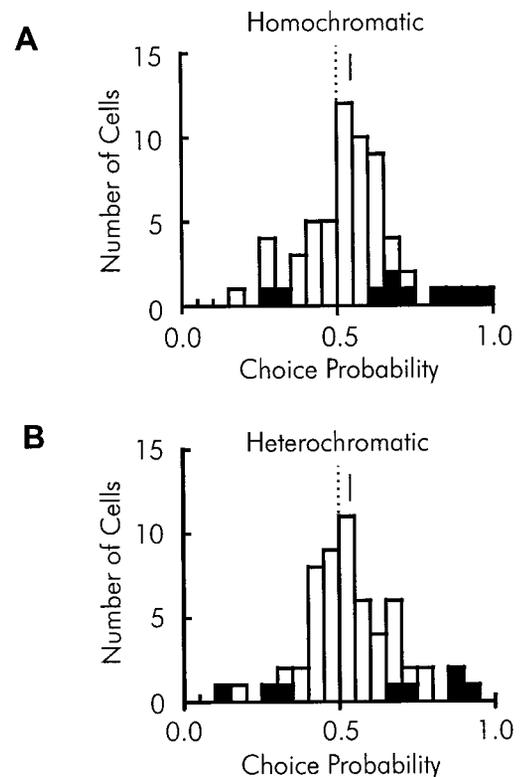
noise evoked changes in responses to motion in the preferred directions of the neurons: these responses were, on average, slightly larger and less variable than responses to the corresponding homochromatic stimuli (Fig. 13*A*). These changes differed from those elicited by increasing the correlation of a homochromatic stimulus, in which case responses to the preferred direction increased and responses to the antipreferred direction decreased (Fig. 13*B*). These findings suggest that segmenting signal from noise by color is not equivalent, in terms of MT responses, to increasing the motion signal strength. Different mechanisms may drive the neurons in these two cases.

### Choice probability

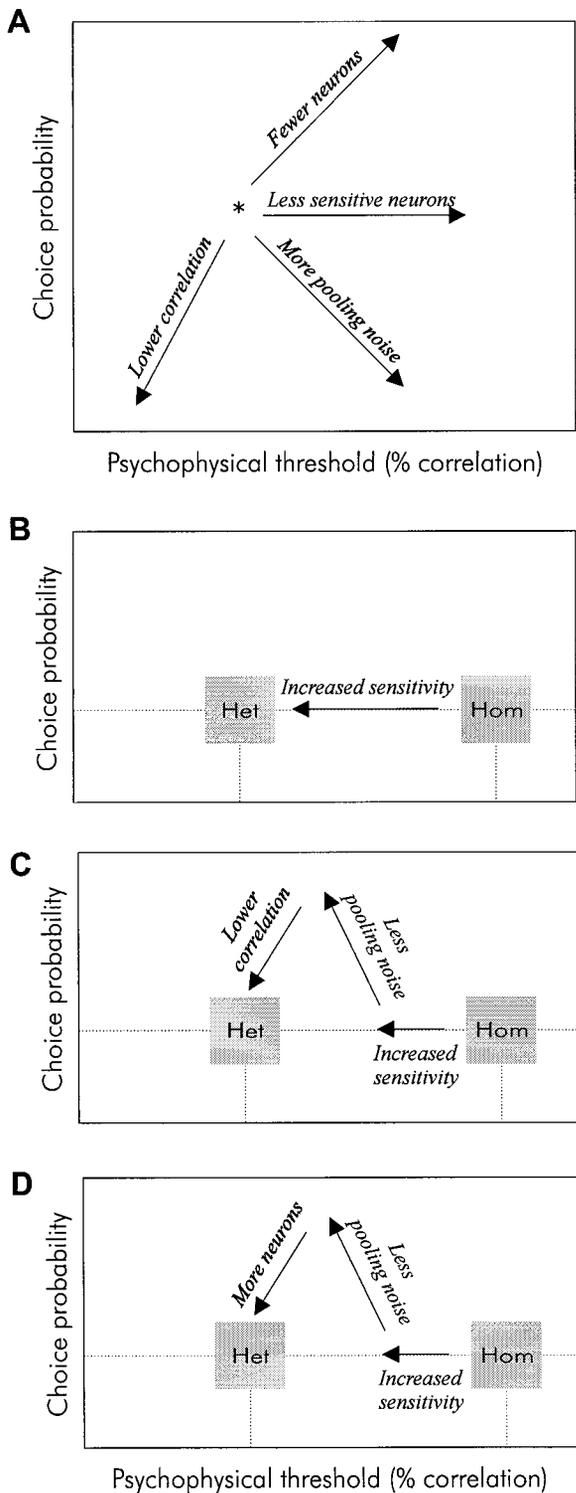
Finally, we investigated how neuronal response and behavioral choice were related on a trial-by-trial basis. Britten et al. (1996) did a thorough analysis of the trial-by-trial relation between neuronal firing rate and judgment of direction in homochromatic stimuli. These investigators found a modest but significant relation between choice and firing rate: for a stimulus moving in one direction and carrying motion of a particular signal strength, MT neurons increased firing rates by an average of 7% on trials for which the animal chose the preferred direction of the neurons.

This relation was quantified as “choice probability”, the probability of correctly predicting the animal’s behavioral choice based on neuronal response during one trial. The relation they found amounted to an average choice probability of  $\sim 0.55$ . In undertaking the same analysis of our data, we wished to know whether the choice probability for our heterochromatic condition differed from that for the homochromatic condition. We reasoned that if the role of MT in direction judgments were the same regardless of color segmentation, then choice probability would be the same for both conditions.

Our analysis followed that of Britten et al. (1996). To calculate representative choice probability values for each neuron, responses were pooled across different stimulus correlation levels using the z-transform method described by Britten et al. (1996). The responses of the neuron on each trial of a given stimulus (preferred or antipreferred direction, homochromatic or heterochromatic) were then assigned to one of two distributions depending on whether the monkey chose the preferred or antipreferred direction of the neuron under study. ROC analysis was performed to generate a choice probability value, representing how well an ideal observer could predict the monkey’s choice based on these two response distributions. We used the permutation test described by Britten et al. (1996) to evaluate whether an observed value was significantly different from that expected by chance. Because choice probability depends on the direction of stimulus motion, we calculated four values for each neuron, based



**Figure 14.** Neuronal choice probability for preferred direction motion. Black bars show neurons whose choice probabilities were significantly different from chance, according to the permutation test described by Britten et al. (1996). Dotted vertical lines indicate chance, and solid vertical line segments are aligned with the means. *A*, Distribution of choice probabilities calculated from responses to homochromatic stimuli. *B*, Distribution of choice probabilities calculated from responses to heterochromatic stimuli.



**Figure 15.** How the Shadlen et al. (1996) MT pooling model could account for enhanced behavioral threshold with color segmentation. *A*, The model predicted average neuronal choice probability and behavioral thresholds, which define a two-dimensional space, depending on the state of four model parameters: number of neurons pooled, sensitivity of the neurons, pooling noise, and correlation between neurons. Asterisk indicates an arbitrary relation between choice probability and behavioral threshold. Arrows indicate how changes in each of the four parameters would affect the simulated choice probability and threshold. (Shadlen et al. 1996, their Fig. 8). *B–D*, Gray boxes represent our data for the homochromatic (*Hom*) and heterochromatic (*Het*) conditions. Behavioral thresholds were lower for the heterochromatic condition, and choice

on neuronal responses to motion in the preferred and antipreferred directions of the neuron, for the homochromatic and heterochromatic conditions.

Only choice probabilities calculated from responses to preferred direction stimuli had averages significantly different from 0.50 (this is consistent with Britten et al. (1996), whose nonpreferred direction choice probabilities were significantly different from 0.50 only for motion correlation levels lower than the minimum we used). Figure 14 displays the distributions of the preferred direction values. The black bars show the distributions for neurons whose choice probabilities were significantly different from chance. The data for the homochromatic distribution (Fig. 14*A*) are similar to data reported by Britten et al. (1996) for the same condition, as expected. The mean of the distribution is 0.546 and is not significantly different from the mean of 0.556 reported by Britten et al. (1996) (their Fig. 5, *top*) (one-sample *t* test;  $p = 0.608$ ). Also as reported by Britten et al. (1996), the majority of statistically significant values are  $>0.5$ . Our data for the heterochromatic condition (Fig. 14*B*) show the same pattern. The mean of the heterochromatic distribution is 0.538 and is not significantly different from our own homochromatic (paired *t* test;  $p = 0.551$ ) or the average homochromatic choice probability of Britten et al. (1996) (one-sample *t* test;  $p = 0.378$ ).

These data show that a monkey's behavioral choice of direction is equally well predicted by MT responses whether the animal views homochromatic or heterochromatic stimuli. That is, whereas for the heterochromatic case the probability of errors is lower (the animal more frequently chooses the correct direction), the predictability of the monkey's choice based on the response remains the same. In terms of neuronal responses, whereas the average response to preferred direction motion may be higher for heterochromatic than for homochromatic stimuli, the responses are distributed such that there is a weak but significant correlation with behavioral choice for both conditions. Therefore, the mechanism that generates direction decisions retains the same relation to the responses of single MT neurons regardless of whether color segments motion signal from noise.

## DISCUSSION

We have evaluated the relation between MT responses and behavioral direction discrimination of motion signals with and without segmentation by color. The average discriminative capacity of MT neurons was enhanced by color segmentation, as evidenced by decreased neuronal thresholds for the heterochromatic condition. For the subset of neurons displaying the strongest enhancement, the decreased threshold stemmed from increased mean and decreased variance of responses to heterochromatic stimuli moving in the preferred directions of the neurons. The average magnitude of the neuronal threshold change for the entire population of studied neurons was, however, smaller than that of the behavioral effect: segmentation decreased behavioral thresholds to  $\sim 0.54$  of their nonsegmented value, whereas it decreased neuronal thresholds to  $\sim 0.70$  of their nonsegmented value (Fig.

← probability was the same for both conditions. *B*, Pooled neurons with sufficiently enhanced sensitivity for the heterochromatic condition could account for our data. *C*, Pooling of neurons with slightly enhanced heterochromatic sensitivity could account for our data if there were less pooling noise and lower correlation between individual neurons. *D*, Pooling of neurons with slightly enhanced heterochromatic sensitivity could also account for our data if there were less pooling noise as well as larger pools.

8). One consequence of this difference was that the ratio of neuronal to behavioral thresholds depended on whether signal was segmented from noise by color. Without segmentation, the average ratio was 1.5, which was statistically indistinguishable from the value of 1.2 reported by Newsome et al. (1989) and Britten et al. (1992) for the same condition. With color segmentation, the average ratio was 2.2, so that observers were slightly more than twice as sensitive as the neuronal population studied. We also found that neuronal choice probability was the same regardless of whether motion signal was segmented by color. In the remainder of the Discussion we first address mechanisms that might underlie enhanced discrimination of motion in heterochromatic stimuli. We then discuss what our findings imply about the role of MT role in direction judgments.

### What mechanisms underlie enhanced discriminability of direction in heterochromatic stimuli?

Two of our findings support the conclusion that heterochromatic motion signals are processed in a fundamentally different way than homochromatic motion signals. First, our covariance analysis of behavioral thresholds showed that, whereas homochromatic thresholds varied predictably with stimulus factors (e.g., stimulus size and motion speed) expected to affect the difficulty of the task, heterochromatic thresholds had no significant correlation with these factors. This suggests that subjects used a different decision strategy when discriminating direction in heterochromatic stimuli. Second, our analysis of the response changes underlying neuronal threshold enhancements revealed different response changes when motion stimulus correlation was increased versus when motion signal was segmented from noise by color. When homochromatic correlation level was doubled, preferred direction responses increased, and antipreferred direction responses decreased; whereas for heterochromatic stimuli, preferred direction responses were both larger and less variable than responses to the corresponding homochromatic stimuli (Figs. 12, 13). This suggests that different mechanisms come into play when heterochromatic stimuli move in the preferred direction of a neuron, causing the neuron to be driven, in some senses, more effectively.

Bringing these two findings together, we are led to propose that the larger and less variable MT responses to heterochromatic preferred direction stimuli reflect, at least partially, the neural implementation of a unique decision strategy used by the monkey to discriminate the direction of color-segmented motion signals. One possibility is that color segmentation of the motion signal allows attention to be directed to signal dots, thus freeing the decision from concern with noise dots. This possibility is supported by two observations: (1) heterochromatic behavioral thresholds were correlated with asymptotic performance, an indicator of attentional state; and (2) the changes we introduced in nonfoveal stimuli to demonstrate that color segmentation enhanced behavioral direction discrimination (longer signal dot sequences, larger dots, and decreased dot density) would all tend to increase the perceptual salience of the signal dots (homochromatic or heterochromatic), as might be required by an attentional mechanism enhancing processing of heterochromatic signal dots. Attentional modulation could occur, at least in part, before motion signals reach MT, and could be implemented as a selective gating of inputs signaling local motion of either signal or noise dots, as we proposed in an earlier publication (Croner and Albright, 1997). Previous studies have demonstrated attentional modulation of MT neurons (Buračas and Albright, 1995; Treue and Maunsell, 1996). Although these other studies found larger

variation of responses with attention than we found in responses to heterochromatic versus homochromatic stimuli, this can be attributed to differences in the stimuli and tasks used. Whether attention is actually engaged by segmenting the motion signal by color, and whether, if engaged, it exerts its effects solely before motion signals reach MT, are open questions. Attention and other components of unique decision strategies for the heterochromatic condition could also be implemented in circuitry involved in pooling MT signals, discussed in the next section.

### The role of MT in direction judgments

Our finding that chromatic segmentation enhances behavioral more than MT neuronal direction discrimination leads to an important question: can MT responses support behavioral performance both with and without segmentation? One possibility is that MT responses underlie judgments about direction in homochromatic stimuli (as suggested by Newsome et al., 1989; Salzman et al., 1990, 1992; Britten et al., 1992) but not heterochromatic stimuli, which may depend on chromatic processing in a separate cortical area. In this case, MT would be just one of multiple areas whose responses influence direction judgments.

It is not necessary, however, to invoke chromatically sensitive neurons to account for the improvement of direction discrimination afforded by color segmentation. Our studies show that MT directional signals are, on average, enhanced for the heterochromatic condition; whether this enhancement is sufficient to support the more accurate judgments of direction in heterochromatic stimuli depends on how MT neurons are pooled to generate the judgments. To demonstrate this explicitly, we examine the pooling mechanism proposed by Shadlen et al. (1996) to support behavioral direction discrimination in homochromatic stimuli. Assuming that direction judgments are based on the average responses of pooled neurons, these investigators simulated how single neuron sensitivity, correlation between neurons, pool size, and noise added to pooled signals would affect the judgments. By simulating judgments for combinations of these four parameters, Shadlen et al. (1996) predicted the average values of two variables that depend on such judgments: behavioral threshold and choice probability. Figure 15A summarizes how the simulation parameters affected these two variables. Changes in neuronal sensitivity affected behavioral threshold without influencing choice probability; changes in each of the other three parameters affected both variables. Shadlen et al. (1996) settled on a combination of parameters that accurately predicted the behavioral thresholds and choice probabilities measured for their homochromatic condition. To account for our heterochromatic data, we can ask what kinds of changes must be introduced into the Shadlen et al. (1996) model to decrease the psychophysical threshold while keeping the same choice probability. There are three possibilities. The simplest involves using only neurons with strongly enhanced sensitivity for the heterochromatic condition (such as the subset of neurons with significantly lower thresholds for the heterochromatic condition) (Fig. 15B); these neurons would support both homochromatic and heterochromatic performance and choice probability via the same pooling mechanism. The other two possibilities involve using neurons that have on average only a modest enhancement for the heterochromatic condition (such as was found across the population of MT neurons we studied), and pooling these neurons differently depending on whether or not the motion signal is segmented by color. Either the neurons must have lower correlation between them and be pooled with less noise (Fig.

15C), or a larger number of such neurons must be pooled with less noise (Fig. 15D) for the heterochromatic condition.

The neural basis of the unique decision strategy used for the heterochromatic condition could conceivably involve pooling MT neuronal signals differently if motion signal is segmented from noise by color (Fig. 15C,D). However, alternative pooling mechanisms need not be proposed if the kind of mechanism illustrated in Figure 15B exists. In this case, the responses of a particular subset of neurons are pooled in the same way to account for both homochromatic and heterochromatic behavioral data. Admittedly, the pooled population is arbitrarily selected in this case to consist only of those neurons with significantly different thresholds for the two conditions. However, if we suppose that MT circuitry may be involved in integrating information about various visual cues, spatial and temporal visual context, and attention to generate an output signal on which direction judgments are based, then only a subset of neurons, probably those projecting to a particular target area, would respond in a manner paralleling perception of motion in complex scenes. Consistent with this idea, other studies have found a minority of MT neurons whose responses parallel perceptions of motion direction in complex visual stimuli (Movshon et al., 1985; Logothetis and Schall, 1989; Rodman and Albright, 1989; Stoner and Albright, 1992). Whether these studies have identified the same population of neurons is unknown.

## Conclusion

An important question in visual science is how the brain integrates different visual cues to form percepts of objects in natural environments. Our studies have opened the door to a new way to address the topic of cue integration. We have previously shown a strong effect of color segmentation on judgments of motion direction and have offered the generalized insight that scene structure along one cue dimension influences how signals along another cue dimension are processed (Croner and Albright, 1997). The neurophysiological studies presented here constitute an important first step in uncovering the neural substrates underlying this fascinating perceptual phenomenon. We have shown that color segmentation influences neurons in a cortical area considered important to motion processing. It remains to be seen whether this effect is all or only part of the neural substrate by which chromatic structure in a visual scene influences motion perception.

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