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Color Signals in Area MT of the Macaque Monkey

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Summary

The relationship between the neural processing of color and motion information has been a contentious issue in visual neuroscience. We examined this relationship directly by measuring neural responses to isoluminant S cone signals in extrastriate area MT of the macaque monkey. S cone stimuli produced robust, direction-selective responses at most recording sites, indicating that color signals are present in MT. While these responses were unequivocal, S cone contrast sensitivity was, on average, 1.0–1.3 log units lower than luminance contrast sensitivity. The presence of S cone responses and the relative sensitivity of MT neurons to S cone and luminance signals agree with functional magnetic resonance imaging (fMRI) measurements in human MT+. The results are consistent with the hypothesis that color signals in MT influence behavior in speed judgment tasks.

Introduction

Early physiological and psychophysical work resulted in the provocative view that color and motion processing are essentially segregated within the central visual pathways (Livingstone and Hubel, 1988; Zeki, 1993). Subsequent studies showed that the strong form of this claim is incorrect: psychophysical observers can see and discriminate motion in isoluminant visual displays (Cavanagh and Anstis, 1991; Mullen and Boulton, 1992a, 1992b), and neurons in motion-processing areas of the monkey cerebral cortex can be influenced by isoluminant chromatic stimuli (Saito et al., 1989; Dobkins and Albright, 1994; Gegenfurtner et al., 1994).

Recent psychophysical evidence has led investigators to suggest a more subtle version of the functional segregation hypothesis. Arguing that there is a quantitative discrepancy between behavioral measurements of judged speed and neural measurements in motion-selective cortex, Gegenfurtner and Hawken (1996) hypothesized the existence of two motion-processing streams. These streams differ in their temporal characteristics and in the way they process color information (Hawken et al., 1994; Gegenfurtner and Hawken, 1996). Contrary to this hypothesis, the first two papers of this series provided (1) psychophysical evidence that the motion of achromatic and chromatic stimuli are analyzed by the same mechanism within the brain and (2) functional magnetic resonance imaging (fMRI) evidence that region MT+ of the human visual cortex responds both to achromatic and chromatic stimuli with amplitudes appropriate to account for the psychophysical data (Dougherty et al., 1999 [this issue of *Neuron*]; Wandell et al., 1999 [this issue of *Neuron*]). In this paper, we show that neurons in visual area MT of the macaque monkey respond well to the same S cone–modulating stimuli employed in the first two papers of this series. Furthermore, S cone responses were directionally selective, indicating that MT is able to encode the motion of isoluminant colored stimuli. On average, the sensitivity of MT neurons to S cone contrast agreed well with the psychophysical and fMRI measurements reported in the first two papers of this series. Interestingly, individual recording sites in MT varied substantially in the strength of their S cone inputs, showing that as a population MT neurons exhibit some degree of color tuning.

The quantitative agreement between the electrophysiological and fMRI measurements supports the proposed homology between a portion of human MT+ and macaque MT, and is consistent with the view that the suprathreshold electrical activity measured in our experiments is closely linked to the hemodynamic signals measured by fMRI. Finally, the similarity of neural and perceptual sensitivity to luminance and S cone stimuli (in the speed discrimination task) suggests that MT supports the perceived motion of colored stimuli.

Results

S Cone and Luminance Signals in MT

Figure 1 shows multiunit responses elicited at one MT site by an S cone–isolating stimulus. The stimulus was shown for 0.5 s and then followed by 0.5 s of a uniform gray background. The large peaks in the average response at 0, 2, and 4 s correspond to the three intervals in which the stimulus moved in the "preferred" direction for that site. The smaller peaks at 1, 3, and 5 s correspond to intervals in which the stimulus moved in the opposite, or "null," direction for that site. The responses at this site show that neurons in MT can be strongly modulated by an S cone–isolating stimulus and that these responses are directional.

For nine single units and 36 multiunit sites, we measured responses to S cone–isolating (85% contrast) and luminance stimuli (37% and 2.2% contrast [see Experimental Procedures]) moving in the optimal direction. The S cone–isolating stimuli elicited statistically significant responses in 42 of the 44 experiments (Student's t test, $p < 0.05$). Figure 2 shows the distribution of a response index (RI) that measures the relative amplitudes of S cone and luminance responses (see Experimental Procedures). Values <0 indicate that the S cone responses were smaller than the responses to 2.2% luminance; values between 0 and 1 represent sites where the S

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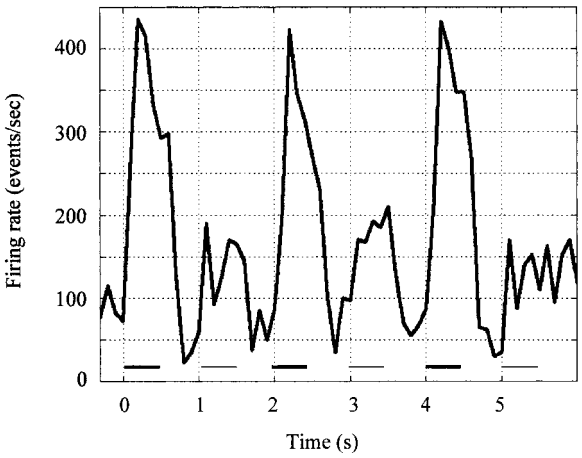

Figure 1. Multiunit Responses to an S Cone–Isolating Stimulus at 42.5% S Cone Contrast

The stimulus sequence begins at time zero and then alternates between 0.5 s of drifting sine wave grating and 0.5 s of uniform gray screen with the same mean luminance. The stimulus motion direction reverses with each presentation so that motion is in the preferred direction (thick lines) at 0, 2, and 4 s and in the opposite direction (thin lines) at 1, 3, and 5 s.

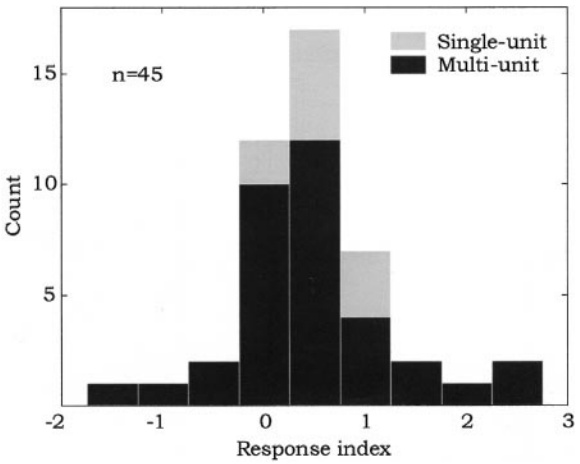

Figure 2. Comparison of S Cone and Luminance Responses in Area MT

Measurements using an S cone stimulus at 85% contrast along with a luminance stimulus at 2.2% and 37% contrast were made for 36 multiunit sites and nine single units. The histogram shows the distribution of RIs measuring S cone responses relative to the luminance responses (see Experimental Procedures).

cone responses were intermediate between 2.2% and 37% luminance responses; values above 1 (7 of the 44 sites) indicate that S cone responses were actually greater than the 37% luminance response. These results show that S cones initiate robust signals in MT. The strength of the S cone responses relative to luminance responses varied strikingly among MT recording sites.

At 10 multiunit recording sites, we obtained full contrast–response curves for both S cone– and luminance-initiated motion stimuli. Figure 3a shows how response increases with S cone contrast, averaged across the 10 sites. Each horizontal line traces a peristimulus time histogram (PSTH) at a single contrast level. As illustrated in the experiment of Figure 1, robust responses to S cone–isolating stimuli are easily identified at high contrast levels. No clear responses are present below 10.5% S cone contrast.

For comparison, Figure 3b shows average responses, measured at the same 10 sites, to luminance stimuli. These sites are exquisitely sensitive to luminance stimuli, as expected for a visual area with extensive magnocellular inputs. Responses to preferred direction motion are quite evident, even for contrasts as low as 2%. Thus, MT is substantially less sensitive to S cone–isolating stimuli than to luminance stimuli.

Figure 4 plots the relationship between stimulus contrast and mean response for luminance and S cone stimuli. The curves were fitted to the data using the model

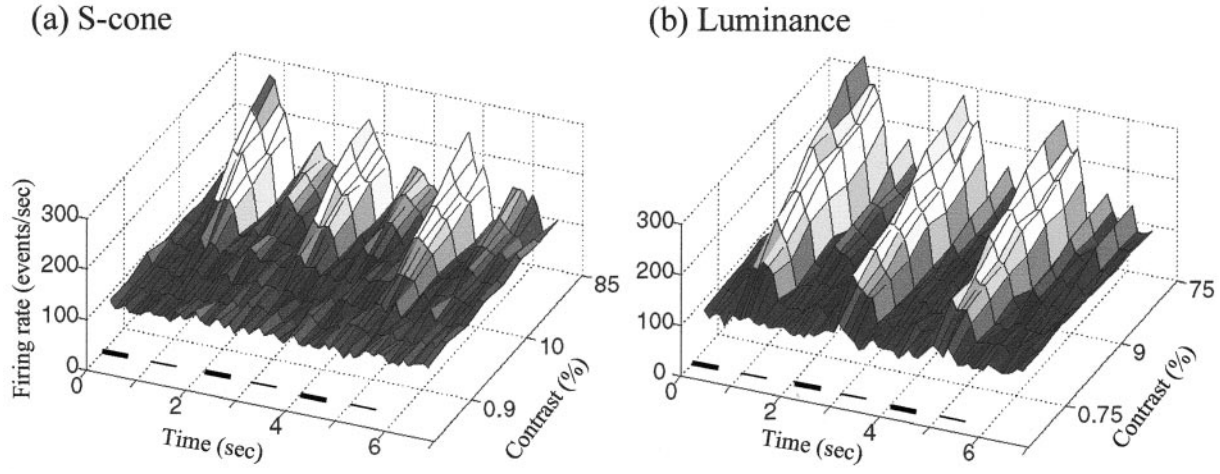

Figure 3. The Effect of Signal Contrast on Unit Activity in Area MT

Measurements using an S cone–isolating stimulus (a) and a luminance stimulus with zero S cone contrast (b) are shown. Each line parallel to the x axis depicts a single PSTH. Each surface is comprised of eight PSTH measurements made at contrast levels ranging from small contrasts at the near edge of the plot to high values at the far edge. The timing and labeling conventions of the visual stimulus are the same as in Figure 1. The data are averaged across 10 multiunit MT sites from the two monkeys.

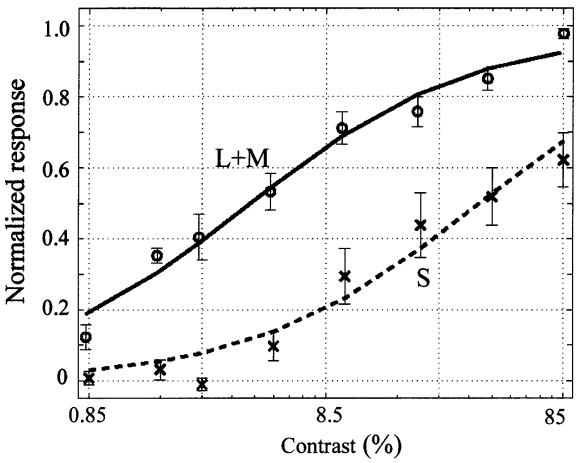

Figure 4. Contrast–Response Curves for Luminance and S Cone–Isolating Stimuli

Each point represents the average and standard error (across 10 MT multiunit sites) of the normalized response to luminance (o) or S cone (x) stimuli at a given contrast. Data are from the same ten experiments illustrated in Figure 3. The best fit is plotted with each contrast–response curve (see Experimental Procedures).

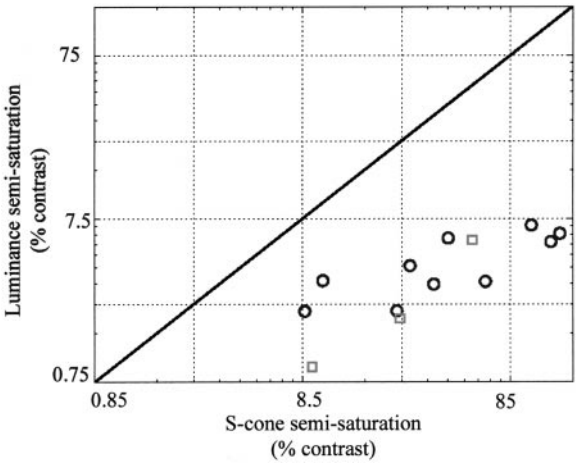

Figure 5. Scatter Plot Summarizing Luminance and S Cone Sensitivity at Each Recording Site

Data for 10 MT multiunit sites (closed circles) and three MT single units (shaded squares) are shown. The sensitivity is summarized by the semisaturation parameter estimated using the model described in the Experimental Procedures.

described in the Experimental Procedures. The semisaturation parameter from the fitted curve measures the contrast level at which the average response reaches half the maximum value. The parameter was 3.5% contrast for the averaged luminance data and 35.9% for the averaged S cone data. Thus, MT is roughly ten times more sensitive to luminance stimuli than to S cone–initiated stimuli.

Figure 5 summarizes sensitivity to luminance and S cone stimuli for 10 MT multiunit sites and three single units (collected simultaneously with multiunit activity at 3 sites). Luminance sensitivity exceeded S cone sensitivity by factors ranging from 3.5 to 23 (mean, 1.15 log units). Nearly all MT sites were stimulated by both S cone and luminance signals, but luminance response is significantly higher per unit of cone contrast.

Adaptation Control Experiments

Calibration errors of the S cone stimulus could result in residual modulation of the L and M cones. Because MT neurons are highly sensitive to L and M cone activity, apparent responses to S cone stimuli could result from these calibration errors. It is also possible that some of the S cone responses are due to rod-initiated signals. To test further for the presence of S cone responses, we repeated the measurements in the presence of a bright yellow adapting light. The wavelength composition of the adapting light was selected in order to activate strongly the L cones, M cones, and rods while sparing the S cones. Were the S cone responses due to residual luminance signals, adaptation to the yellow background should reduce responses to luminance and S cone stimuli equally. The adapting light (>200 scotopic cd/m^2) is well into the rod-saturation region (Aguilar and Stiles, 1954; Hood and Finkelstein, 1986).

Figure 6 shows the effect of the yellow background on MT responses to luminance- (Figure 6a) and S cone–isolating (Figure 6b) stimuli. Luminance sensitivity was reduced by a factor of more than 4, while S cone sensitivity at the same sites was reduced by a factor of 1.6. Because the two responses are not reduced equally, we conclude that MT responses to the S cone–isolating stimuli are not due primarily to residual luminance or rod-initiated signals.

Direction Selectivity

As part of the measurement protocol, we obtained direction-tuning curves for both luminance and S cone stimuli. Figures 7a and 7b illustrate direction-tuning curves at 2 MT recording sites. Measurements shown in Figure 7a illustrate a site where the direction-tuning curves for S cone and luminance stimuli were virtually identical, both in terms of preferred direction and overall response level. Across the data set, the preferred direction was almost always the same for S cone and luminance stimuli. At some sites, such as the one illustrated in Figure 7b, S cone direction selectivity was less pronounced than luminance direction selectivity. In these cases, responses to motion in the opposite (null) direction were stronger for the S cone stimulus than for either the high or low contrast luminance stimuli. At the site illustrated in Figure 7b, for example, the responses to S cone–isolating stimuli appeared to be more orientation selective than direction selective.

Figures 7c and 7d compare the directionality of the luminance and S cone responses across the entire data set. The distribution of directionality indices (DIs) (see Experimental Procedures) is shown separately for monkey S (Figure 7c) and monkey M (Figure 7d). In monkey S, DIs were similar for luminance and S cone stimuli (mean DI: 0.96, 1.08, and 0.92 for S cone, low contrast luminance, and high contrast luminance stimuli, respectively). In monkey M, however, S cone responses were less directional; the mean DI for the responses to S cone stimuli (0.52) was significantly lower than the mean DI for the high contrast luminance stimulus (0.98; Student's t test, $p < 5 \times 10^{-4}$), as well as for the low contrast

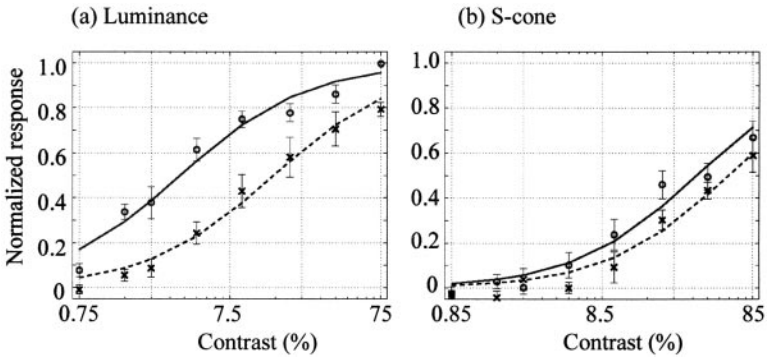

Figure 6. The Effect of Adapting the L, M, and Rod Receptors on Contrast–Response Functions

Contrast–response curves for luminance stimuli (a) and S cone–isolating stimuli (b) are shown in the two panels. Responses under gray (o) and yellow (x) illumination are denoted by the two symbol types. At each site, measurements were made on gray, yellow, and then again on gray backgrounds. Data from 10 sites were included in this analysis. Sites were included only if the two separate measurements made on gray backgrounds, before and after the yellow adaptation condition, were consistent with each other (i.e., if the recordings appeared stationary).

luminance stimulus (mean DI: 1.04; Student's t test, $p < 5 \times 10^{-3}$). For monkey M, the S cone data are consistent with prior reports that the direction selectivity of MT neurons is weaker for low salience motion stimuli (Albright, 1992; Olavarria et al., 1992). The difference in the directionality of some MT neurons under S cone stimulation further supports the conclusion that the S cone responses are not due to residual luminance signals. But the directionality measurements must be regarded tentatively because the results in the two animals differ.

Discussion

This study and others have demonstrated that MT units can be influenced by isoluminant colored stimuli (Saito et al., 1989; Dobkins and Albright, 1994; Gegenfurtner et al., 1994; Thiele et al., 1999). Thus, the strong hypothesis of complete segregation of color and motion processing within the visual cortex appears untenable (Hubel and Livingstone, 1987; Livingstone and Hubel, 1987, 1988; Zeki, 1990; Zeki et al., 1991). Rather, the key questions now are (1) what sorts of color signals reach MT,

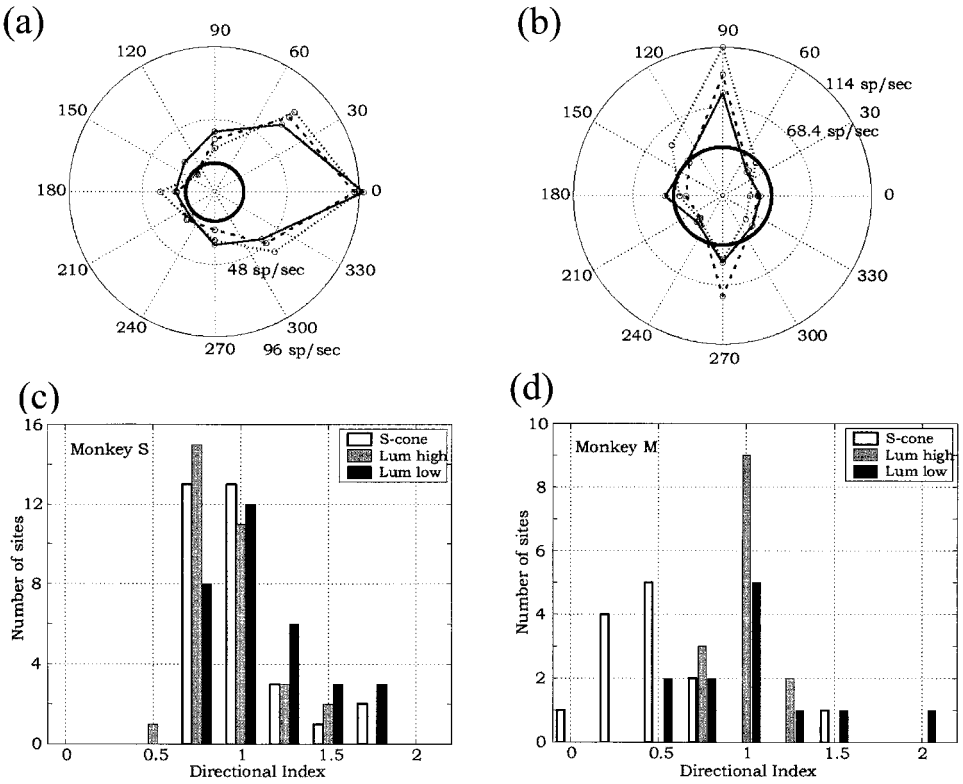

Figure 7. Direction Tuning of Two MT Multiunit Sites to 2.2% and 43% Contrast Luminance and 85% Contrast S Cone–Isolating Stimuli

(a and b) Each polar plot shows the mean response as a function of the direction of motion. The dark circle at the center indicates baseline activity rate. The dashed, dotted, and solid lines represent S cone, high luminance contrast and low luminance contrast responses, respectively. (c and d) Distribution of directional indices for S cone, low luminance contrast, and high luminance contrast stimuli from all single units and multiunit recording sites. (a) and (c) show results from monkey S, and (b) and (d) show those from monkey M. For monkey S, all three histograms contain data from 32 recording sites. For a few sites in monkey M, responses were not significantly greater than baseline for low luminance– or S cone–isolating stimuli. Direction indices are presented only for sites with significant activity (n = 14, 13, and 12 for high luminance, S cone–isolating, and low luminance histograms, respectively).

(2) does MT use these signals to encode the motion of colored stimuli, and (3) can the color inputs to MT account for the effects of chromatic composition on speed perception, or must another pathway be invoked to account for the perceived motion of colored stimuli?

Our results are pertinent to all three of these questions. The clear demonstration of S cone responses in MT, coupled with the known magnocellular input driven by L and M cones, shows that MT receives signals initiated from all three cone types. MT neurons respond in a directionally selective manner to S cone signals, showing that MT neurons actually encode the motion of isoluminant colored stimuli. Finally, the fact that MT neurons are less responsive to S cone than to luminance signals by roughly a factor of 10 agrees remarkably well with the perceptual observations and the fMRI data reported in the first two papers of this series (Dougherty et al., 1999; Wandell et al., 1999). Together, the data suggest that the physiology of MT neurons can account for the effects of color on perceived speed in human observers and that a second motion pathway need not be invoked.

Although a coherent view of the role of MT in processing color signals is gradually emerging, important questions remain unanswered. For example, exactly how are luminance and chromatic signals organized within MT? One possibility is that MT units combine input from luminance and color opponent mechanisms in a nonselective manner, according to the "color energy" model proposed in the first paper of this series (Dougherty et al., 1999). In this view, MT neurons can process motion defined by color signals, but they retain no information about the color identity of the stimulus. A few recent studies, however, suggest that MT neurons may utilize chromatic identity information under some circumstances (Dobkins and Albright, 1998; Croner and Albright, 1999). Our observations lend some support to this point of view: the large variability in the contribution of S cone signals among MT sites (Figure 2) suggests that some degree of color tuning may be present in MT. Thus, it seems possible that in addition to computing the motion of colored stimuli, there may be neural mechanisms in MT that can identify signals using this color information. More detailed analyses of the chromatic properties of MT neurons will be necessary to resolve this issue.

How are the S cone signals communicated to MT? Physiological studies indicate that the magnocellular layers of the lateral geniculate nucleus (LGN), which provide the dominant input to MT (Maunsell et al., 1990), receive no S cone–initiated signals (Rodieck, 1998). Rather, S cone "on signals" originate in the small, bistratified ganglion cells of the retina and appear to be transmitted to primary visual cortex via the koniocellular pathway of the LGN (Dacey and Lee, 1994; Martin et al., 1997). There may also be an S cone "off signal" in the parvocellular pathway (Klug et al., 1993). Thus, our data suggest that the S cone inputs received by MT originate in the color-opponent koniocellular pathway, and perhaps in the parvocellular pathway, as well. A physiological study of Gegenfurtner and colleagues (1994) found unequivocal evidence for red–green color opponent input, presumably originating in the parvocellular pathway, in 11% of the MT neurons they tested, consistent with the inactivation studies of Maunsell and colleagues (1990). The available data, therefore, suggest that MT receives inputs from all known LGN pathways, as envisioned in the color energy model presented in the first paper of this series (Dougherty et al., 1999). Preliminary anatomical data from the retina suggest that some S cones may project to the magnocellular pathway (D. Calkins, personal communication; S. J. Schein, personal communication). If these connections prove to be physiologically significant, our model of color inputs to MT may require revision.

A prior investigation of single units in MT reported no evidence for S cone responses (Gegenfurtner et al., 1994). It is unclear whether the difference between their study and ours reflects actual differences in data or merely differences in interpretation. Gegenfurtner and colleagues measured the responses to eight different isoluminant stimuli in 17 cells. They report that isoluminant stimuli generated appreciable responses for 13 of the 17 cells tested (in comparison with 42 of 44 sites in our sample tested for S cone inputs). For all 13 of these neurons, Gegenfurtner and colleagues reported that the strongest responses were generated by red–green isoluminant stimuli (L−M), rather than by S cone–modulating stimuli like those used in our study. These data alone do not preclude the possibility that S cone responses were in fact present in the neurons tested, only that these responses must have been smaller in amplitude than the red–green responses. Gegenfurtner and colleagues go on to say, however, that "there was very little if any S cone input to these cells" (Gegenfurtner et al., 1994, p. 459), leading us to suspect that our data differ substantially from theirs. The different results in the two studies are not likely to derive from differences in the stimulus contrasts used. The S cone stimuli employed by Gegenfurtner and colleagues were lower contrast (66.7%) than ours (85%), but their luminance stimuli were lower contrast than ours, as well. It is conceivable that our multiunit recordings may have detected weak S cone responses more effectively by summing signals from many neurons near the electrode tip, but the single unit data illustrated in our Figures 2 and 5 do not differ noticeably from the multiunit data (although the number of single units is small). In short, we remain perplexed by the apparent difference in the two studies. Possible contributing factors may include anesthesia, small sample sizes, or subtle stimulus differences.

Comparison of fMRI and Unit Activity

The electrophysiological measurements of S cone and luminance signals in macaque MT agree well with parallel fMRI measurements in human MT+ (Wandell et al., 1999). Both studies demonstrated robust responses to S cone–isolating stimuli, and both found that S cone sensitivity is about ten times lower than the luminance sensitivity. It is worth remembering that this level of quantitative agreement is obtained despite vast differences in measurement methods. The fMRI measurements are the result of changes in local magnetic fields caused by blood oxygenation levels. The single unit measurements are based totally on action potentials,

and the multiunit measurements are dominated by action potentials. The agreement between electrophysiological and fMRI measurements provides (1) further evidence in support of the homology between macaque MT and human MT+ and (2) an important confirmation of the quantitative validity of the fMRI measurements as a report of the underlying electrical activity.

Color Signals in MT

Previous studies have shown that MT contributes importantly to the performance of tasks involving motion and disparity computations (Salzman et al., 1992; DeAngelis et al., 1998). Taken together, the findings reported in this paper and the two companion studies support the view that MT performs these basic computations for all visual stimuli, irrespective of color composition. The electrophysiological and fMRI data indicate that MT has modest access to color information. Thus, MT, like other visual areas, receives inputs from all three LGN pathways, albeit in different proportions than do other visual areas. The color sensitivity of psychophysical observers in making speed judgments is strikingly similar to the color sensitivity revealed by the electrophysiological and fMRI measurements (Dougherty et al., 1999; Wandell et al., 1999). This agreement suggests that the responses of MT neurons underlie the perceived motion of colored stimuli. Together, these three studies suggest that MT plays a substantial role in the perception of visual motion, for stimuli of all colors.

Experimental Procedures

A central goal of the current study was to compare quantitatively our electrophysiological measurements with the fMRI measurements obtained in a companion study (Wandell et al., 1999). Several aspects of our experimental design were adopted specifically to facilitate this comparison. First, our visual stimuli were nearly the same as those employed in the fMRI experiments. Second, we used a fixed battery of visual stimuli at each recording site, irrespective of the tuning properties of individual sites. This procedure reflects the fact that the spatially coarse fMRI signal reflects contributions from all sites in MT+, not just from those that are well tuned to a specific stimulus. Finally, most of our measurements were obtained from multiunit clusters rather than from single units. Again, this procedure simply allows us to cast a broad net in each experiment, gathering information from more of the neural elements that might contribute to an fMRI signal. We collected data from single units whenever possible, but recording sites were not selected on the basis of isolated action potentials. All procedures used in this study conformed with guidelines established by the National Institutes of Health for the care and use of laboratory animals.

Visual Stimuli

The stimuli were 0.8 cycles/° of grating contrast patterns drifting at 5°/s. The stimuli subtended 14° × 14° of visual angle and were centered on a fixation point. To assess the relative contributions of the cones to MT responses, the contrast pattern was set to one of two types of colored patterns: (1) an S cone–isolating stimulus that had zero L and M cone contrast or (2) a luminance stimulus with L and M cone contrasts set in a ratio of 1:1.6 and zero S cone contrast. Contrast patterns were generated using a Cambridge Research graphics board (VSG 2/3) and presented on a Nanao 17 inch Flexscan monitor (model T2-17ts, 60 Hz screen refresh rate) placed 57 cm away from the monkey. Cone-isolating stimuli were created using the methods described in Appendix B in Wandell (1995) and in Dougherty et al. (1999).

In most experiments, the contrast patterns were presented on a uniform gray background (~50 cd/m^2). In the adaptation experiments, yellow light from two slide projectors was superimposed on the display, producing a 189 cd/m^2 background (241 scotopic cd/m^2). The spectral composition was similar to that shown in Wandell et al. (1999) (Figure 4), but the cathode ray tube display produced more power in the short wavelengths than did the liquid crystal display used in those experiments, accounting for the high scotopic luminance levels. The monkey was allowed to adapt to each new illumination condition for 3–5 min prior to recording.

Behavioral Task

Two rhesus monkeys were trained to fixate a central spot on a computer monitor while viewing the grating stimuli. Eye position was measured continuously using a scleral search coil system (CNC Engineering, Seattle, WA). Throughout each trial, the monkey was required to maintain fixation within a window (3° × 3° or smaller) centered around a small fixation point. Trials in which the monkey broke fixation prematurely were aborted without reward and were excluded from the analysis.

Each trial began with onset of the fixation point. After the monkey established fixation for 0.5 s, six stimuli of 0.5 s duration were presented, each separated by 0.5 s intervals of gray screen of the same mean luminance as the grating stimuli. To minimize motion adaptation effects, the direction of motion was reversed every second so that the first, third, and fifth seconds contained motion in one direction, and the second, fourth, and sixth seconds contained motion in the opposite direction. For each multiunit site or single unit studied, we first measured direction-tuning curves for three types of grating stimuli: 37% luminance contrast, 2.2% luminance contrast, and 85% S cone contrast. The axis of motion on each trial was chosen pseudorandomly from four possibilities, such that the entire stimulus set consisted of eight directions of motion at 45° intervals around the clock. For a subset of recording sites, we measured full contrast–response curves for luminance and S cone–initiated stimuli. For these measurements, we used a single axis of motion, approximating the preferred–null axis of the multiunit cluster or single neuron. The contrast level was selected pseudorandomly in each trial. In all experiments, each stimulus condition was repeated at least four times.

Electrophysiology

Neuronal activity was recorded using parylene-coated tungsten microelectrodes (MicroProbe, Bethesda, MD; impedance = 1–2 MΩ at 1 kHz). Electrodes were inserted into the occipital lobe through stainless steel guide tubes held in place by a plastic grid attached to the inside of the recording cylinder (Crist et al., 1988). MT was identified in preliminary mapping experiments based on its high percentage of direction-selective units, its characteristic topography, and the stereotyped sequence of gray matter, white matter, and sulci along the electrode tracks.

For multiunit recordings, an "event" was considered to be any excursion of the voltage trace above a set threshold (this might correspond to an action potential from a single neuron or a signal from several superimposed spikes). The threshold was set by hand so that baseline activity (in the absence of a stimulus) was 50–100 events/s. This multiunit measurement is likely to reflect the summed spiking activity of several neurons near the tip of the recording electrode. Single units were isolated using a conventional time–amplitude window discriminator. For each site, the multiunit receptive field location and the preferred direction were first mapped using a random dot stimulus that was controlled interactively by the experimenter. Additional details regarding our experimental methods can be found elsewhere (Heeger et al., 1999; Seidemann and Newsome, 1999).

Data Analysis

Contrast sensitivity data were compiled into plots of neural response as a function of stimulus contrast. These data were then fitted using the function $R = (c^p/c^p + \sigma^p)M$, where R is the response level (in events per second or spikes per second), c is the stimulus contrast, M is the maximum response level, σ is a semisaturation constant, and p is an exponent that defines the slope of the curve. When

comparing the sensitivity of S cone and luminance targets, we used the common values of M and p for the S cone and luminance stimuli.

The DI was computed using the formula $DI = 1 - R_{null}/R_{pref}$, where R_{pref} and R_{null} are the response levels above or below the spontaneous firing rate (in events per second or spikes per second) for motion in the preferred and null (or antipreferred) directions, respectively.

To compare the activity level elicited by 85% S cone contrast stimulus and luminance stimuli of 2.2% and 37% contrast, we computed the following RI: $RI = (R_{s\text{-}cone} - R_{low\text{-}lum})/(R_{high\text{-}lum} - R_{low\text{-}lum})$, where $R_{S\ cone}$ and $R_{low\text{-}lum}$ and $R_{high\text{-}lum}$ are the response levels above baseline (in events per second or spikes per second), for S cone, low luminance contrast (2.2%), and high luminance contrast (37%) stimuli, respectively.

Acknowledgments

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