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Color Signals in Human Motion-Selective Cortex

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Summary

The neural basis for the effects of color and contrast on perceived speed was examined using functional magnetic resonance imaging (fMRI). Responses to S cone (blue–yellow) and L + M cone (luminance) patterns were measured in area V1 and in the motion area MT+. The MT+ responses were quantitatively similar to perceptual speed judgments of color patterns but not to color detection measures. We also measured cortical motion responses in individuals lacking L and M cone function (S cone monochromats). The S cone monochromats have clear motion-responsive regions in the conventional MT+ position, and their contrast–response functions there have twice the responsivity of S cone contrast–response functions in normal controls. But, their responsivity is far lower than the normals' responsivity to luminance contrast. Thus, the powerful magnocellular input to MT+ is either weak or silent during photopic vision in S cone monochromats.

Introduction

Stimulus color and contrast influence perceived stimulus speed. For example, a stimulus can be made to appear to move at a different rate by adjusting its color or contrast (Cavanagh et al., 1984). The theory of functional segregation of color and motion provided an interesting and provocative explanation of this phenomenon (Livingstone and Hubel, 1988; Zeki, 1993). According to the theory, color and motion information are represented in independent processing streams, with extrastriate motion areas receiving luminance but not chromatic signals. Subsequent investigations have shown that the strong form of functional segregation is incorrect. Stimuli with zero luminance contrast do appear to move (Cavanagh and Anstis, 1986, 1991; Lindsey and Teller, 1990; Chichilnisky et al., 1992; Mullen and Boulton, 1992), and such stimuli do evoke responses in extrastriate visual areas (MT) involved in motion perception (Saito et al., 1989; Gegenfurtner et al., 1994; McKeefry and Zeki, 1997; Thiele et al., 1999). Careful examination of the data, however, revealed apparent quantitative discrepancies between behavioral measurements and area MT responses (Hawken et al., 1994; Gegenfurtner and Hawken, 1996b). These discrepancies led to the interesting proposal that there are two motion streams and that these process color information differently (Gegenfurtner and Hawken, 1996a).

In this paper, the second in a series of three, we describe functional magnetic resonance imaging (fMRI) measurements in human motion-selective cortex of responses to chromatic and achromatic stimuli. These experiments are designed to detect discrepancies between the color signals measured in the human motion complex (MT+) and the influence of stimulus color and contrast on perceived speed measured in the first study (Dougherty et al., 1999 [this issue of *Neuron*]). Corresponding measurements of unit activity are described in the third paper (Seidemann et al., 1999 [this issue of *Neuron*]).

The experiments described in this paper mainly compare responses to contrast patterns initiated in the S cones with responses initiated in the L and M cones. The S cone contrast patterns have zero contrast with respect to physically defined luminance (Judd, 1951). The S cone modulations appear violet–green when superimposed on a gray background. The L and M cone modulations are a powerful luminance stimulus. They appear yellow–black when seen on a gray background. For convenience, we describe the stimuli using color names, but there is no evidence to suggest that the signals measured in motion-selective cortex cause the conscious experience of color appearance.

The S cone and luminance responses were compared for three reasons. First, S cone stimuli appear to move slowly compared with luminance stimuli of similar contrast and identical physical speed (Dougherty et al., 1999). The apparent speed difference is very large and should be associated with a correspondingly large difference in neural responses in the relevant neural pathways. Second, the ratio of S cone to luminance responsivity in speed judgments differs from the ratio in detection tasks. Hence, this color comparison offers a clear chance at distinguishing whether MT+ color responses are specific to motion judgment or reflect a general sensitivity difference. Third, S cone stimuli can be presented over a larger contrast range than red–green isoluminant stimuli, and the S cones are more securely isolated than the L or M cones. Thus, the comparison provides a good experimental stimulus for measuring the influence of color on perceived motion.

The fMRI measurements reveal that human MT+ responds powerfully to S cone stimuli as well as to luminance and isoluminance stimuli initiated in the L and M cones. The response amplitude per unit of S cone contrast (i.e., responsivity) is lower than the responsivity for luminance stimuli. These differences are consistent with measurements of perceived speed judgments described by Dougherty et al. (1999), but they are not consistent with the detection thresholds of the same stimuli. Consequently, we suggest that the color responses measured in MT+ specifically influence the

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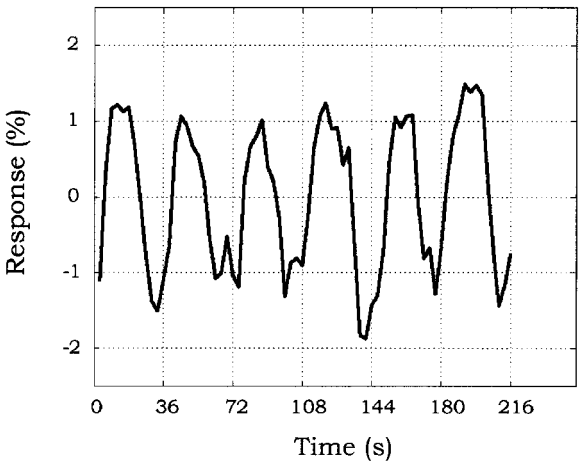

Figure 1. The Time Series in MT+ as a Moving 60% Contrast S Cone–Isolating Stimulus Alternates with a Neutral Gray Background

The vertical axis measures the percent modulation about the mean for all voxels in MT+. The data were smoothed by convolution with a three tap kernel (0.126, 0.747, 0.126) (subject: H. B.).

motion judgment and that they are not a general measure of color responsivity. These measurements support the view set forth by Dobkins and Albright (1998) that "chromatic information is processed by multiple visual subsystems, but in a different manner by each as befits their broader functions in visual perception" (p. 54).

To verify that we have properly isolated S cone signals, we have measured cortical responses in two S cone monochromats. These are individuals whose retinae contain only S cones and rods. In these individuals, too, responses to S cone stimuli are present in human region MT+. In addition to their importance as a control, the measurements in S cone monochromats offer a unique opportunity to understand developmental plasticity within the color and motion pathways.

Results

S Cone Responses

Figure 1 shows an fMRI time series measured in MT+ while the subject was viewing a moving S cone stimulus at 60% cone contrast (18 s) that alternated with a uniform gray background (18 s). The fMRI signal modulates by more than 1%, many standard deviations larger than the noise and in synchrony with alternation between the S cone stimulus and neutral background. For this observer, and four others we have tested, MT+ responds robustly to a moving S cone isoluminance stimulus.

Figure 2 shows how response amplitude increases with stimulus contrast in area V1 (Figure 2a) and in region MT+ (Figure 2b). Each panel contains contrast–response functions for both luminance and S cone stimuli. In area V1, the shape of the two curves differs substantially. The response levels spanned by S cone responses are comparable to those spanned by luminance responses, but much lower luminance contrasts are required to reach any given response level. Hence, color sensitivity differences between the two areas are not described by a single scale factor. To reach low response levels (0.3), the S cone contrast must be more than 1.0 log unit greater than the luminance contrast. To reach higher response levels (0.7), the S cone contrast need only be 0.3 log units higher than the luminance contrast.

Sensitivity is greater in MT+ than V1 for both luminance and S cone stimuli. Compared with V1, sensitivity in MT+ to luminance stimuli is roughly six times greater, and sensitivity to S cone stimuli is roughly two times greater. Also, the luminance response function reaches saturation at quite low contrast levels, on the order of 2%–5% (Tootell et al., 1995). While the luminance and S cone contrast–response functions differ, they are more nearly parallel in MT+ than are the corresponding curves

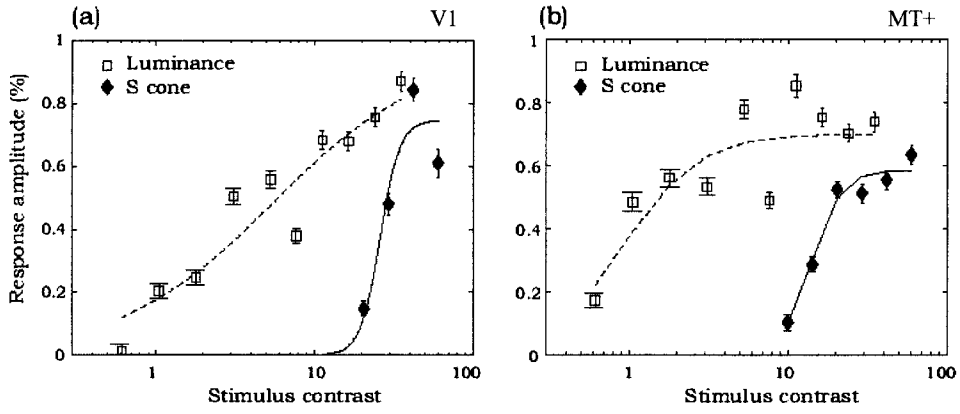

Figure 2. The Increase of Response Amplitude with Stimulus Contrast Measured in Area V1 and Region MT+

The response amplitudes measured using S cone–isolating stimuli (closed diamonds) and luminance stimuli (open squares) are shown. For the S cone stimuli, contrast is simply the S cone contrast level. For the luminance stimuli, the relative L and M cone contrasts were 1.0:1.6, and the stimulus contrast is the vector length (square root of the sum of the squares) of these two contrasts. The smooth curves fit to the data, and their parameters are described in the Experimental Procedures. In V1, the curve parameters (σ, M, p) were 0.06, 0.97, 0.89 for luminance and 0.26, 0.76, 6.0 for S cone stimuli. In MT+, the parameters were 0.01, 0.70, 1.84 for luminance and 0.15, 0.59, 4.6 for S cone stimuli. Error bars are one standard error of the mean response amplitude. The data represent the fit to combined data from two subjects (subjects: H. B., G. B.).

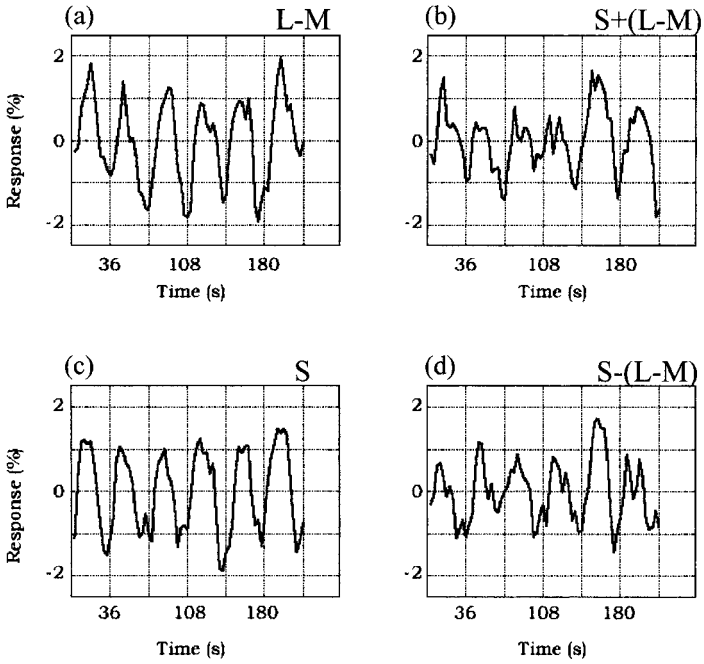

Figure 3. Responses to Isoluminance Stimuli

fMRI time series in MT+ in response to four different isoluminant moving stimuli modulated about a neutral gray background. All four stimuli evoked significant responses in MT+. (a) shows the time series response to an L − M stimulus, and (b) is the response to an S + (L − M) stimulus. (c) represents the time series to the S cone stimulus alone, and (d) is the response to S − (L − M) (subject: H. B.).

in V1. Across all MT+ response levels, the S cone contrast needed to match the luminance contrast ranges from about 1.0 to 1.3 log units. At a given stimulus contrast level, the signal-to-noise ratio in MT+ of responses initiated in the S cones will be substantially lower than that of responses initiated by luminance stimuli of the same contrast.

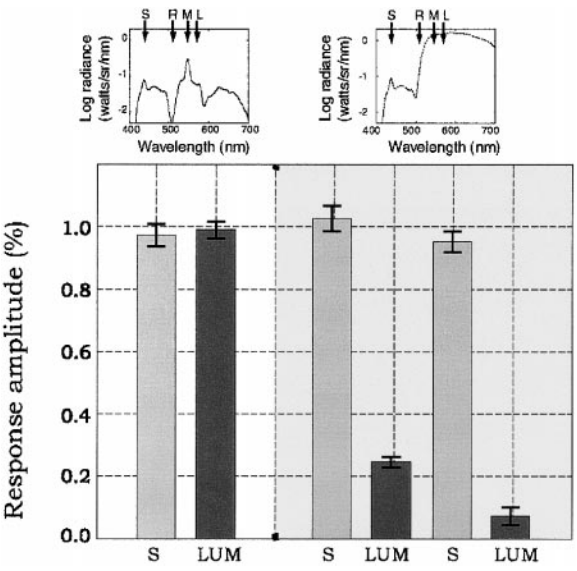

Figure 4. Adaptation Experiments

The mean fMRI response modulation in response to a 6% luminance stimulus (closed bars) and a 60% S cone stimulus (shaded bars) are shown. The bars shown on the left superimposed on the white background represent responses measured in the presence of a gray background. Those shown on the right (shaded background) represent measurements made in the presence of an intense yellow background superimposed on the gray background (two replications are shown). The insets above the bar graph describe the spectral power distribution of the background under the two conditions. The locations of the peak wavelength sensitivities of the four photoreceptor classes are indicated by the arrows. Error bars show 1 SEM of the six modulations measured during each scan (subject: G. B.).

In addition to the S cone isoluminance responses, we also made measurements of L − M cone–initiated responses containing zero CIE luminance. Figure 3 shows the fMRI time series to an isoluminance L − M cone stimulus (Figure 3a), the isoluminance S cone stimulus (Figure 3c), and the sum and difference of these two stimuli (Figures 3b and 3d). The mixture of these stimuli spans the isoluminance plane; all of these stimuli cause a robust MT+ response. Human region MT+ is slightly more responsive to L + M stimuli than L − M stimuli. All of these results were confirmed in a second observer.

The data in Figures 2 and 3 show that MT+ is very responsive to moving targets initiated in the L and M cones. This sensitivity is evident when these two cone types respond in phase to produce a luminance signal or out of phase to produce an isoluminant signal. The data also show that L and M cone contrasts of 2% cause an MT+ response comparable to that produced by an S cone contrast of 20%. The sensitivity to the L − M stimuli compared with responses to L cone– and M cone–isolating stimuli (data not shown) indicate that MT+ does not respond simply to the weighted sum of three cone signals, as for a pure luminance mechanism (Chichilnisky et al., 1993).

Adaptation Experiments

Given the high MT+ sensitivity to L and M cone stimuli, small calibration errors could cause MT+ responses measured with the S cone–isolating stimuli. Also, at the relatively low mean luminance levels of the projecting display, the MT+ responses could be caused by rod-initiated signals. To examine whether the MT+ responses are truly S cone–initiated signals, we performed

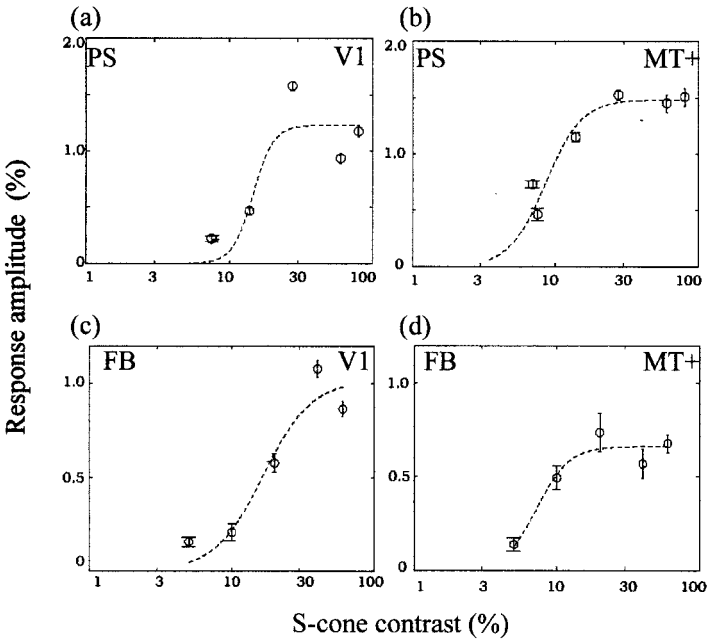

Figure 5. The Dependence of Response Amplitude on Stimulus Contrast in Two S Cone Monochromats

Response amplitudes for subjects P. S. (a and b) and F. B. (c and d) are similar to one another within area V1 (a and c) and region MT+ (b and d). The curve parameters (σ, M, p) in (a) through (d) are 0.15, 1.23, 6.0; 0.085, 1.48, 3.45; 0.17, 1.02, 2.55; and 0.073, 0.66, 3.82. Other details as in Figure 1.

a control experiment in which the moving stimuli were presented on a bright yellow adapting background.

In these adaptation experiments, the spectral power distribution of the yellow background was chosen to reduce the contrast of stimuli initiated in the L cones, M cones, and rods while relatively sparing S cones (see insets in Figure 4). The contrast seen by every receptor type is reduced when the yellow light is added to the background, and this reduction can be calculated from the change in mean background absorptions. In the presence of the yellow background, the contrasts in the L, M, and S cones and in the rod receptors are reduced, respectively, by factors of 20, 15, 1.5, and 10. Hence, the addition of the yellow light to the background strongly reduces the contrast of any residual L, M, or rod signals but relatively spares the contrast of the S cone signal. In addition to reducing the rod stimulus contrast, the yellow background light also greatly increases the mean level, from 7 cd/m^2 to 120 cd/m^2, (112 scotopic cd/m^2), well above the level of rod saturation in normal observers (Hood and Finkelstein, 1986).

The main panel in Figure 4 shows the fMRI response amplitudes measured in MT+ while subjects viewed a 6% contrast luminance stimulus (closed bars) and a 60% contrast S cone stimulus (shaded bars). When measured on a neutral background, the two stimuli produced essentially identical responses. The bars shown on the right are measurements in the presence of the yellow adapting light. Responses to the L + M stimulus are significantly reduced, but responses to the S cone stimulus are little changed. Were the S cone responses due to unwanted L and M absorptions, the amplitude of all the responses would be reduced in the same way by the added background light. Two repetitions of these adapting effects are shown for one observer in Figure 4. The same effect was also confirmed in a second observer.

S Cone Monochromat Experiments

To further verify that S cone–initiated signals drive activity in MT+, contrast–response measurements were repeated on two observers who have S cones and rods but are missing L and M cones. These S cone monochromats only have two photoreceptor types, so it is straightforward to isolate the S cones using conventional three-primary displays. Hence, S cone monochromats serve as a useful control against calibration errors.

A second potentially interesting feature of these observers is that the absence of L and M cones will dramatically reduce the signals from the magnocellular pathway, which is known to be the dominant input to area MT (Maunsell et al., 1990). Hence, measurements of the response in MT+ of S cone monochromats also permits us to measure developmental plasticity in the motion pathway.

Figure 5 shows response versus stimulus contrast curves for S cone signals in area V1 and region MT+ of two S cone monochromats. The curves are similar to the S cone–initiated signals measured in normal observers, though there is a sensitivity increase of roughly a factor of 2. The response to each stimulus in each of the S cone monochromats (Figure 5) exceeded the average response of the normals (except near saturation; Figure 2). The response versus contrast curves support the main conclusion of this paper, namely, that S cone signals reach region MT+. In separate measurements (data not shown), rod-initiated responses were measured under low illumination conditions. Under these conditions, the rod responses in region MT+ also show slightly higher contrast sensitivity than measurements in normal controls.

Discussion

Strong S cone responses can be found both in human V1 and motion-selective cortex, MT+. The S cone responsivity in MT+ is on the order of 1 log unit lower

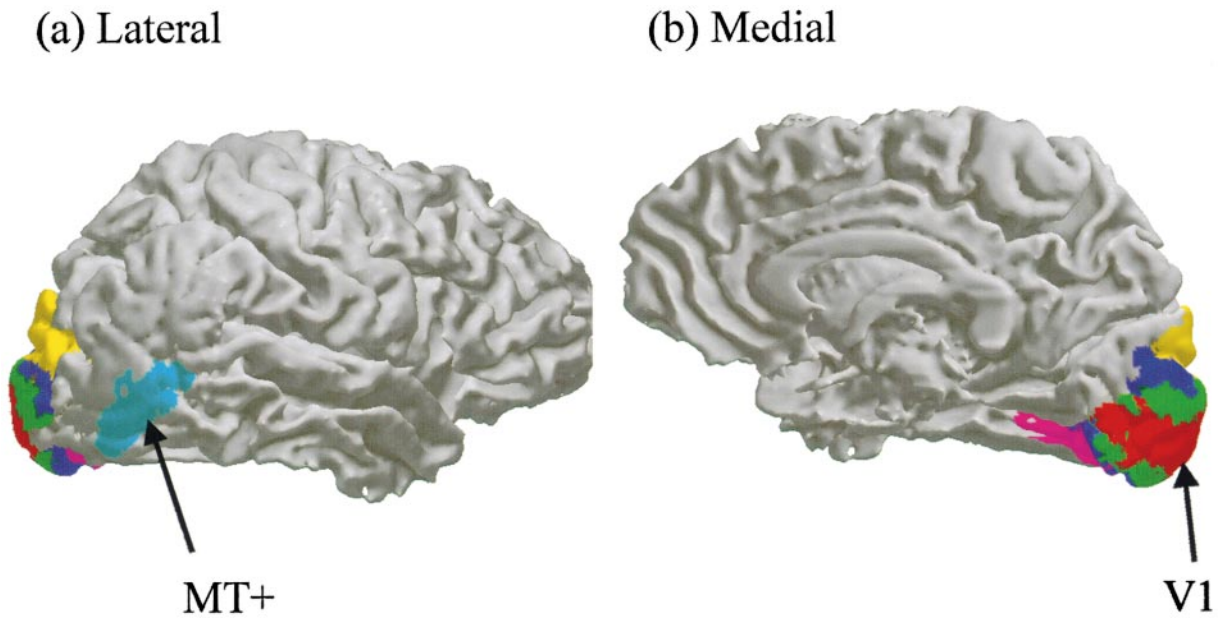

Figure 6. Visual Area Locations

The locations of V1 (red), V2 (green), V3 (blue), V3A (yellow), V4 (magenta), and MT+ (cyan) in the right hemisphere of a normal control (H. B.) are shown in lateral (a) and medial (b) views. Retinotopic visual areas were located by analyzing the traveling wave of activity caused by rotating wedges and expanding rings (Wandell, 1999). Region MT+ was identified using the localizing scan described in the text.

than L + M cone responsivity. This difference is consistent with the influence of contrast and color on relative speed judgments (Dougherty et al., 1999). This MT+ color responsivity does not parallel the threshold differences between S cone and luminance targets. Hence, the color responsivity in MT+ follows the color responsivity of the speed judgment task but not that of the detection task.

How are S cone signals transmitted to MT+? S cone on signals are carried by the koniocellular pathway (Dacey and Lee, 1994); S cone off signals appear to be carried by the parvocellular pathway (Klug et al., 1993). Preliminary anatomical data from the retina suggest that some S cones project to the magnocellular pathway via diffuse bipolars (D. Calkins, personal communication; S. J. Schein, personal communication). To date, however, there is no strong evidence that S cone signals make a functional contribution to the magnocellular pathway (Rodieck, 1998). The fMRI signal pools across many different cells and does not show whether S cone responses in MT+ are part of (1) a color energy representation derived from these postreceptoral pathways (Dougherty et al., 1999), (2) a conventional opponent-colors representation, or (3) something else entirely. We discuss this question again after describing the unit measurements (Seidemann et al., 1999).

To understand the relationship between the amplitude of MT+ responses and that of speed judgments, it will be necessary to develop an explicit theory of perceived speed. A general theory is beyond the scope of this paper, but one can envision an explanation for coupling response amplitude and perceived speed using arguments that have been proposed in the computational vision literature. The speed and motion of achromatic

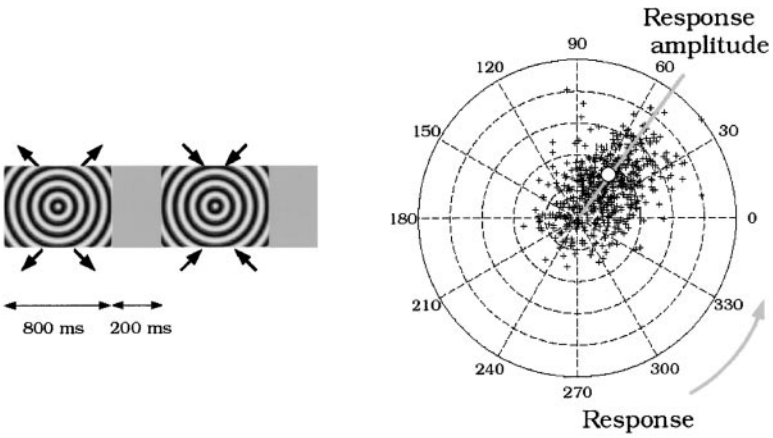

Figure 7. The Trial Structure and Data Analysis

(a) The stimulus trial structure. A series of moving stimuli were shown, either contracting or expanding. The stimulus duration was 800 ms. In the 200 ms blank interval that followed, the subject responded as to the direction of motion.

(b) The computation of response amplitude of the fMRI response. Each cross measures the amplitude (radial position) and phase (angular position) at the stimulus frequency (1/36 Hz) of the time series of a voxel. The shaded unit length vector is drawn at the angle of the average phase of all MT+ responses during the localizer scan. The mean projected response is computed by projecting the individual points onto the unit length vector and computing the mean length of these projected values (white dot).

targets have been modeled using Bayesian theory (Simoncelli et al., 1991; Heeger and Simoncelli, 1992; Weiss, 1998). Perceived speed errors are explained by the relatively low signal-to-noise ratio of the neural signals of certain low contrast stimuli. Hence, it is reasonable to retain the hypothesis that the low responses to S cone stimuli measured in the motion-selective region of cortex play a role in the perceptual judgments of relative speed. Specifically, the Bayesian argument is that visual computations are biased to estimate that objects are moving slowly and smoothly such that weak signals are interpreted as moving relatively slowly. As the size and reliability of the response increase, perceptual judgments deviate from the a priori assumptions. A Bayesian theory would explain relative speed judgments between low and high stimuli, or S cone and L cone stimuli, using the same computational mechanism.

We conclude by describing two implications of our results for the interpretation of motion processing in human cortex. First, these measurements support the view that color information is widely distributed, though different areas may have different color tuning (Cavanagh and Favreau, 1985; Chichilnisky et al., 1993; Dobkins and Albright, 1998; Dougherty et al., 1999). In this view, the speed of a high contrast, clearly visible, S cone signal is similar to that of a low contrast, barely visible, luminance signal because of the intrinsic color properties of the motion pathways. Further, relative velocity judgments between stimuli of different colors and contrasts arise for the same reason, namely, the strength of the responses in MT+. The visibility of these targets, however, depends on other cortical processes with other color sensitivities.

The data described here have implications for the analysis of neurological deficits. For example, consider the observation that individuals with cerebral achromatopsia perceive the motion of colored targets well when these are presented at high stimulus contrasts (Cavanagh et al., 1998). Arguing from the assumption that chromatic information is weak in motion-selective cortex, Cavanagh and colleagues concluded that cortical responses outside of MT must mediate motion perception in cerebral achromatopes. The measurements reported here suggest that the MT pathway contains enough information to permit individuals with cerebral achromatopsia to perform chromatic motion judgments.

Second, we conclude with several observations concerning developmental plasticity in the motion-selective area in the S cone monochromats. Ordinarily, the L and M cone inputs to MT+ are powerful, and these signals are presumably communicated via the magnocellular pathway. The absence of the L and M cone types in the monochromats offers the opportunity for plastic reorganization whereby S cones increase their input to the magnocellular pathway.

The S cone responsivity is a factor of 2 higher in the monochromats compared with the normal trichromats. In V1, the semisaturation parameter (σ) for S cone stimuli is 0.26 for the trichromats and 0.16 for the monochromats. In MT+, the parameter is 0.15 for the normal controls and 0.078 for the S cone monochromats. Hence, the S cone responses in the monochromats are roughly twice those of the normal controls.

The S cone responsivity in the monochromats, however, is roughly eight times lower than normal L and M cone responses in MT+. The low MT+ responsivity in the monochromats suggests that even in the absence of two other cone classes, S cone signals do not make full use of the powerful magnocellular pathway. Rather, this pathway remains relatively silent in the S cone monochromat under photopic conditions. The inability of the S cone signals to utilize the potentially powerful magnocellular pathway appears to represent a fundamental limit on developmental plasticity.

Experimental Procedures

Subjects

fMRI signals were measured in two color-normal subjects (H. B., G. B.) and two S cone monochromats (P. S., F. B.). S cone monochromacy (also known as blue cone monochromacy or X-linked incomplete achromatopsia) is a rare genetic condition in which the individual is born without functional long (L) and middle (M) wavelength–sensitive cones, the main receptors for daytime and color vision. Thus, their vision is mediated solely by the short (S) wavelength-sensitive cones and the rods, which they appear to have in normal abundance (Sharpe et al., 1999). Because they only have two classes of receptors, designing a visual stimulus to isolate the S cones in these individuals can be done with greater precision than for normals.

The S cone monochromats were identified by genetic (Nathans et al., 1993) and behavioral (Zrenner et al., 1988; Hess et al., 1989; Reitner et al., 1991; Sharpe et al., 1992; Stockman et al., 1999) measurements. Their visual field sensitivity and fixation have been evaluated in separate experiments. Both S cone monochromats show evidence of a central scotoma when tested using automated visual perimetry. Measurements of visual fixation using a Rodenstock scanning laser ophthalmoscope revealed that the monochromats fixate at a position 2° (F. B.) or 3° (P. S.) outside the central fovea. Eye movement measurements made using a Powerrefractor (Multichannel Systems, Tübingen, Germany) verified that both subjects have very stable fixation.

Magnetic Resonance Protocols

During the fMRI measurements, subjects were supine within the bore of the magnet and used a bite bar to minimize head movements. Structural and functional MR measurements were made using a GE 1.5T scanner. Anatomical images were acquired using T1-weighted contrast images (TE = minimum full, TR = 33 ms, FA = 40°) at a spatial resolution of ($0.9 \times 0.9 \times 1.2$) mm^3. Functional MR images were measured using a gradient-echo BOLD T2* weighted spiral k space sequence (Kwong et al., 1992; Meyer et al., 1992; Ogawa et al., 1992; Glover and Lai, 1998). Spiral fMRI sequences compare favorably with echo-planar imaging in terms of spatial resolution and sensitivity (A. M. Sawyer-Glover and G. H. Glover, 1998, Proc. Sect. Magn. Reson. Technol., abstract). Functional data were acquired in eight planes parallel to the midsagittal boundary of the cerebellum and occipital lobe. The functional acquisitions used two interleaved spiral scans (187.5 ms/spiral), a TE of 40 ms, a TR of 1500 ms, and a 90° FA. Spatial resolution within the measurement plane was 1×1 mm^2, and the through-plane resolution was 4 mm. The functional measurements were made using a custom built semicylindrical surface coil that cradled the back of the head, near the occipital lobe.

Display Apparatus

In the experiments with normal subjects, stimuli were projected from a liquid crystal projection display (Sanyo model 2000) via a relay lens onto a screen 1.28 m from the subject, located at the opening of the magnet's bore. In some experimental conditions, light from a pair of Kodak Carousel slide projectors was superimposed upon the LCD projection screen. In the experiments with S cone monochromats, stimuli were presented on a flat panel LCD (NEC 2000) contained within a shielded box in the magnet room, 4.3 m from

the observers. Subjects viewed the flat panel LCD through a set of binoculars with ~8-fold magnification, yielding an effective viewing distance of about 0.54 m.

The displays were calibrated using a PhotoResearch Spectroradiometer. The calibration involved first verifying the additivity of the red, green, and blue display channels. Then, the spectral power distributions of each display channel was determined at 4 nm wavelength sampling intervals. Finally, the (nonlinear) relationship between the digital frame buffer values and each channel's display intensity was characterized. These measurements, which were repeated throughout the experiments, are sufficient to provide the information needed to create cone-isolating stimuli (Brainard, 1989; Appendix B in Wandell, 1995). Because of spatial inhomogeneities in the relay lens and rear-projecting screen, from repeated calibrations we estimate that the color calibration of the projecting system is accurate to better than 10%. These inhomogeneities are not present in the flat panel system, which is accurate to a precision of better than 3%.

Localizing Scans

In separate experimental sessions, the positions of primary visual cortex (V1) and several other visual areas were identified using phase-encoded retinotopic stimuli (Engel et al., 1994, 1997). The experimental sessions devoted to contrast–response function measurements always included two functional localizing scans that served to identify the active regions associated with motion-selective cortex (MT+) and primary visual cortex. The localization scans served to identify those portions of these regions that fell within the MR measurement planes during that session. The active locations within the boundaries of V1 were identified using a flickering white–black checkerboard pattern (8 Hz flicker, 14° × 10° area, 0.25°/pair of black/white checks) that alternated every 18 s with a neutral gray field. This stimulus elicits powerful activity in the retinotopically organized brain regions but relatively less activity in MT. The visual stimulus used to localize MT+ was a sparse (3% density) field of small white dots, moving radially inward and outward, seen against a black background (12°/s; 14° × 10° area, 0.1°/dot). The moving dots alternated every 18 s with a field of static dots. The stimulus exchange between moving and static dots modulates the signal within retinotopically organized areas, including V1, as well as in two regions located on the lateral surface of each hemisphere. The locations on the lateral aspect of the brain appear to contain the human homolog of macaque MT (Zeki et al., 1991; Tootell and Taylor, 1995; Wandell, 1999), and we refer to it as MT+.

The positions of several retinotopic visual areas and MT+ in the right hemisphere of a normal observer (H. B.) are shown in Figure 6. Region MT+, as shown, was selected using a low threshold criterion. The region analyzed in each session was a subset of this region chosen by running a second localizer scan. In this and other studies, we have identified MT+ in more than 12 observers. We find that MT+ is larger in the right hemisphere than left, and the region spans an area 1 cm wide and between 2 and 3 cm in length.

Heeger et al. (1999) have shown that the luminance responses in MT+ are directionally selective. We have not measured whether the fMRI responses to S cone stimuli are directionally selective, but based on the single unit measurements described in the third paper of this series we expect to find such selectivity.

Experimental Scans

Moving radial harmonic patterns were used to measure contrast response functions in MT+. The stimuli (Figure 7a) were presented as a series of brief trials consisting of a moving target (800 ms) followed by a neutral field (200 ms). During the 200 ms neutral field display, subjects pressed a switch to indicate whether the pattern they had just seen had moved inward or outward. The moving stimulus was a 0.5 cycles/° spatial radial sinusoid contrast pattern (concentric rings) expanding or contracting at 8°/s. The 18 s of experimental trials was followed by 18 s of a uniform field. Each experimental scan comprised seven alternations of the stimulus–blank cycle. The first cycle was discarded to remove transients in the fMRI signal, and analyses are based on the amplitude modulation of the final six repetitions.

Data from normal observers were obtained in two background conditions. In one condition, the stimulus was presented upon a neutral gray background in the middle of the display range. This background had CIE coordinates x,y,Y = 0.31, 0.41, 7.0 cd/m^2. This intensity level is slightly above the mesopic luminance level (Wyszecki and Stiles, 1982). To verify further that the fMRI signals were not due to rods, or L or M cones, additional experiments were carried out using an intense yellow adapting light. The additional light was provided by superimposing the outputs of two slide projectors, transmitted through a yellow filter (Kodak Wratten 12) and projected symmetrically about the fixation point. The CIE coordinates of the background with the superimposed yellow light were x,y,Y = 0.49, 0.48, 126.4 cd/m^2, with scotopic luminance of 112 cd/m^2 (3.5 log scotopic Trolands, assuming a 3 mm pupil). The spectral power distribution of the yellow adapting light was chosen to selectively reduce the sensitivity of both the long (L) and middle (M) wavelength cones, sparing sensitivity of the S cones. The high background luminance is quite close to the level of rod saturation, making it very unlikely that the signals are rod initiated (Aguilar and Stiles, 1954; Hood and Finkelstein, 1986).

Contrast–response functions also were measured in two S cone monochromats. In these experiments, stimuli were presented using the flat panel LC display; the relative absorption rates due to the background were S cones, rods = 1, 1.6; CIE coordinates were x,y, Y = 0.29, 0.34, 70 cd/m^2. Because S cone isolation is relatively simple to achieve for these observers, and there are no L or M cones to suppress, no data were collected with the superimposed yellow background.

Data Analysis

After each scanning session, the eight fMRI measurement planes were aligned to a high resolution anatomical scan of the subject's brain using custom software. The anatomical scan provides a common reference frame for all conditions. Activity levels, cortical flattening, and three-dimensional renderings of the brain were performed using methods described elsewhere and distributed on the Internet (Engel et al., 1997; Teo et al., 1997). Figure 7b illustrates how a single value, the mean projected amplitude, is measured from the fMRI time series. First, the fMRI time series for each voxel in the region of interest is measured. Second, the time series are summarized by percent modulation and phase at the stimulus frequency. The position of each cross in the polar plot represents the percent modulation and phase of one voxel out of the ~400 voxels within MT+. The unit length vector extending from the center of the polar plot, the standard phase vector, is drawn at an angle equal to the phase of the average MT+ response in the localizing scan. Third, a perpendicular from each voxel is projected onto the standard phase vector, and the average distance from the origin of these projected values is computed (white dot). The mean of these values is the mean projected amplitude and serves as a dependent measure of response amplitude. The standard error of these values is plotted in several of the figures, but due to the correlation between individual voxels the plotted error bars are smaller than the true variation. A better estimate of the variation can be obtained from visual inspection of the deviations of the data points from the smooth curves.

In some figures, a smooth curve is plotted to summarize how response amplitude varies with stimulus contrast. These response versus contrast functions are summarized by the function $R = (c^p/c^p + \sigma^p)M$. In this formula, R is the response amplitude, c is the stimulus contrast, M is the maximum response amplitude, σ is a semisaturation sensitivity parameter, and p is an exponent that defines the slope of the curve. These parameters were estimated separately for each curve and are only used to summarize and compare data obtained in different conditions. The values of these parameters for individual fits are included in the figure legends.

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