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Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli

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Summary. Based on the fact that a great majority of cells in the middle temporal (MT) area of the macaque respond to movement of luminance contours with directional selectivity, this area has been thought to be concerned with the analysis of visual motion. However, objects can be discriminated from the background not only by differences in luminance but also by differences in color. It is possible that color signals are also used for motion analysis in MT. In the present study, we examined whether MT cells respond to movement of a pattern composed of pure color-contours. Using a color TV system, a moving color bar was displayed on a uniform background whose color was opponent with that of the bar. The main bar/background color combination we examined was magenta/cyan. Yellow/blue and cyan/magenta combinations were also examined for some cells. The response of MT cells to movements of opponent-color stimuli was recorded while the bar/background luminance ratio was changed from 1/10 to 10/1. In half of 89 cells tested in 3 monkeys, the response decreased considerably (disappeared completely in some cells) at a luminance ratio close to the human equiluminous condition. In the other half, a directional response persisted at any bar/background luminance ratio, though the response decreased to a varied extent (30–90% of the maximum response) near the ratio 1 (human equiluminous condition). The average magnitude of the equiluminous response to the magenta/cyan stimulus for the overall population was about 35% of the maximal response when the length of the bar (0.5° in width) and the movement amplitude were set to be optimal for individual cells, i.e. smaller than 15° and 10° of visual angle, respectively. This fall to 23% when the bar length and movement amplitude were limited to 2°. The same cell responded to pure color-contours of yellow/blue as well as of cyan/magenta combinations. Thus, MT can detect the direction of movement of pure color-contours, although the sensitivity is less than for luminance contours.

Key words: Middle temporal (MT) area – Visual motion analysis – Directional selectivity – Color contour – Monkey

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Introduction

The MT (middle temporal) area of the macaque has been thought to be concerned specifically with the analysis of visual motion. This is based on the following evidence: 1) Most cells in this area show selectivity for the direction of movement of visual patterns (Zeki 1974, 1978; Van Essen et al. 1981; Maunsell and Van Essen 1983a; Tanaka et al. 1986; Mikami et al. 1986a, b), whereas they are quite insensitive to the shape (Zeki 1974; Tanaka et al. 1986) and the wavelength (Zeki 1978; Van Essen et al. 1981) of the pattern. 2) Direction of movement is represented systematically in this cortical area: that is, the direction of movement detected by cells changes regularly on the cortical surface (Zeki 1974; Albright et al. 1984).

Since objects can be segregated from a background by differences in either luminance or color, it must be desirable for a motion analyzing system to have the ability to use either of these cues for the analysis. The stimulus pattern used in most earlier studies was composed of luminance contrast only, and the color pattern used in some earlier studies contained a luminance difference with the background. It is therefore not yet clear whether the MT cells respond to the movement of patterns of pure color-contrast.

The purpose of the present study is to find out whether MT cells can analyze the direction of movement of pure color-contours. We examined the response of MT cells to a color bar moving on a differently-colored background. The bar/background luminance ratio was changed over a wide range, including that of the human equiluminous condition. We found that in a considerable proportion of MT cells directionally selective responses do not disappear at any value of the luminance ratio, though the magnitude of the response decreases when this is close to 1 (human equiluminous condition). We thus conclude that the MT area can analyze the direction of movement of a color pattern which has no luminance contrast. The conclusion is parallel with the psychophysical observation that a pattern composed of pure color-contours provides a sensation of motion to human observer even though the sensation is less vivid than that caused by a pattern which contains luminance contrast. The result is more consistent with a schema based on the redundant representation of sensory cues in the prestriate area (DeYoe and Van Essen 1988), than with a schema of a strict segregation of the cues in the same area (Livingstone and Hubel 1987).

Methods

Preparation and recording

Four Japanese monkeys (*Macaca fuscata*) weighing 4.5–6.4 kg were semichronically prepared to be used for repeated recordings. Surgery for attaching a brass block to the dorsal top of the skull for head-fixation and craniotomy (15 mm square) in the posterolateral part of the skull of the right hemisphere for microelectrode recordings was done long before the recording session under anesthesia with pentobarbital sodium (33 mg/kg initial intraperitoneal injection followed by supplementary intramuscular injection of 2–8 mg/kg/h). The opening of the skull for the recording was covered with acrylic resin after injecting antibiotics. All wounds were infiltrated with a mixture of Xylocain jelly and antibiotics during the surgery and for several days after. To record from the MT area in each recording session, we only had to make a small hole in the acrylic resin, and no wounds were given to the animal in the recording session.

In each recording session, the animal was anesthetized with inducing anesthetic (ketamine hydrochloride, 7 mg/kg) and fixed on an iron stage through the brass block. Throughout the recording, anesthesia was maintained by respiring the animal with a gas mixture of N_2O and O_2 (70 : 30 to 80 : 20). Muscles were relaxed with gallamine thriethiodide (initially 10 mg/kg, followed by hourly 4 mg/kg intramuscular injections). Artificial ventilation was maintained at 25 strokes/min, and the end tidal CO_2 was maintained at 4.5–5.0% by adjusting the stroke volume (55–85 ml/stroke). The EEG and ECG were monitored throughout the experiment to ensure that the experiment caused no distress to the animal. When necessary, a small dose of pentobarbital sodium (up to 0.5 mg/kg/h) was injected intramuscularly. The body temperature was kept at 38.0–38.5 ° C. To reduce salivation, 0.5 mg atropine sulfate was injected every 3 h. The pupils were dilated with 0.5% phenylephrine hydrochloride and 0.5% tropicamide. Black opaque contact lenses with a central clear zone 2 mm in diameter and of appropriate power were attached to both eyes to keep the corneas moist and to focus the stimulus on the retina.

The MT cells were extracellularly recorded with a glass-coated platinum-iridium electrode (exposed tips: 10–15 μm long; 1.5–2.5 MΩ at 1 kHz). A small circular opening (4–5 mm in diameter) was made in a region of the acrylic cover set at the posterolateral part of the skull, and the dura was exposed. Then a pinhole was made in the dura using a stainless needle. The electrode was introduced into the brain through this pinhole, and was advanced anteromedially in the horizontal plain at an angle of 30° with the parasagittal plain. The opening was covered with paraffin to prevent the exposed dura from drying and to reduce movements of the brain caused by pulsation or respiration. To ensure a systematic penetration into MT, the position of each penetration was determined with reference to a point made on the resin-coated skull.

At the vertical level we examined (18–20 mm above the interaural line), the electrode entered MT, which lies on the posterior bank of the superior temporal sulcus (STS), after passing through three intervening regions of gray matter, i.e., the posterolateral gyrus and the posterior and anterior banks of the lunate sulcus. MT was identified by the physiological properties of the recorded cells; that is, in the medial half of the posterior bank of the STS, clusters of directionally selective cells with relatively small receptive fields are found (Zeki 1974; Maunsell and Van Essen 1983a; Tanaka et al. 1986). On the other hand, in the lateral half of the same bank, most cells are not directionally selective. Thus the lateral border of MT could be determined easily. Medially, MT adjoins MST (the medial superior temporal area) in which directionally selective cells are also clustered. However, MST can be distinguished easily from MT because the size of the receptive field of MST cells is very large (mean, about 40°, Van Essen et al. 1981; Tanaka et al. 1986), and particularly in the dorsal part of MST, directionally selective cells which respond only to changes in size (expansion or contraction) or only to rotation (clockwise or counterclockwise) are intermingled with directionally selective cells which respond to a straight frontoparallel movement of a pattern (Saito et al. 1986). It was later confirmed histologically that all the recorded positions were well localized within the densely myelinated region in the posterior bank of the STS (see below).

At the end of each recording session, the opening was filled with acrilic resin after an antibiotic agent had been injected. Injection of gallamine triethiodide was stopped at the end of the recording. Spontaneous respiration resumed, and became normal 2–3 h later. In some later experiments, the recovery of spontaneous respiration was assisted by an intramuscular injection of neostigmine (5 mg/kg).

Histology

After the last recording session, the monkey was deeply anesthetized with pentobarbital sodium and perfused with warm saline, followed by 10% formal saline. A block of the brain was removed and placed in 30% sucrose in 10% formalin until it sank. Frozen sections were cut at a 50 μm thickness in the horizontal plane, and two neighboring sections were taken at every 1 mm. One series of sections was stained for myelin with hematoxylin (a modified Heidenhein's method. Hutchins and Wever 1983), and the other series was stained with cresyl violet. The extent of MT was determined by the dense and uniform myelinated band in the cortex (Ungerleider and Mishkin 1979; Van Essen et al. 1981).

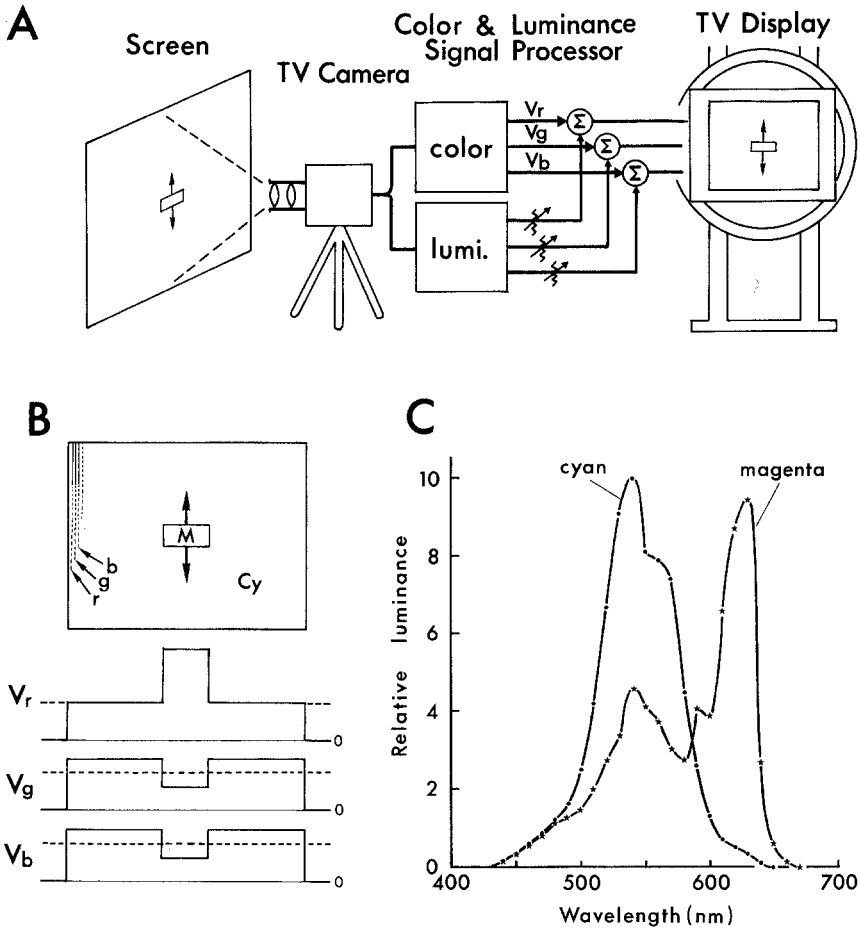

Fig. 1. A A block diagram of a TV system to produce a moving color bar on a colored background, the color and luminance of both of which can be changed independently. A moving light slit is rear-projected onto a half-transparent screen by means of a conventional projector. Picture signals taken by a TV camera are fed to two signal processors, one of which determines the chrominance and the other the luminance of the bar and the background. A TV display is placed on a stage so that the display can be moved horizontally and vertically, and also rotated. **B** Relative voltage levels of signals fed to r (red), g (green), and b (blue) channels to produce a magenta bar on a cyan background. Three kinds of phosphors (r, g, b) are aligned so that they form parallel vertical stripes on the TV screen (Trinitron tube, Sony Corp.). The bar was oriented at right angles to the stripes and moved parallel to the stripe, so that neither the leading edge nor the trailing edge of the bar stimulated any one or two phosphors separately at any moment. Thus, unintended changes in color and luminance never occur at the moving edges. **C** Relative spectral luminance distribution of equiluminous magenta and cyan used in the present study

Photic stimulation

As a stimulus we used a moving bar of a different color from that of the background. In order not only to examine the sensitivity of MT cells to movements of pure color contours but also to re-examine their sensitivity to the kind of color at the same time, we used two different color combinations: i.e., magenta/cyan (and cyan/magenta, for some cells) and yellow/blue. These opponent-color combinations are very frequently used in human psychophysical experiments on color vision, because human beings show the highest spatial resolution for the magenta-cyan combination and the lowest spatial resolution for the yellow-blue combination (Isono and Sakata 1976).

If there is an equiluminous condition at which the response of MT cells decreases or even disappears, this luminance ratio between bar/background colors might be different for different cells. Therefore, it is necessary to investigate the response of MT cells for various values of the bar/background luminance ratio, while keeping the chrominance of the bar and background constant. Only a color TV system can achieve the independent control of luminance and chrominance easily and precisely. In TV systems, however, moving patterns are displayed on a screen as a sequence of stationary patterns which change their position by a small distance every 1/60 s (in the NTSC system). It is well known that if the time interval and the distance between two successive patterns are set properly, we perceive a smooth pattern movement called 'apparent movement'. It has recently been shown that the MT cells of the macaque respond to stimuli which produce apparent motion in humans in the same way as they do to real movement (Mikami et al. 1986a, b; Newsome et al. 1986). This allows us to use a TV system as a moving pattern generator.

A block diagram and a description of our stimulator are given in Fig. 1. As shown in Fig. 1A, a light slit was rear-projected onto a screen and moved up and down by means of a mirror mounted on a galvanometer. The moving pattern on the screen was taken by a TV camera, and the picture-signal was fed to two processors. One determines spatio-temporal signals for luminance, and the other for chrominance. Signals from the processors were fed to the r (red), g (green) and b (blue) channels, and the magnitude of the signal fed to each channel was set independently by individual attenuators. By using this system, we can control the luminance and chrominance of the bar and the background independently. The luminance of the bar and that of the background for different values of the attenuators were measured by a spot-photometer (Tektronix, J16 digital photometer with J6503 detector unit).

The TV screen we used was a 'Trinitron' (Sony Corp.) in which the red (r), green (g), and blue (b) phosphors form parallel vertical stripes (instead of a dot matrix, depicted schematically in Fig. 1B). The bar was always oriented on the screen at right angles to the stripe and the bar moved parallel to the stripe, so that neither the leading edge nor the trailing edge of the bar stimulated any one or two phosphors separately at any moment. Thus, no unintended changes in color or luminance occurred at the moving edge.

When the bar/background luminance ratio was set at 1 (equal luminance condition, i.e., human equiluminous condition), the absolute luminance of the bar and that of the background was 100 cd/m^2. This level was chosen so that the minimum and

maximum luminance of the stimulus needed to produce a bar/background luminance ratio of 10/1–1/10 fell well within the photopic range. To obtain a different luminance ratio, the luminance of the slit and that of the background were changed in a complementary manner. For example, to obtain a ratio of 10/1, the absolute luminance of the bar was set at 300 cd/m^2, and that of the background at 30 cd/m^2. The luminance of the bar/background was set at 30/300 cd/m^2 to obtain the ratio of 1/10.

In an experiment to test the response of visual cells to an equiluminous stimulus, one should consider an effect of luminance changes which appear at color borders because of chromatic aberration in the optics of the eye. For the magenta/cyan stimulus used in the present study, we estimated the magnitude and spatial extent of this luminance change as follows: Since magenta and cyan contain wide spectral components, the spectral energy distributions were first measured for equiluminous magenta and cyan, respectively, at 10 nm intervals from 400 nm to 700 nm using a spectroradiometer (UDT-11A radiometer with 1100A spectral analyzer equipped with interference filters. United Detector Tech. Inc.). They were transformed into relative spectral luminance distributions in reference to the CIE standard luminous efficiency function for photopic vision (1924). These distribution curves are shown in Fig. 1C. The spatial distribution of the luminance near the magenta/cyan border was calculated for a 'nearly worst case', in which an image formed by 540 nm light, which is the dominant wavelength of the cyan (see Fig. 1C), is just focused on the retina and images transmitted by other wavelengths are blurred forming an S-shaped luminance distribution along the axis orthogonal to the color border. The procedure and results are given in Fig. 2. The luminance at a distance x (magenta side, positive) from the color border for a wavelength w was calculated by the following formula, taking the hyperbolic tangent function as the S-shape:

$$L_w(x) = \tfrac{1}{2}\{(L_{C(w)} + L_{M(w)}) - (L_{C(w)} - L_{M(w)}) \cdot \tanh(3x/b)\}$$

where b is the width of the blurred image formed by w. By referring to Ivanoff's data about the difference in the refractive power of the human eye (at maximum, the difference of the refractive power relative to 540 nm light is +0.8 D for 430 nm light and –0.8 D for 650 nm light, cf., Ivanoff 1947), the width b of the blurred image of the border was calculated. As shown in Fig. 2A and C, it was assumed that the width b corresponds to the distance between x_1 and x_2 where the value of $\tanh(3x/b)$ is –0.9 or +0.9. The above calculation was done for each spectral component at 10 nm intervals from 430 nm to 650 nm. All the curves were summed up to make a final luminance distribution curve.

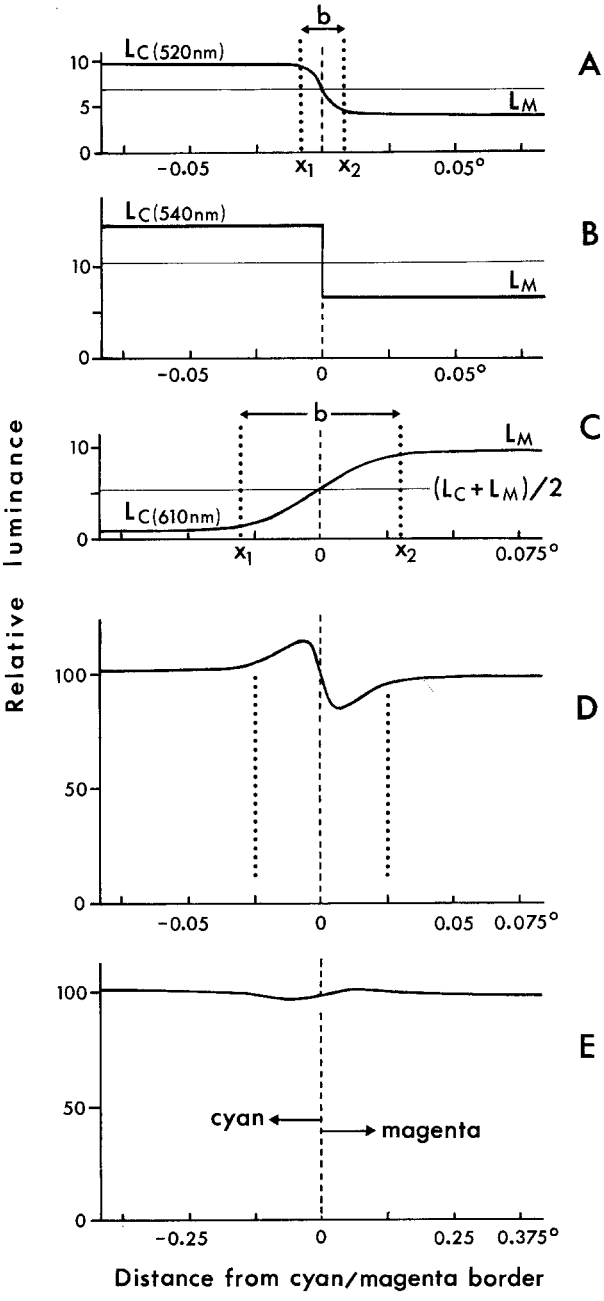

Fig. 2A–E. Estimation of transient luminance change generated at an equiluminous magenta/cyan border by chromatic aberration of the eye. **A–C** Calculated retinal luminance distributions of the light components of the wavelength of 520 nm (**A**), 540 nm (**B**), and 610 nm (**C**) contained in the cyan/magenta stimulus. $L_{C(w)}$ and $L_{M(w)}$ are the luminances of the light component w at a position far from the cyan/magenta border. If $L_{C(w)} \neq L_{M(w)}$, there is a luminance edge as to w at the cyan/magenta border ($x = 0$) in the original stimulus. For 540 nm light (dominant wavelength of cyan used in the present study, see Fig. 1C) for which the eye optics are assumed to be just in focus, the retinal image forms a sharp edge, as shown in **B**. For light of other wavelength, the retinal image of the edge is blurred. The shape of the luminance distribution of the blurred image is hypothesized as an S-shape and approximated by the hyperbolic tangent function: $L_w(x) = \tfrac{1}{2}\{(L_{C(w)} + L_{M(w)}) - (L_{C(w)} - L_{M(w)}) \cdot \tanh(3x/b)\}$, x: magenta side positive. The width of the blurred image of the edge is calculated by the optical geometrics referring to Ivanoff's data on aberration (see the Method section for details), and it was assumed that this value corresponds to the distance between x_1 and x_2 where the value of $\tanh(3x/b)$ is –0.9 or +0.9. The luminance distribution was calculated for the wavelengths at 10 nm interval from 430 nm to 650 nm, and all the curves were summed to obtain the final luminance distribution shown in **D**. The amplitude of the transient luminance change at the border is about ± 15%. Note that the changing region (lying between two dotted lines) is very narrow (0.05°). **E** Calculated luminance distribution of the retinal image of equiluminous cyan/magenta border when the image was intentionally blurred with an additional lens of the power of +3 D. The amplitude of the luminance change is greatly reduced (about ± 3%), though the width is increased (note that scale of the abscissa in **E** is different from the others)

This final curve is shown in Fig. 2D. The magnitude of the luminance change at the magenta/cyan border produced by chromatic aberration is ±15% in this calculation. This seems relatively large, but note that the luminance change takes place in a very narrow region. It is about 0.05° (fundamental component, 20 Hz/deg). Using two animals, we tested 28 MT cells (half of which showed a good response to the movement of a pure color contour: see Result section) for whether they do or do not respond to achromatic bars (both light and dark bars 0.5° in width) when the bar/background luminance contrast was set at the high value of 100% (bar/background luminance ratio was 2 for the light bar and 0.5 for the dark bar). No cells responded to these bars. For 16 of them, the effectiveness of bars of double width (0.1°) of the same luminance contrast was tested. For most cells, the stimuli were ineffective. Therefore, even if the above estimation using human data might underestimate the luminance change by a factor of 1/2 in both peak amplitude and width, it would be safe to say that the luminance change caused by chromatic aberration has no effect in eliciting a response in MT cells.

To study the effectiveness of equiluminous color contours in eliciting responses from MT cells, two series of experiments with different stimulus settings were done on three animals: In one series, in which we intended to examine the behavior of MT cells under an optimally stimulated condition (we thus called this series the 'optimal-stimulus experiment'), the length of a bar and its amplitude of motion were set to be smallest within a range in which individual cells showed a maximal response to the bar with luminance contrast. The width of a bar was usually fixed at 0.5° because an increase in the width did not improve the response further except for a few cells. For such exceptional cells, the width was set at 1°. The length of a bar was usually between 1° and 8°, but for 1 cell it was 15°. The amplitude of motion was set between 2.5° and 10°. In the optimal stimulus experiment, the TV screen was placed 80 cm in front of the eye. At this distance, the stripes of phosphors (pixels) are not resolvable. The visible part of the screen subtended about 11° × 15° (a central 50% area of the whole screen was used and the peripheral regions were masked). The response to different color combinations (bar/background combinations of magenta/cyan, yellow/blue, and cyan/magenta) was compared in this series of experiments.

In the second series of experiments (we called this series the 'small-stimulus experiment'), the size of the bar and its amplitude of motion were made as small as possible in the range in which the stimulus with a clear luminance contrast was still effective in producing a reliable response in individual cells. This was done to reduce the effect of possible regional differences in equiluminous condition over the retina. The maximum length of a bar and the maximum amplitude of motion were 2°. The width of a bar was usually 0.5°, but for a few cells, it was 0.25°. The distance between the animal's eye and the TV screen was set at 114 cm, and the visible part of the screen subtended 7.5° × 10° in this setting. This was greater than the largest receptive field of MT cells examined in the present study.

The speed of motion was optimized in all the experiments. It was between 1.5° and 20°/s for most cells. For two cells in the optimal-stimulus experiment, it was 40°/s.

In some of the small-stimulus experiments, the response to the color stimulus was compared when the image of the bar was focused on the retina (normal condition) and when it was intentionally blurred by placing an additional lens close to the eye. This was done to confirm that chromatic aberration has little effect on the response of MT cells. An achromatic lens with a power of +3 D was used to defocus the retinal images formed by any wavelength. By calculation, the peak amplitude of the luminance change is reduced to ±3% by this blurring (Fig. 2E).

When a single MT cell was isolated, its receptive field, and the preferred direction of movement were explored using a hand-moved bar. The TV screen was then moved along the x-y coordinates so that its center coincided with the center of the receptive field, and was rotated so as to fit the axis of movement of the bar with the preferred-null direction of the cell.

Quantitative measurements of the response to each opponent-color stimulus of different luminance contrast were made by the multiple histogram method (Henry et al. 1973) to minimize the effect of slow changes in the responsiveness of the cell; that is, a set of values for the luminance contrast of a particular stimulus (magenta/cyan, for example) was predetermined and tabulated for the cell to be studied. In the odd-numbered trials, the response was measured by increasing the contrast values step by step, as indicated in the table. In the even-numbered trials, the sequence of contrast values was reversed. This was repeated until the PSTHs grew to an adequate size (6–20 repetitions). The magnitude of the response was calculated by subtracting the background discharge rate (mean rate of discharge during 1 s before stimulation) from the mean discharge rate during the stimulating period (i.e., the total number of discharges for a time window which had a duration equal to the passing-through-time of the stimulus over the receptive field). The opening time of the window was set appropriately in reference to the latency of the response.

Results

The present results were based on observations of 89 MT cells which showed a strong directional selectivity (direction index[1], greater than 0.5) to a moving light slit. Of these, 41 cells were subjected to the optimal-stimulus experiment in which the size of the bar and the amplitude of motion were set so that the cell was activated maximally, and the rest were subjected to the small-stimulus experiment in which the size of the bar and the amplitude of motion were reduced to the smallest values which still produced reliable responses. These two series of experiments were necessary because either seems to have limitations in assessing the responsiveness of MT cells to pure color-contrast. In the optimal-stimulus experiment, it is quite possible that the minimum response includes a response elicited by luminance contrast. This is because a rather large size of the stimulus bar and a long moving distance are generally required to elicit the optimal response (the largest stimulated area was 15° × 8°) but there is no guarantee that the equiluminous condition is homogeneous over a wide retinal region. On the other hand, in the small-stimulus experiment a weak input may be hidden by some nonlinearity, e.g. a threshold nonlinearity, in the contrast-response function of the cell. The possibility of being disturbed by a nonhomogeneity of equiluminance over the retina would be low in a small-stimulus experiment. On the contrary, the possibility of being disturbed by a nonlinearity in

1 Direction index (DI) is defined by the commonly used formula: DI = 1 – Rn/Rp, where Rp and Rn represent the magnitude of the response to a stimulus moving in the preferred direction and in the null direction (opposite to the preferred one)

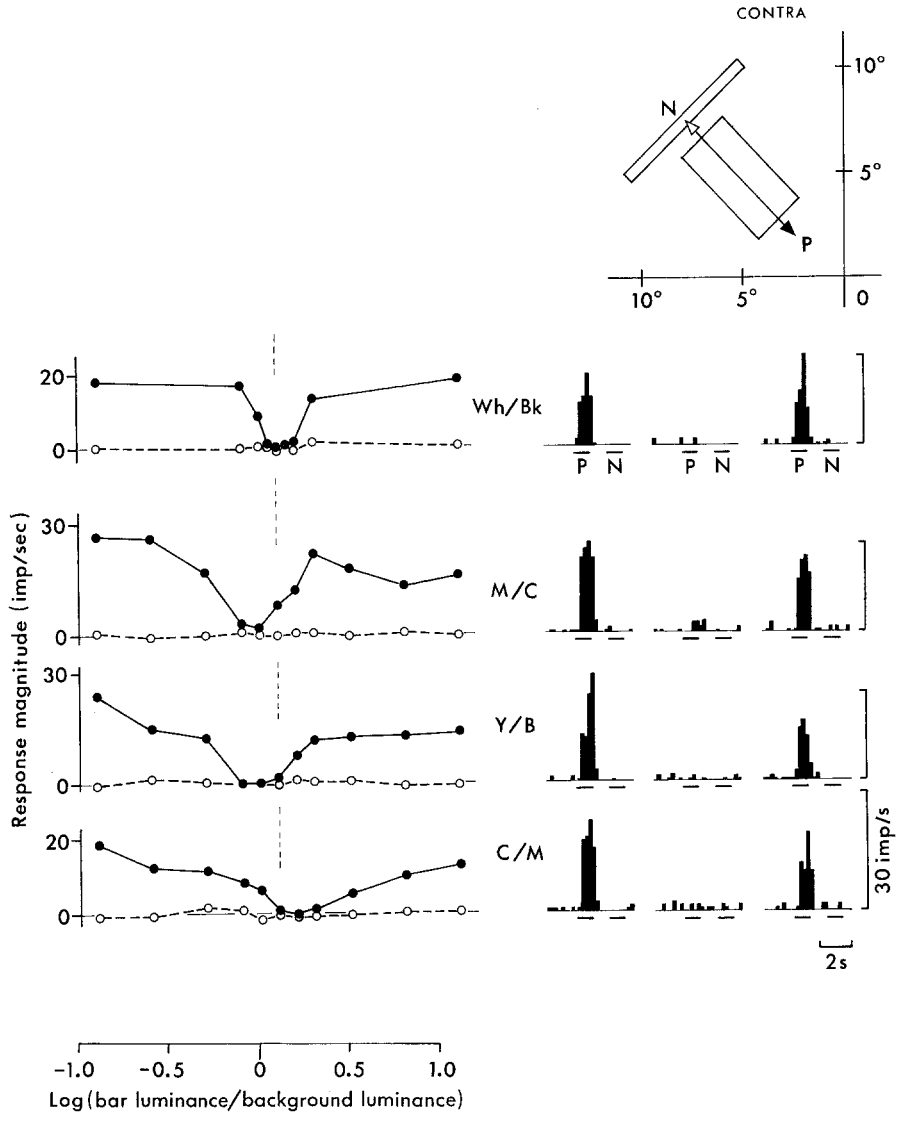

Fig. 3. Response of an MT cell which did not respond to movements of an equiluminous opponent-color stimulus. An example taken from the optimal-stimulus experiment. Left column: Magnitude of response plotted against luminance contrast between the bar and background. Filled circles: the magnitude of the response to a bar moving in the preferred direction. Open circles: the magnitude of the response to a bar moving in the direction opposite to the preferred direction (null direction). Top row: Response to a black-and-white pattern. Second row: chromatic combination of bar/background, magenta/cyan. Third row: yellow/blue combination. Bottom: cyan/magenta combination. For the lower three combinations, only the luminance contrast was changed, and the chromatic contrast was kept constant. For all three color combinations, the response disappeared almost completely near the human equiluminous condition. Right column: PSTHs of, from left to right, the maximum response to a bar darker than the background, the minumum response near the human equiluminous condition (zero on the abscissa of the left graph), and the maximum response to a bar brighter than the background. Lines with marks P and N beneath the histograms show the period of bar-movement towards the preferred direction and the null direction, respectively. Top inset shows the receptive field of the cell with the illustration of the moving bar used in the measurements

stimulus-response would be low in an optimal-stimulus experiment.

The distribution of the eccentricity of the receptive field center did not differ between the cells studied in the two kinds of experiments. It ranged from near 0° to 15°.

First, we will describe the results of the optimal-stimulus experiment. In Fig. 3, an example of a cell which showed the most extreme response behavior is illustrated. In the left-hand column, the magnitude of the response to a bar moving in the preferred direction (filled circles) and in the null direction (opposite to the preferred one, open circles) is plotted against the bar/background luminance-contrast. In the three lower graphs, there was a constant chromatic-contrast (magenta/cyan, yellow/blue and cyan/magenta combinations for the upper, middle and lower graphs) between the bar and the background in addition to a luminance contrast of different values between 1/10 and 10/1. For all color combinations, the response of the cell decreased almost to zero when the luminance ratio was close to 1 (human equiluminous condition). This means that the cell cannot signal the direction of motion of a pattern if there is no luminance difference between the pattern and its background. The contrast-response plot designated by Wh/Bk was for an achromatic stimulus. The cell gave virtually full-sized responses even when the luminance contrast was as low as 0.2 log unit of both sign (positive and negative contrast, i.e., luminance of the bar to that of the background is 1 : 1.58 and 1.58 : 1, respectively), indicating that the cell has high sensitivity to luminance contrast. Thus, the cell seems to have a property which is typical to the so-called the magnocellular stream (Livingstone and Hubel 1987). But

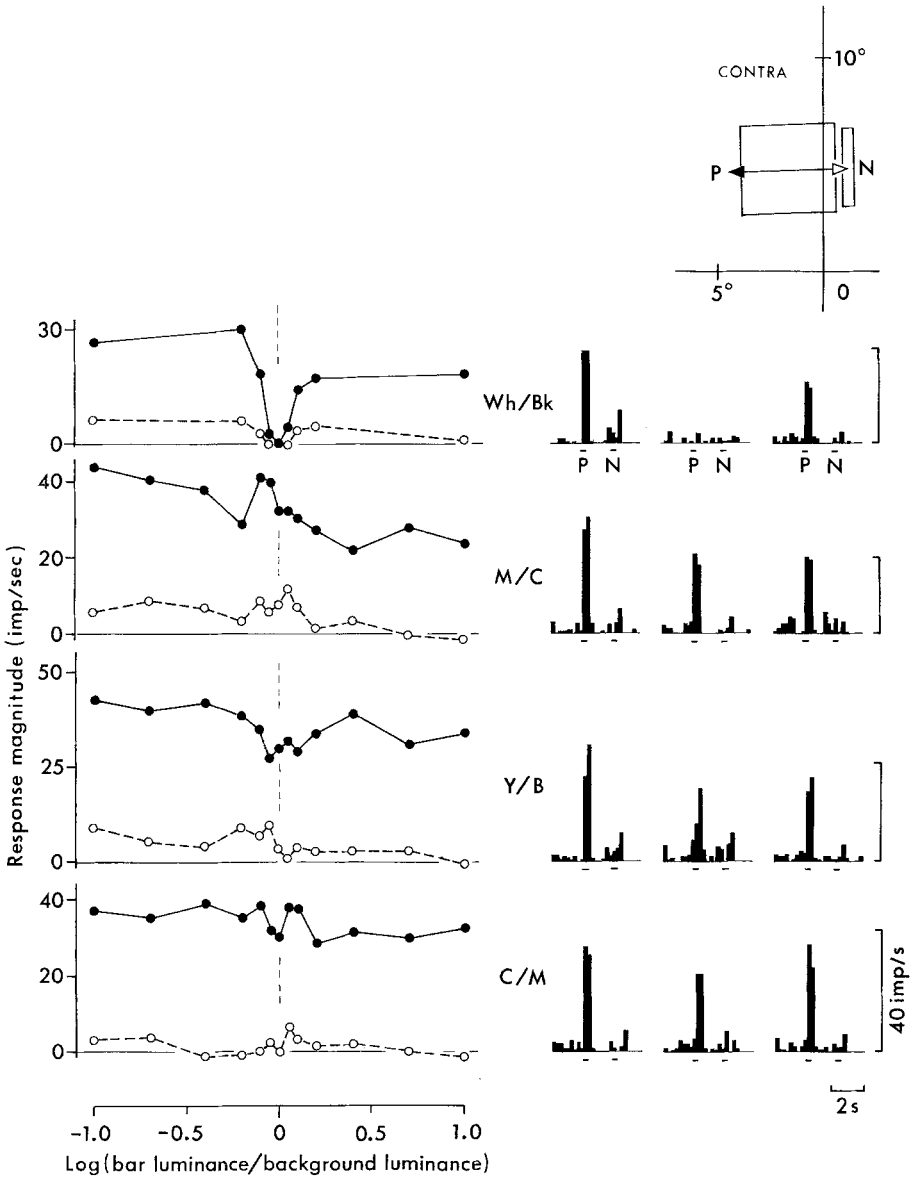

Fig. 4. Response of an MT cell which showed clear contrast with the cell in Fig. 3. This cell showed no systematic dip in the response to a color stimulus. The format is the same as in Fig. 3. This example is also taken from the optimal-stimulus experiment

to show this was not our purpose in examining the response to an achromatic stimulus. The reason for this test will be described below.

The extreme reverse was the cell shown in Fig. 4. There is no obvious dip in the magnitude of the response of the cell to the movement of color patterns of different luminance contrasts. Since this cell showed higher sensitivity to luminance contrast than the cell shown in Fig. 3, as seen in the top graph (the response of the cell increased to more than half the maximum at a luminance contrast of 0.1 log unit), we examined the response thoroughly by changing the luminance contrast of the colored stimuli in steps of 0.05 log unit near the human equiluminous condition. Though there is a little irregularity in the magnitude of the response, we did not observe a systematic dip in the amplitude of the response. The main reason for examining achromatic responses was to determine a reasonable step of luminance contrast for testing. Figure 4 also shows that the response is directionally selective at any luminance contrast.

The large majority of MT cells showed a response behavior in between the above two extremes. As will be shown in the next section, the average magnitude of the residual response at equiluminance was about 35% of that of the maximum responses of individual cells.

Before entering the quantitative analysis, we will introduce the results of the second series of experiments, i.e., the small-stimulus experiment. This series of experiments was designed to find out whether a non-null phenomenon, exemplified in

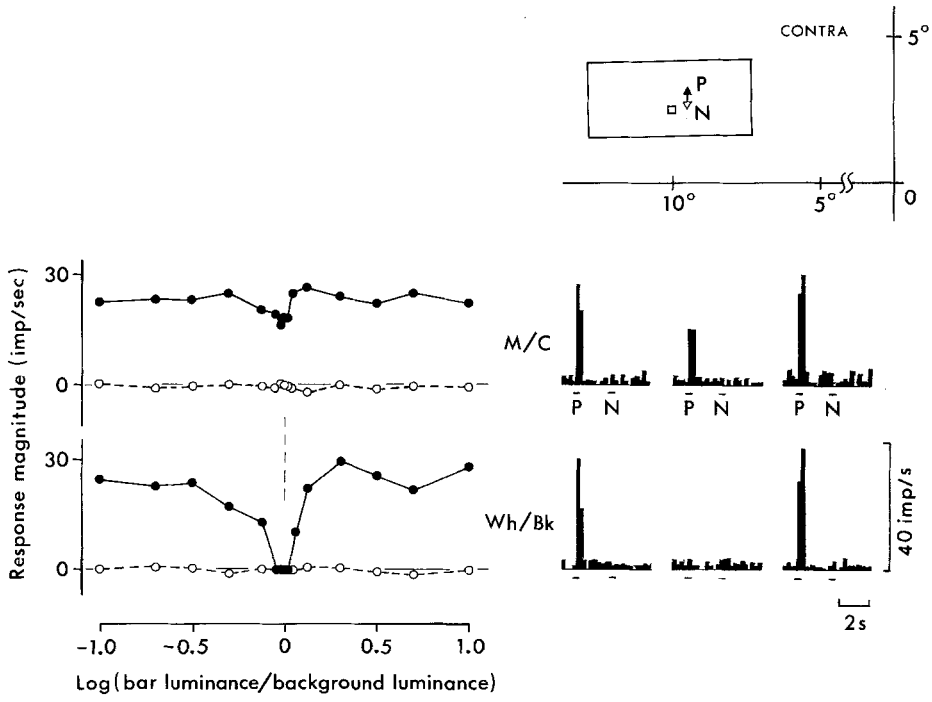

Fig. 5. A cell which did not show a complete null in the small-stimulus experiment. The response to the magenta/cyan stimulus did not disappear at any luminance combinations. The format is similar to that in Figs. 3 and 4

Fig. 4 is truly indicative of receiving a color-contrast input or merely the reflection of a non-homogeneity in the equiluminous condition over the retina (cf. Livingstone and Hubel 1987).

The results of the small-stimulus experiment (in which only the color combination magenta/cyan was examined together with the responses to the achromatic stimulus) were qualitatively the same as those of the optimal-stimulus experiment. Many cells failed to respond to the magenta/cyan stimulus near the human equiluminous condition, whereas a definite proportion of cells continued to respond clearly at any bar/background luminance ratio. Figure 5 illustrates the contrast-response plots for a cell which belongs to the latter type. As can be seen, there is no bar/background ratio at which the response to the magenta/cyan stimulus decreased considerably, though the response curve shows a dip near the human equiluminous condition. There is no possibility that we might have overlooked a null point, because the step of luminance-contrast we examined for the magenta/cyan stimulus around the minimum response condition is fine enough judging from the contrast-response function of the cell for the achromatic stimulus. The response of this cell obtained with a small stimulus is assumed to be mostly free from regional differences of equiluminance on the retina for two reasons. First, the retinal eccentricity of the center of the receptive field is relatively large (10.1° contralateral and 3.2° superior in the visual field, see Fig. 5 upper inset). Therefore, in the central region of the receptive field, the change in the equiluminous condition is supposed to be gradual. Second, the bar was moved only 1.5° in the *vertical* direction, so that there was only a slight change in the retinal eccentricity of the stimulated region. It is thus very difficult to infer that the origin of the minimum response obtained near the human equiluminous condition is a breakdown of equiluminance.

Quantitative evaluation I: null index

To evaluate quantitatively the responsiveness of MT cells to the movement of equiluminous color patterns, we calculated the ratio between the minimum response to a color stimulus moving in the preferred direction (the minimum response was obtained generally near the human equiluminous condition, cf. Fig. 10) and the maximum response to the same color stimulus with a clear luminance contrast. As a maximum response, we took the average of two maxima, one obtained for a luminance ratio less than 1 (the bar darker than the background, negative contrast) and the other for a luminance ratio greater than 1 (the bar brighter than the background, positive contrast). We called this ratio the 'null index (NI)'. NI was not calculated for three exceptional cells which showed a big imbalance between the response to positive and negative luminance contrast (1 cell in the optimal-stimulus experiment and 2 cells

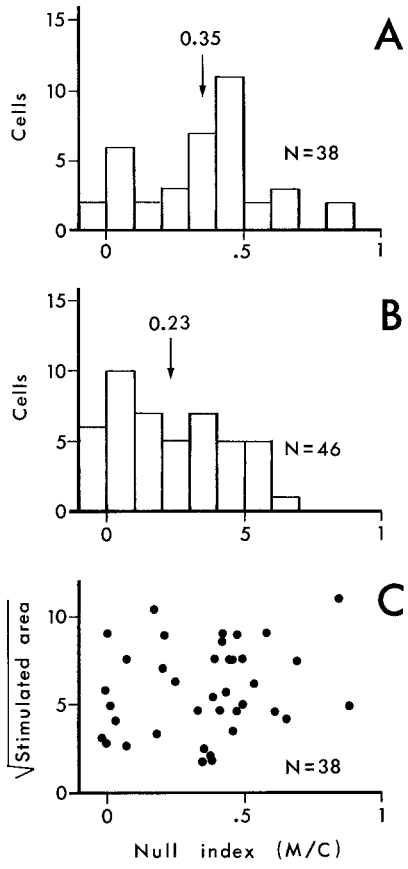

Fig. 6. A, B Distribution of null index (NI) for the magenta/cyan combination in the optimal-stimulus experiment (**A**) and in the small-stimulus experiment (**B**). **C** A scatter diagram representing the relationship between the stimulated area and NI for the magenta/cyan stimuli in the optimal-stimulus experiment. Stimulated area is represented by the square root of (bar-length × (moving amplitude + bar-width)). All the parameters within the parenthesis were expressed by visual angle in degree. Abscissae for all three graphs are the value of NI for the magenta/cyan stimuli

in the small-stimulus experiment gave responses more than twice as strong to a stimulus of positive contrast than to one of negative contrast).

In the optimal-stimulus experiment, the value of NI for magenta/cyan combination varied from 0 to 0.9, and the mean for 38 cells was 0.35 (Fig. 6A). Thus, at equiluminance the response of MT cells reduces, on the average, to about 1/3 the maximum. The distribution of NI for the magenta/cyan combination is also plotted for the small-stimulus experiment (Fig. 6B). It is evident from the two histograms that the residual response at equiluminance is stronger on the average in the optimal-stimulus experiment than in the small-stimulus experiment in which the mean of NI for 46 cells is 0.23. One might think that a cause of this difference could be a breakdown of equiluminance in the optimal-stimulus experiment with a long traverse of a large stimulus across the receptive field. However, we can indicate evidence that this factor will be small, if present. We examined the relation between the value of NI and the size of the stimulated area to find out whether they show high correlation. As shown in the scatter diagram of Fig. 6C, the correlation was very weak (correlation coefficient, 0.22, $N = 38$). This fact strongly supports the notion that the minimum response at equiluminance is not seriously influenced by a breakdown of equiluminance due to non-homogeneity of the equiluminous condition over the retina. In fact, the use of large stimuli did not break the null phenomenon in many cells (see Fig. 3). A plausible cause of the shift of the NI-distribution towards the left in the small-stimulus experiment would be a nonlinearity in the contrast-response function of the cells. That is, with a small stimulus which moved a small distance, MT cell activation was generally weaker, and in such a situation, the response could be blocked by some threshold mechanism.

In our sample, the value of NI and the eccentricity of the receptive field were not correlated. The correlation coefficient was –0.16 ($N = 38$) and 0.18 ($N = 46$) for the optimal-stimulus and the small-stimulus experiments, respectively.

Before coming to the conclusion that the residual response at equiluminance is a 'response to a pure color-contour', we must consider the effect of the transient luminance change generated at the fringes of the bar by chromatic aberration in monkey optics. Because MT cells generally show a high sensitivity to luminance-contrast, such a luminance change might cause the residual response. We estimated that the peak luminance change generated at the magenta/cyan border is about ± 15% and that the width of the changing region is about 0.05° (Fig. 2D, detailed descriptions are given in the Methods section). Using light and dark bars 0.05° in width and a luminance contrast of 100% (bar/background luminance ratio was 2 for the light bar and 0.5 for the dark bar), we tested 28 MT cells, including 12 cells which showed NI larger than 0.23 (0.26–0.88) with a small stimulus, for whether they do or do not respond to a narrow bar of high luminance contrast. None of the tested cells responded to these bars. For 16 of them, the effectiveness of bars of double width (0.1°) and of the same luminance contrast was tested. Six cells did respond to the light bar, but the amplitude of response was less than a half that of the residual response at equiluminance. The stimuli were completely ineffective for the 10 other cells. Thus, it would be safe to say that chromatic aberration is not a cause of the residual response at equiluminance. To confirm this, we tested whether the residual response

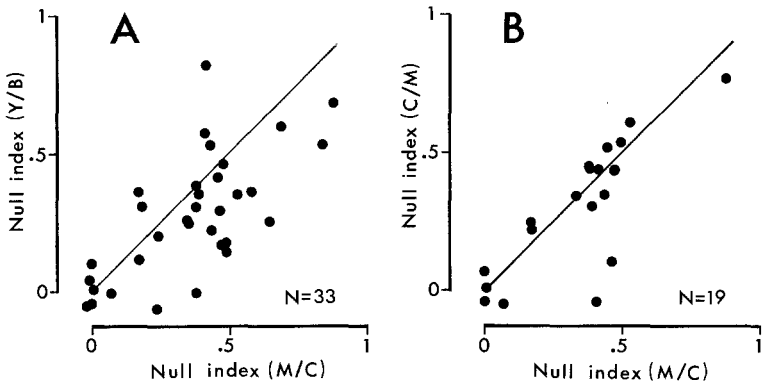

Fig. 7A, B. Scatter diagrams representing the relationship between the NIs for magenta/cyan and yellow/blue color stimuli (**A**) and those between the NIs for magenta/cyan and cyan/magenta color stimuli (**B**). Each dot represents a single cell

at equiluminance decreased when the retinal image of the chromatic-edge was blurred by placing an additional lens (+3 D) close to the monkey's eye. By calculation, the peak amplitude of the luminance change caused by chromatic aberration should have been reduced by blurring to about ± 3% (see Fig. 2E and Method section). Of 5 cells tested, which showed different levels of NI for the focused stimulus (0.1–0.5), one cell showed a slight decrease (by –0.05) but the rest showed an increase (by 0.15–0.3) rather than a decrease of NI value when the image was blurred. It is thus not possible to say that the luminance change generated by chromatic aberration is the cause of the residual response at equiluminance. Incidentally, the increase of stimulus size towards the optimum by blurring would have made the NI larger in some cells.

From all these considerations, we conclude that the residual response of MT cells at equiluminance has its origin largely in a color-contrast input. Thus, although the magnitude of the average output of MT decreases at equiluminance to about 1/3 of the maximum, MT can still detect the direction of motion of a pattern composed of a pure color-contour. In particular, cells such as those shown in Fig. 4 can code information about the direction of movement of a pattern, even when the pattern shows no other difference than chromaticity with its background.

The null index was also calculated for the response to other color combinations tested in the optimal-stimulus experiment. The mean of the null indexes for the yellow/blue color pattern was 0.27 (average of 33 cells) and that for cyan/magenta was 0.30 (average of 19 cells). In order to see whether the individual MT cells show a different degree of the null phenomenon for magenta/cyan (M/C) and yellow/blue (Y/B) color-contrasts, a scatter diagram, representing the relationship between NI for M/C and NI for Y/B measured on identical cells, has been made and is shown in Fig. 7A. Although the NIs for

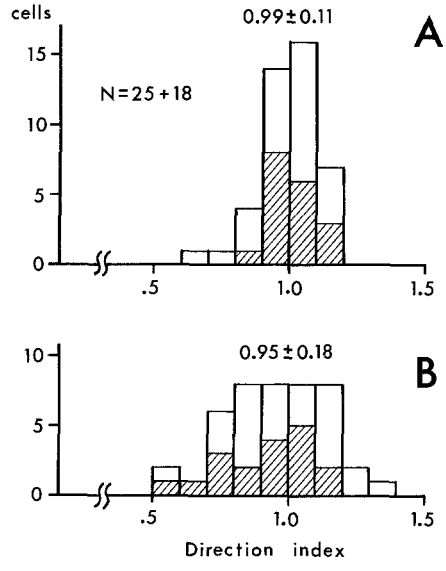

Fig. 8A, B. Distribution of direction index (DI) calculated for the maximum response (**A**) and for the minimum response (**B**). Clear and hatched histograms are obtained from the optimal-stimulus experiment (25 cells) and from the small-stimulus experiment (18 cells), respectively. Inset figures represent mean and standard deviation

the two color contrasts are not strictly equal in individual cells, the difference is small in the majority (the ratio of the two NIs falls between 0.5 and 2) so that the plotted points are distributed along the regression line represented by NI(M/C) = NI(Y/B). As a population, however, there is a tendency for the NI for Y/B to be a little smaller than for M/C. Relationships between the NIs for M/C and C/M in individual cells were studied by making a similar scatter diagram (Fig. 7B). In all cells except for two which showed a remarkable imbalance, the two NIs are well balanced, indicating that their response behavior is independent of a bar/background color reversal.

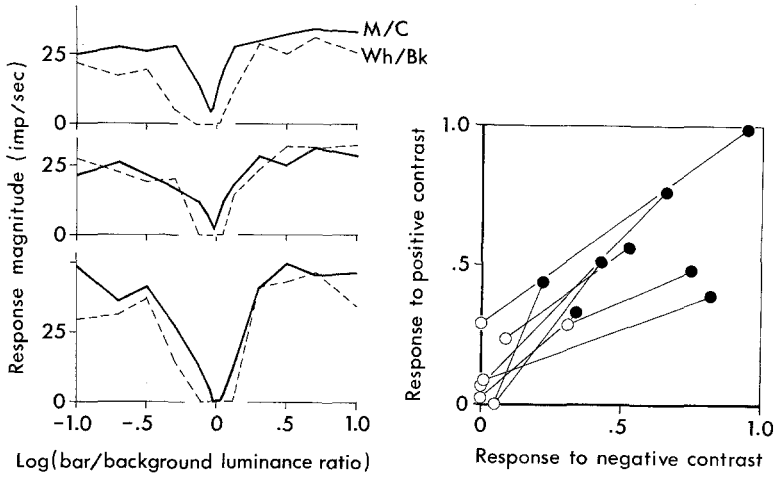

Fig. 9. Evidence for inputs of color-contrast signals in cells which showed equiluminous null phenomenon. Left graphs show contrast-response plots in three cells for the magenta/cyan (solid curves) and achromatic (broken curves) stimuli obtained in the small-stimulus experiment. The range of the bar/background luminance ratio for which the response disappeared is narrower for the magenta/cyan than the black-and-white stimuli in all cells. The right graph shows an improvement of threshold responses to black-and-white stimulus (open circles) by adding chromatic signals without altering luminance contrast (filled circles). Detailed explanations are given in the text. Responses of 8 cells are shown.Lines connect the responses of the same cell. Both responses to the negative luminance-contrast (abscissa) and positive luminance-contrast (ordinate) are normalized by the maximum response of the individual cells to the contrast of the same sign

It is worthy of note that the preferred direction was not altered by reversing the sign of the luminance contrast, and except for 3 cells out of a total of 89 cells the magnitude of the response to stimuli of positive and negative luminance contrast was well balanced. This is very different from the directionally selective cells in layer 4B of V1: the preferred direction of many of these was reversed by reversing the sign of the luminance contrast (Livingstone and Hubel 1984).

Quantitative evaluation II: direction index

The second index introduced for the evaluation of the response behavior of MT cells is the direction index (DI, for definition, see footnote 1). DIs were calculated both for the maximum response to the magenta/cyan pattern with luminance contrast and for the minimum response to the same color combination at near the human equiluminous condition. Figure 8 shows histograms of these DI values calculated for cells in which the minimum response exceeded 30% of the maximum (25 cells subjected to the optimal-stimulus experiment (clean histogram) and 18 cells subjected to the small-stimulus experiment (hatched histogram)). Although the mean is a little smaller and the scattering is somewhat wider for the DIs in the minimum response (Fig. 8B) than for the DIs in the maximum response (Fig. 8A), (mean and standard deviation for 8A are 0.99 and ± 0.11, and those for 8B are 0.95 and ± 0.18, respectively), the difference is very small and the mean is close to 1. This indicates that the direction selectivity of MT cells is well maintained for movements of an equiluminous color pattern.

Evidence that a color-contrast signal is also fed to cells which showed complete null at equiluminance

We noticed that in cells whose response to color-contrast stimuli disappeared almost completely for some range of the bar/background luminance ratio, the contrast-response curves plotted for the color stimulus and the achromatic stimulus did not coincide. That is, the range of the null is always narrower for the color stimulus than for the achromatic one. Three examples are illustrated in the left half of Fig. 9. If the response to the color stimulus was determined solely by the luminance imbalance presented in the stimulus, then the two curves would coincide. We thought that the separation of two curves might indicate that a color-contrast signal improved the response to patterns of very low luminance contrast. However, to conclude this only from the above observations may be dangerous, because the response curves for the color and the achromatic stimuli were obtained sequentially in a different set of trials, and therefore could be influenced by a slow change in responsiveness. We carried out another set of experiments, in which the following four stimuli were combined in a single multi-histogram trial: achromatic stimuli of a weak positive and a weak negative contrast of an equal absolute value (between –0.125 and +0.125 log units) to produce a near threshold response, and magenta/cyan stimuli whose bar/background luminance ratio was adjusted so that it was separated from the equiluminous value of each cell by an amount equal to the luminance contrast value set for the achromatic stimuli. That is, we compared the response to black-and-white stimuli and magenta/cyan stimuli of equal luminance contrast.

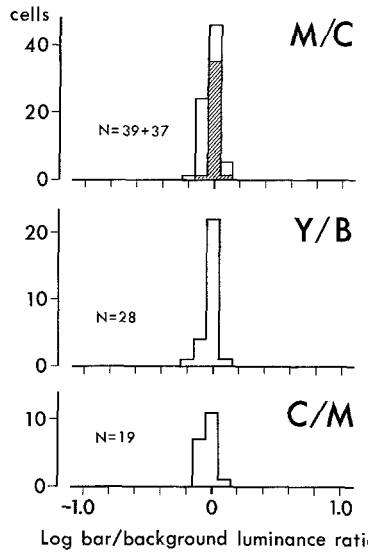

Fig. 10. Distribution of the equiluminous point of MT cells for magenta/cyan (M/C), yellow/blue (Y/B), and cyan/magenta (C/M) color combinations. Zero on the abscissa indicates the human equiluminous condition. Clear and hatched histograms for M/C combination are obtained from the optimal-stimulus experiment (39 cells) and from the small-stimulus experiment (37 cells), respectively. Cells which showed complete null over some range of the luminance contrast are not included in this figure

The results for 8 cells are shown in the right half of Fig. 9. For each cell, the response to the achromatic stimuli is plotted with an open circle by taking the magnitudes of the response to a negative and positive contrast on the abscissa and ordinate, respectively. The response of each cell to the magenta/cyan stimuli whose luminance contrast was determined as described above is plotted in the same way with a filled circle. The two plots for the same cell are connected by a line. It is evident that the response to the magenta/cyan stimulus is much larger than the response to the achromatic stimulus of the same luminance contrast. The magnitude of increase ranged from 0.3 to 0.99 as normalized by the maximum response. This suggests that color-contrast signals are also fed to cells which showed an equiluminous null phenomenon.

Distribution of the equiluminous point

This provides further information on the degree of similarity of the wavelength-luminosity relationships betwen the monkey visual system and our own. The bar/background luminance ratio at which the cells' response fell to a minimum is shown in Fig. 10 in the form of a frequency histogram. In all cases (magenta/cyan, yellow/blue, and cyan/magenta combinations), this luminance ratio (referred to as the equiluminous point) in MT cells is concentrated very near the human equiluminous condition.

Discussion

Although the magnitude of the response of most directionally selective MT cells decreased when the bar/background luminance ratio of the color stimulus was close to 1, the response did not disappear and directional selectivity was maintained in a significant proportion of MT cells. We conclude that the MT area can analyze the direction of movement of a pattern composed of pure color-contours, though the strength of the output is considerably weaker than for the movement of patterns with luminance contrast.

Relation to psychophysical observations

If we assume that MT plays a crucial role in the sensation of motion[2], the above conclusions is consistent in all aspects with many psychophysical observations on human subjects; namely, that the movement of equiluminous color patterns can produce a good motion sensation, though somewhat weaker than that produced by a pattern with luminance contrast (Cavanagh et al. 1985; Isono and Yasuda 1986, 1987). Furthermore, Cavanagh and Favreau (1985) concluded that color and luminance share a common motion pathway, on the basis of the observation of the effect of adaptating stimuli on a motion after-effect. They suggested the existence of cortical cells responding both to the movement of a pattern composed of luminance contrast and that composed of pure color-contrast.

Based on the observations that many psychophysical phenomena which relate to motion perception break down at equiluminance, Livingstone and Hubel (1987) reached just the opposite conclusion, namely that the color contrast signal might not be used in visual motion analysis in humans. The exact reason for this discrepancy is not known at present. However, since a threshold is generally examined in psychophysical studies, it is not surprising that the physiological properties of MT does not match some of the psychophysical phenomena directly, because it is reasonable to assume that the way in which signals from MT are involved in different perceptual attributes need not have the same threshold.

2 This assumption is not groundless, since Newsome et al. (1986) have shown that there is good coincidence between the spatio-temporal conditions of the sequential presentation of flashing slits producing a directionally selective response in MT cells of the macaque and those producing apparent motion sensation in human observers

Advantage of responding to pure color-contrast

In most MT cells, the degree of nulling at equiluminance is not greatly influenced by differences in the color of the moving slit and the background. Though the magnitude of the response to yellow/blue combination is somewhat smaller than that to magenta/cyan combination, it seems reasonable to assume that the MT cells do not provide information about the color of a moving object. This is consistent with earlier studies which showed that MT cells are insensitive to the wavelength of a moving stimulus (Zeki 1974; Van Essen et al. 1981). In addition, in all the cells studied, the preferred direction was not reversed by changing the sign of the luminance contrast, i.e., light on dark or dark on light. All this indicates that MT cells analyze visual motion independently of stimulus parameters such as color and sign of luminance contrast.

Another important item of information gained from color patterns than to know the kind of color are cues for 'figure/ground separation': an animal may be aware of the existence of an object by the discontinuity of color between the object and the background. Present results indicate that MT cells do use a color-contrast signal in this way. The addition of a color-contrast to a low-contrast achromatic pattern considerably improved the responses of cells even those which showed a complete null at equiluminance. This fact indicates that the great majority, if not all, of cells in MT are not truly free from a color-contrast input, and that the color-contrast signal can assist the analysis of movement of contours even in the case of cells which show the null phenomenon.

All the above rationale is consistent with the hypothesis proposed by DeYoe and Van Essen (1988) that there is redundant representation of sensory cues in the different anatomical streams found within the monkey prestriate area.

Input of color-contrast signal

From what type of cells do the MT cells receive the color-contrast signal? There are at least two possibilities: 1) they receive converging inputs from wavelength-selective cells, but the best wavelength is different for different cells; 2) they receive signals from cells which are broadband for stimulus wavelength but which respond to the passage of a color-contrast border.

Wavelength selective cells with broad or no orientation selectivity are commonly found in areas V1 (Michael 1978; Zeki 1978, 1983; Livingstone and Hubel 1984; Vautin and Dow 1985), V2 (Zeki 1978; Hubel and Livingstone 1985; Burkhalter and Van Essen 1986) and V4 (Zeki 1978, 1983; Desimone et al. 1985). It has been shown that all these areas send fibers to MT (Maunsell and Van Essen 1983b; Van Essen 1985) and could thus be candidate sites from which color-contrast information might be fed to MT. However, combined studies of cytochrome oxidase (CO) staining, the tracing of afferent connections, and the functional mapping of V2 showed that projections from V2 to MT originate in the thick CO-rich stripes in which directionally selective cells are common and color selective cells rare (DeYoe and Van Essen 1985; Shipp and Zeki 1985). It has also been shown that the direct projections from V1 to MT originate in layer 4b (see Van Essen 1985), and the majority of cells in this layer are again selective for direction of movement (Dow 1974: Livingstone and Hubel 1984) but insensitive to wavelength (Dow 1974). It seems likely that the MT-projecting V1 and V2 cells which are insensitive to wavelength are also able to respond to color contrast borders, although the possibility remains that wavelength-selective V4 cells also project to MT.

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