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Analysis of Local and Wide-Field Movements in the Superior Temporal Visual Areas of the Macaque Monkey

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The middle temporal (MT) and medial superior temporal (MST) areas of the macaque cortex have many cells that respond to straight movements in the frontoparallel plane with directional selectivity (D cells). We examined their responses to movements of a bar, of a wide dot pattern, and to combined movements of the two in anesthetized and immobilized animals. D cells in MT showed a wide variety in the strength of the inhibitory field surrounding the excitatory center field. Responses of SI^+-type cells to a bar moving across the excitatory field were suppressed when a wide dot pattern moved over the surround field in the same direction and at the same speed as the bar. Inhibition was selective to the direction and speed of the surround movement, and the effective area for inhibition occupied a wide area, which expanded in all radial directions. Responses of SI^--type cells to a center bar movement were changed little by a conjoint movement over the surround field. Consequently, SI^--type cells responded to wide-field movement as well as to stimuli confined within the excitatory field. Although D cells in MST commonly had large excitatory fields, a proportion of them (Figure type) responded to bar movement much more strongly than to wide-field movement. Their responses to a bar movement were suppressed direction-selectively by a conjoint movement of a wide dot-pattern background. The effective area for inhibition coexisted with the excitatory field in these cells. MST cells of the Nonselective type responded comparably well to the two stimuli, and those of the Field type responded much more strongly to wide-field movement than to bar movement. It is thus suggested that MT cells of the SI^+ type and MST cells of the Figure type can detect a difference between movements of an object and its wide background, whereas MST cells of the Field type can detect a conjoint movement of a wide field, neglecting the movements of a single object.

Among the multiple visual areas of the macaque prestriate cortex, the MT (middle temporal) area, located at the posterior bank and fundus of the superior temporal sulcus (STS), is capable of performing the analysis of visual motion. This idea is based on two lines of observation. First, most cells in this area prefer moving stimuli to stationary stimuli, and their responses to moving stimuli are selective to the direction of motion (Maunsell and Van Essen, 1983a; Van Essen et al., 1981; Zeki, 1974). Second, the preferred direction of motion shown by MT cells changes systematically along the surface of the cortex, which indicates that the direction of motion is represented in this cortical area (Albright et al., 1984; Zeki, 1974). The area that adjoins MT anteriorly receives fiber projections from MT (Maunsell and Van Essen, 1983b; Ungerleider et al., 1982; Yukie et al., unpublished observations) and is called the MST area (the medial superior temporal area; Maunsell and Van Essen, 1983b). Since it was recently reported that there were many directionally selective cells with large receptive fields (Maunsell and Van Essen, 1983b; Van Essen et al., 1981; Wurtz et al., 1984; Zeki, 1980a), MST may also be involved in the analysis of visual motion.

To elucidate the functional significance of the directionally selective cells in these two cortical areas, we paid special attention to movements of the background. Information on background movement is indispensable for the animal not only for the perception of net movements of objects relative to a moving background, but also for the perception of the animal's own movement, which causes background movement (for reviews, see Gibson, 1968; Nakayama, 1985). With regard to the influence of background movement on the responsiveness of neuronal cells to a moving object, some interesting results have been reported on the brain of several species other than the macaque (Allman et al., 1986, in press; Frost, 1978; Frost and Nakayama, 1983; Grünau and Frost, 1983; Hammond and MacKay, 1977, 1981). However, the analysis of background movement itself has not been studied experimentally in previous physiological works.

The present study aimed to learn whether cells in MT and MST of the macaque can analyze the movements of an object relative to its background, and whether they can analyze the conjoint movements of a wide visual field. We examined their responses in anesthetized and immobilized monkeys, and found that a population of cells in both areas responded selectively to objects that moved differently from the background. In addition, a group of cells unique to MST responded selectively to the conjoint movements of a wide visual field, neglecting the movements of a single object. Part of this study has been previously reported in an abstract (K. Tanaka et al., 1984).

Materials and Methods

Preparation

Four Japanese monkeys (*Macaca fuscata*) weighing 4–7 kg were used for experiments repeatedly (9–14× for each). Three to seven days prior to the first recording session, surgery was performed under pentobarbital sodium anesthesia (32 mg/kg). A brass block, which would be used for head fixation, was attached to the dorsal top of the skull, a spherical skullectomy (12–20 mm long) was made along the lateral part of the lunate sulcus, and a plastic well was attached around the hole so that it could be covered by a plastic lid.

Each recording session was initiated by inducing anesthesia by an intramuscular injection of alphaxalone (10 mg/kg) or ketamine hydrochloride (7 mg/kg). A ventilation tube was inserted into the trachea, the

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animal was made prostrate on an iron stage, and the head was fixed to an arm of this stage through the brass block. Throughout the recording, the animal was immobilized with gallamine triethiodide (initially 10 mg/kg, followed by hourly 4 mg/kg intramuscular injections) and anesthetized with a gas mixture of N_2O and O_2 (70:30 to 80:20). Artificial ventilation was maintained at 25 strokes/min with a 40:60 inspiration/expiration ratio, and the end tidal CO_2 was maintained at 4.5–5% by adjusting the stroke volume. The body temperature was kept at 38°C. To reduce salivation, 0.5 mg atropine sulfate was injected subcutaneously at the beginning, midway, and towards the end of the recording. Injection of the agent for paralysis was stopped 1 hr before the end of the recording. Spontaneous respiration resumed and became normal within 2–3 hr after this. Two successive recording sessions were separated by at least 3 d. The antibiotic was injected subcutaneously and applied to the exposed dura after each recording session.

Recording and histology

Extracellular single-cell recordings were made in the deep portion of the STS by glass-coated platinum-iridium electrodes with exposed tips 10–15 μm long (2.5–4 MΩ at 200 Hz). The electrodes were held by a three-dimensional micromanipulator fixed to an arm of the iron stage, and advanced in the horizontal plane anteromedially at an angle of 30°–45° against the parasagittal plane (Fig. 1). The exposed dura, which was not dissected, was covered with paraffin to prevent it from drying and to reduce movements of the brain caused by pulsation and respiration. Each penetration was made with reference to a point on the plastic well, in order to constitute systematic tracking. A total of 17–27 penetrations were made in each hemisphere. Small electric lesions (10 μA tip negative, 20 sec) were made at the end of several penetrations to reconstruct the electrode tracks. After the last recording session, the animal was deeply anesthetized with pentobarbital sodium and perfused intracardially with warm saline, followed by 10% formol saline. A block of the brain was removed and placed in 30% sucrose in 10% formalin until it sank. Frozen serial sections were cut at a 50 μm thickness in the horizontal plane. Every fifth section was stained with modified Heidenhain's myelin stain (Hutchins and Wever, 1983) or Gallyas' silver stain (Gallyas, 1979), and the other sections were stained with cresyl violet. The extent of the MT area was determined by the dense and uniform myelinated band in layers IV, V, and VI of the cortex, as shown in Figure 2 (Ungerleider and Mishkin, 1979; Van Essen et al., 1981), and the electrode tracks were reconstructed by reference to the electric lesions and traces of penetrations.

Photic stimuli

The pupils were dilated by local application of 0.5% tropicamide and 0.5% phenylephrine, and the corneas were kept moist by covering them with neutral contact lenses. Eyes were focused on a translucent tangent screen at 57 cm from the corneas through artificial pupils 3 mm in diameter and appropriate lenses. Several retinal landmarks, such as a crossing of vessels and the center of the optic disk, were projected by a reversible retinoscope on the screen, and the position of the area centralis was determined geometrically from them by referring to photographs of the fundus.

When a single cell was isolated, its optimal stimulus was studied by using real objects held by hand as well as images projected on the screen. The stimuli were presented monocularly or binocularly. The disparity of binocularly presented stimuli was changed by the use of a Risley prism in front of one eye. The equipment used to examine whether a cell selectively responded to a disparity change, size change, and rotation is described in the accompanying paper (Saito et al., 1986). The present paper concentrates on directionally selective cells responding to straight movements in the frontoparallel plane. To study the response properties of these cells, two types of white light patterns were independently back-projected on the screen from two projectors, each of which was equipped with a movable mirror mounted on a galvanometer. One of the two photic patterns was a light bar, which was 1 log unit brighter than the background illumination (4 cd/m²). The other was a two-dimensional array of small light spots expanding over 70° in the direction of motion and 55° in the orthogonal direction. Usually the spots were 0.7° in diameter and the interval between the centers of the two neighboring spots was 2°. The axis of the array was 45° oblique to the direction of motion. For excitatory fields smaller than 3°, it was replaced by a pattern with a 0.35° spot diameter and 1° interval. Randomly textured patterns, one-dimensional rectangular gratings (striped patterns), and patterns with larger spots were also used in some cells. Light parts of the patterns were 1 log unit brighter than the background. To shield a part of the screen from the dot pattern, one polarizing filter was placed in front of the projector, and another, with a polarizing axis orthogonal to that of the first filter, was attached to the screen from behind. The luminance of the dots within the masked area was 3 log units lower than that of the outside dots. Because of the loss of energy through a single polarizing filter, the contrast between a bar projected within the masked area and that of the outside dot pattern was reduced to 0.5 log units.

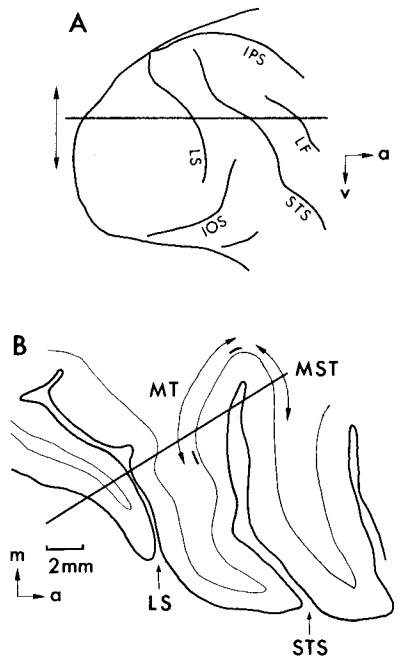

Figure 1. Typical electrode penetration through MT and MST. *A*, Lateral view of the posterior half of the right hemisphere. *B*, Horizontal section at the dorsoventral level indicated by the *straight line* in *A*. Electrodes advanced anteromedially on the horizontal plane with an angle of 30°–45° against the parasagittal plane. The extent of MT was determined histologically by the dense myelinated band in deep layers of the cortex. The *short lines* in *B* indicate the transition from heavy to light myelination, and the *vertical arrows* in *A* indicate the dorsoventral extent of MT. The area that anteriorly adjoined MT and had a mediolateral width of about 4 mm is referred to as *MST* in this study. *IOS*, Inferior occipital sulcus; *IPS*, intraparietal sulcus; *LF*, lateral fissure; *LS*, lunate sulcus; *STS*, superior temporal sulcus.

The x–y coordinates on the screen were translated to the azimuth (Ax) and elevation (Ay) of the spherical polar coordinate (vertical axis) system (Bishop et al., 1962) by the following formulae, where (x_0, y_0) represents the foot of a perpendicular line from the eye to the screen, and d represents the distance between the eye and screen:

$$Ax - Ax_0 = \arctan\left(\frac{x - x_0}{d}\right)$$

and

$$Ay - Ay_0 = \arctan\left(\frac{(y - y_0)\cos(Ax - Ax_0)}{d}\right)$$

Results

D cells in MT and MST

In both MT and the area that anteriorly adjoins it, the majority of cells responded to a straight unidirectional movement of patterns in the frontoparallel plane. Their responses were selective to the direction of motion: the response magnitude to the null direction (opposite to the best) was less than 10% of that to the best direction. These directionally selective cells respond-

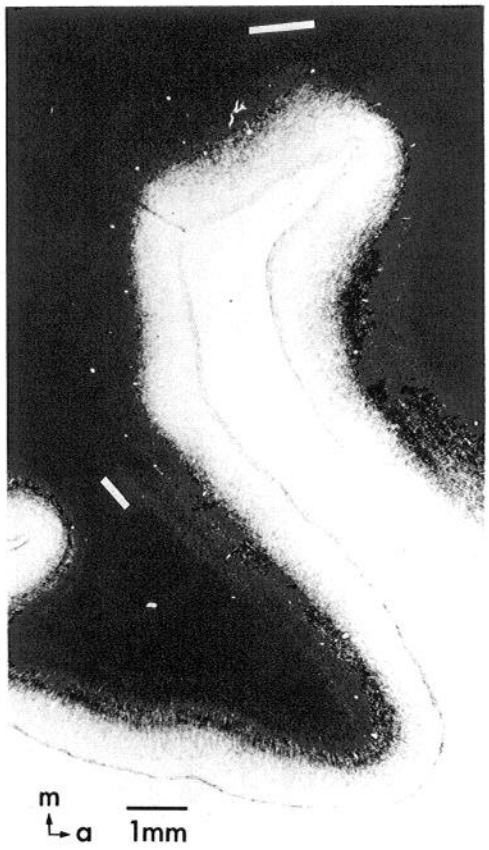

Figure 2. Horizontal section stained for myelin with Gallyas' silver stain. *White lines* indicate the medial and lateral borders of MT.

ing to straight frontoparallel movements will be referred to as D cells. The extent of MT was determined histologically (see Materials and Methods). D cells constituted 76% (350) of 463 cells located within MT. Most of them responded well to monocular stimuli through either eye. Disparity sensitivity of these cells was not examined systematically in this study. However, binocular stimulation with a particular range of disparity was required for activation of 22 D cells in MT. The other cell types encountered in MT are given in Table 1. In the area that anteriorly adjoined MT and had a mediolateral width of about 4 mm, D cells also constituted the largest population (285/519; 55%). More lateral to this area in the anterior bank of the STS, most cells were unresponsive to the visual stimuli used. The dorsoventral extent of the clustering of D cells in the anterior bank roughly coincided with that of MT in the posterior bank (see Fig. 12 of Saito et al., 1986). Based on the above geography, the area seems to correspond to a large part of MST that was defined by fiber projections from MT (Maunsell and Van Essen, 1983b). Hereafter, it will be referred to as MST. The other major cell types encountered in MST are S cells, which were excited only by size changes of patterns, and R cells, which were excited only by rotary movements of patterns (Table 1). Properties of these cells are described in the accompanying paper (Saito et al., 1986). Most of the D cells in MST responded well to either eye.

This paper concentrates on D cells in both areas. A marked difference between D cells in MT and those in MST existed in the size of their excitatory receptive fields. In Figure 3, the square root of the area of the excitatory field is plotted as a function of the eccentricity of the center of the excitatory field. The extent

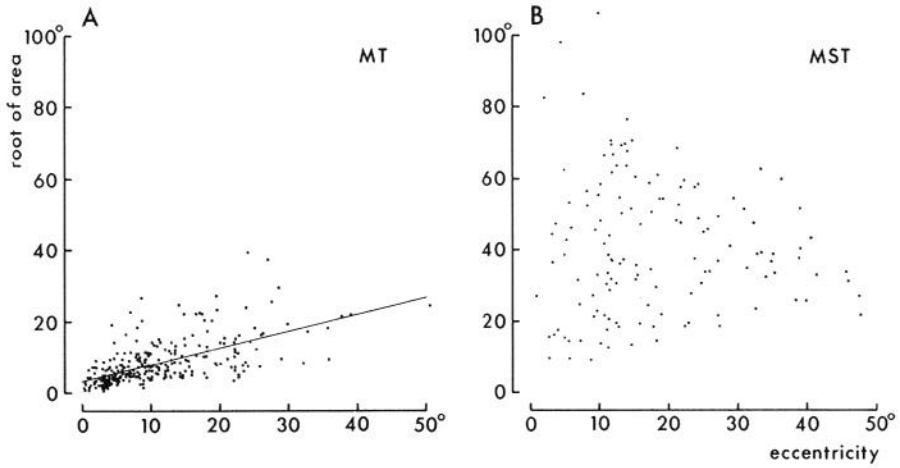

Figure 3. Receptive field size of D cells in two areas. *A*, For 289 *MT* cells, the square root of the area of the excitatory field is plotted against the eccentricity of its center. The field size increased with the eccentricity. The slope and *y*-intercept of the regression line are 0.47 and 0.33, respectively. *B*, For 141 *MST* cells, plotted as in *A*. The field size was large, irrespective of the eccentricity. The mean value is 41°.

Table 1. Types and populations of cells recorded in MT and MST

	MT	MST
D cell	350 (75.6)	285 (54.9)
Directionally biased cell	23 (5.0)	5 (1.0)
Bidirectional cell	27 (5.8)	6 (1.2)
Pandirectional cell	7 (1.5)	5 (1.0)
S cell[a]	10 (2.2)	70 (13.5)
R cell[b]	0	58 (11.2)
Dynamic disparity cell[c]	6 (1.3)	2 (0.4)
Other visually responsive cell[d]	2 (0.4)	15 (3.3)
Visually unresponsive cell[e]	38 (8.2)	73 (14.1)
Total	463	519

Figures indicate the number of cells in each response type and those in the parentheses indicate the percentage.

[a] Cells activated only by size changes of patterns.

[b] Cells activated only by rotary movements of patterns.

[c] Cells activated only by a combination of a left-directional movement in one eye and a right-directional movement in the other eye.

[d] Including ON-cells, OFF-cells, cells responding to jerky movements.

[e] Cells not activated by any visual stimuli used in the present study, and not activated by conventional auditory or tactile stimuli.

of the excitatory fields was determined as the "minimum response field" (Barlow et al., 1967): an oscillating object was shifted laterally from the center of the receptive field, and the border of the field was determined by the end position of the stimulus at which excitatory responses disappeared. Therefore, the field size of the cells that will require the stimulus summation over a large part of the excitatory field for activation may have been underestimated. In MT, the size of the excitatory field increased with eccentricity, in accordance with the previous study, which examined excitatory fields of multiunits in this area (Gattass and Gross, 1981). The linear regression line for 289 cells was

$$(\text{square root of area}) = 0.47 \times (\text{eccentricity}) + 0.33; \quad (\gamma = 0.62)$$

In MST, the average of the square root of the area for 141 cells

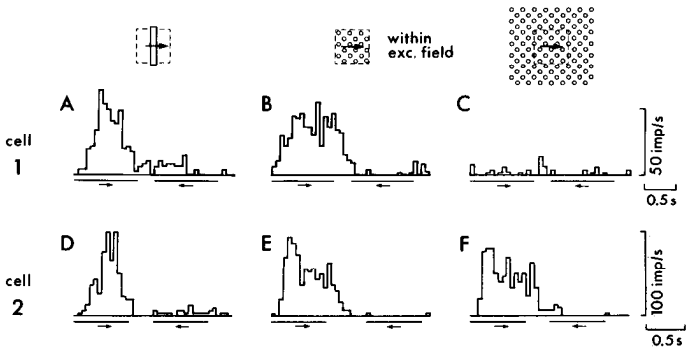

Figure 4. Responses of two MT cells to the movements of a bar and of a dotted pattern. The pattern moved in the optimal direction and speed during the period marked by the *left underline,* and moved in the reverse direction during the period marked by the *right underline. A–C, Cell 1* responded comparably well to a bar movement (*A*) and a dot-pattern movement confined within the excitatory field (*B*). However, it failed to respond to a dot-pattern movement that was extended over a 70° × 55° area (*C*). This indicates that the excitatory field was surrounded by an inhibitory field. Size of the excitatory field, 5.5° (along the axis of motion) × 6.5°; bar size, 1° × 6°; amplitude of movement, 10°. *D–F, Cell 2* responded well to all of the three kinds of moving stimuli. It had no inhibitory surround field. Field size, 6° × 9°; bar size, 1° × 7°; amplitude, 10°.

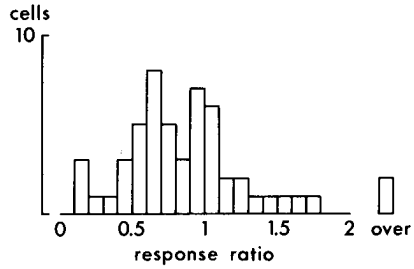

Figure 5. Comparison of response magnitude to movements of the two kinds of patterns confined within the excitatory field. The response magnitude was defined as the mean firing rate for the period during which the pattern moved over the excitatory field in the optimal direction, subtracted by the spontaneous firing level. The comparison was made for 53 MT cells by calculating the ratio, (response magnitude to a dot-pattern movement)/(response magnitude to a bar movement).

was 41°, and there was no simple correlation between size and eccentricity. In the central visual field, D cells in MST had much larger excitatory fields than those in MT. No retinotopical organization has been noticed in MST.

Responses of MT cells to dot patterns

Most of the MT cells responded equally well to the movement of a single bar and that of a regularly spaced, two-dimensional dot pattern if the stimuli were limited within the excitatory field. This is illustrated for two cells in Figure 4. The direction and speed of the movement were determined beforehand as optimal. In Figure 4, the pattern moved in the optimal direction during the period marked by the left underline, and in the opposite direction during the period marked by the right underline. The size of the bar was also optimized for each cell, but the diameter of the dot elements (0.7°) and the interval between them (2°) were not changed. Quantitative evaluation as to the effectiveness of these two kinds of stimuli was made for 53 MT cells by calculating the ratio of the magnitude of the response elicited by the dot-pattern movement to that elicited by the bar movement. The response magnitude was defined by the mean firing rate for the period during which the pattern moved over the

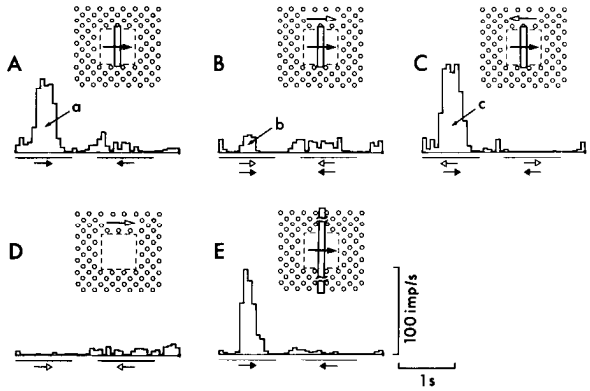

Figure 6. Properties of surround inhibition observed in a MT cell. *A,* Response to a bar movement with a dot pattern held stationary. *B, C,* Response to the bar movement was suppressed by 84% when the dot pattern moved in the same direction with the bar (*B*), but was facilitated by 35% when the dot pattern moved in the opposite direction (*C*). Therefore, the inhibition was directionally selective. *Filled arrows,* Direction of the bar movement; *open arrows,* direction of the dot-pattern movement. *D,* The dot-pattern movement by itself never evoked excitatory response. This was also true when the dot pattern moved while a bar remained stationary at the center of the excitatory field. *E,* Lengthening of the bar caused only slight suppression of response (−16%). Field size, 7.5° × 7.5°; bar size, 1° × 3°; amplitude of movement, 20°.

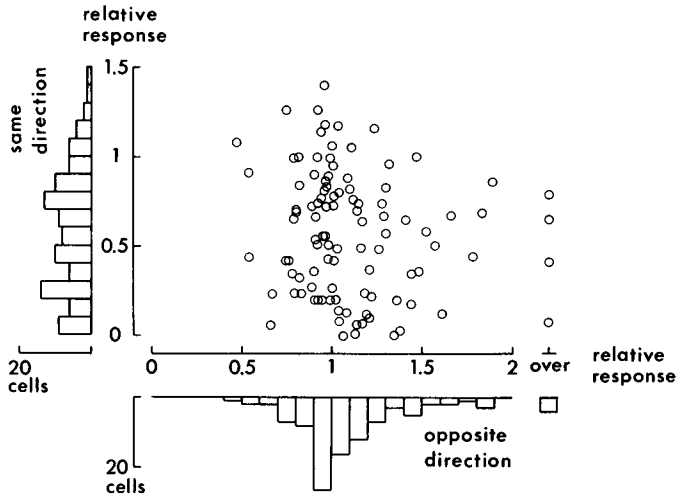

Figure 7. Strength of the surround effect for 105 MT cells. Distribution of the surround effect when the dot pattern moved in the same direction with the bar (*left histogram*), when the dot pattern moved in the opposite direction (*bottom histogram*), and scatter diagram between the effects in the two situations (plotted by *open circles*). The surround effect is quantified by the relative magnitude of the response to the combined movements of the bar and dot pattern with reference to bar movement response, with the dot pattern held stationary. The effect of the dot-pattern movement in the same direction is evenly distributed from complete suppression (0) to no effect (1). Cells with a ratio less than 0.5 are classified as SI^+-type; those with a larger ratio are classified as SI^--type. The effect of the dot-pattern movement in the opposite direction is distributed around 1 (no effect), except for 10% of the cells, which showed facilitation by more than 50%. Neither positive nor negative correlation was observed between effects for the two situations.

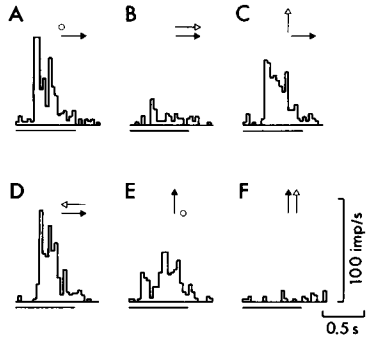

Figure 9. Surround inhibition of a directionally nonselective MT cell. This cell had a 6° × 7° excitatory field activated by movements in any direction. *A*, Response to a right-directional bar movement with a stationary dot pattern in the surround field. *B*, The response was suppressed by a right-directional movement of the dot pattern. *C, D*, Response was not changed by an upward or left-directional movement of the dot pattern. *E*, Response to an upward bar movement with the dot pattern held stationary. *F*, The response was suppressed by an upward (same as the direction of the bar movement) movement of the dot pattern. Bar size, 1.5° × 1.5°; amplitude of movement, 20°.

cell's excitatory field. Most cells (40/53) had a ratio between 0.5 and 1.5 (Fig. 5).

When the area of stimulation by the dot-pattern movement was increased far beyond the excitatory field (to 70° × 55°), some of the MT cells failed to respond to it, but the others continued to respond. Cells 1 and 2, illustrated in Figure 4, are typical examples (Fig. 4, *C* and *F*). It was thus indicated that the excitatory field of some MT cells was surrounded by an inhibitory field, while the other cells lacked such an inhibitory surround field.

Surround inhibition of MT cells

To examine the properties of surround inhibition, the excitatory center field and the inhibitory surround field were stimulated independently—the center with the optimal single bar and the surround with the wide dot pattern. The dot pattern was presented only outside the excitatory field because we wanted to observe the inhibitory effect of the surrounding area separately. Complex interactions might occur when the excitatory field was stimulated by both the bar and dot pattern at the same time. Typical results of the experiments are shown in Figure 6. Response to the central bar movement (Fig. 6*A*) was strongly suppressed when the dot pattern moved with the bar in the same direction and at the same speed (Fig. 6*B*). However, the response

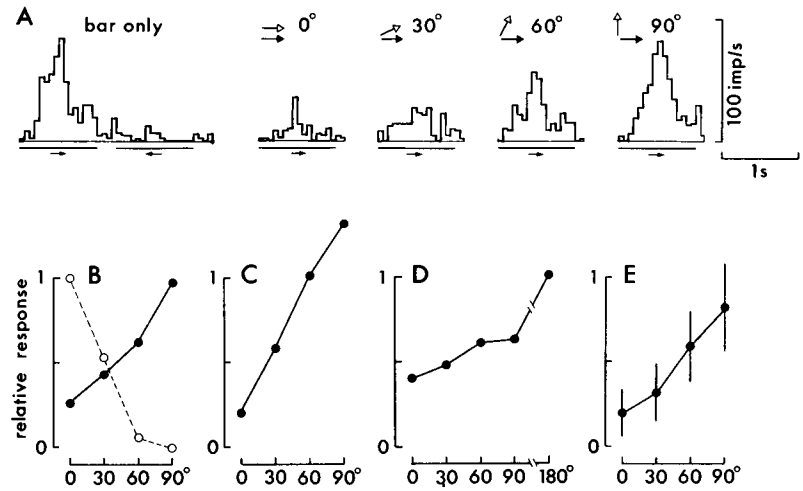

Figure 8. Directional tuning of the surround inhibition. *A and B*, Response of one MT cell to a bar movement with a dot pattern held stationary (*leftmost histogram* in row *A*) and to combined movements of the bar and dot pattern (*others in A*). The bar moved across the excitatory field in the optimal direction, while the direction of the movement of the dot pattern over the inhibitory surround field deviated by 0°, 30°, 60°, and 90°, respectively, from that of the bar movement. *Filled circles* in *B* plot the relative magnitude of the response to the conjoint movements with reference to the response to the bar movement. *Open circles connected by broken lines* show the directional tuning of the excitatory response of the same cell. Field size, 4° × 4.5°; bar size, 1° × 4°; amplitude of movement, 7.5°. *C–E*, Sharpest tuning curve (*C*), broadest one (*D*) and mean values (*E*) of the 20 MT cells tested. *Vertical bars in E*, Standard deviation.

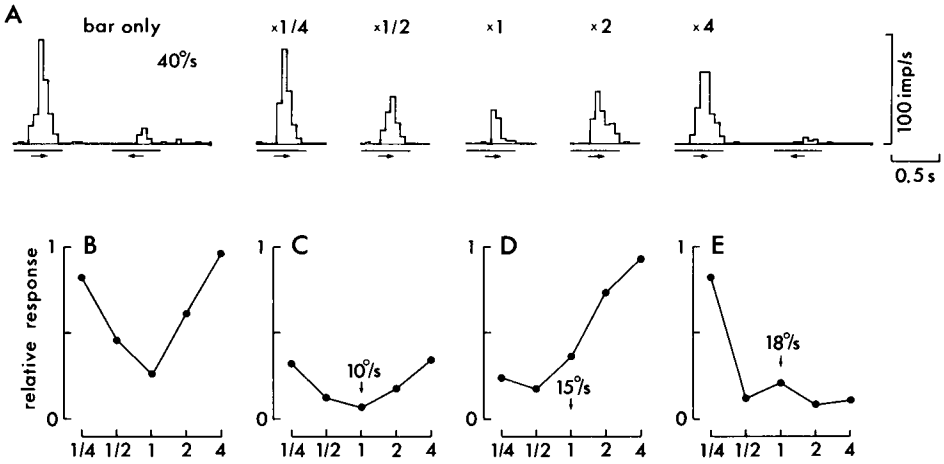

Figure 10. Speed-tuning of the surround inhibition. *A, B,* Responses of one MT cell to a bar movement with a dot pattern kept stationary (*leftmost histogram* in row *A*), and those to combined movements of the bar and dot pattern (*others in A*). The bar moved across the excitatory field in the optimal direction and speed, while the dot pattern moved over the surround field in the same direction as that of the bar movement, but at a speed of ¼, ½, 1, 2, and 4× as fast as that of the bar movement. The relative response magnitude to the combined movements with reference to the response to the bar movement is plotted in *B* against the relative speed of the dot-pattern movement. Field size, 9° × 11°; bar size, 1° × 11°; amplitude of movement, 20°. *C–E,* Tuning curves of other three MT cells.

was not influenced, or in some cells facilitated, when the dot pattern moved in the direction opposite to that of the bar movement (Fig. 6*C*). From this, it is evident that the surround inhibition is directionally selective. Because no excitatory response was elicited by the surround stimulation alone (Fig. 6*D*), the surround field can be called a "pure inhibitory field." When a cell had spontaneous activity, as in Figure 6, it was suppressed by a movement of the surround stimulus in the direction preferred by the excitatory field. In most cells, the reduction of the response magnitude caused by a lengthening of the bar was much less than that caused by a conjoint movement of the dot pattern (Fig. 6*E*). Therefore, the surround inhibition of MT cells is quite distinctive from the "hypercomplex" properties defined by Hubel and Wiesel (1965).

Effects of the surround stimulation were quantitatively evaluated for 105 MT cells by calculating the ratio of the magnitude of the response elicited by the combined center and surround movements to that elicited by the center movement with the stationary dot pattern in the surround. The response magnitude was given by the total number of impulses contained in the response above the spontaneous firing level. As shown in Figure 7, the value of the effect of the dot pattern's moving with the bar in the same direction (b/a in Fig. 6) was evenly distributed from complete suppression (0) to no effect (1). Suppression of more than 50% was seen in 40% of the cells. The effect of the dot pattern's moving in the opposite direction (c/a in Fig. 6) was distributed around 1 except for 10% of the cells. Facilitation of more than 50% was seen in the latter 10%. Figure 7 also shows that there is no correlation between the strengths of surround effects in the two combinations. The cells that showed strong inhibition when the dot pattern moved with the bar in the same direction did not necessarily show strong facilitation when the dot pattern moved in the opposite direction.

Next, we examined tuning properties of the surround inhibition to direction and speed by changing the direction or speed of the surround movement, while those of the center movement were fixed to the optimal parameters. When the direction of the surround movement was progressively shifted by 30° steps from that of the center bar movement, inhibitory effects of the surround stimulation decreased steadily. Typically, they were halved by a 60° deviation and lost by a 90° deviation. However, the shape of the tuning curve varied from cell to cell. A typical one is illustrated in Figure 8, *A* and *B*. Figure 8 also shows two extremes and the average of the 20 cells tested in *C, D,* and *E,* respectively. These tuning curves are, on average, a little broader than the directional tuning curves of excitatory responses (a 50% average reduction by 30°–45° deviation; e.g., see open circles in Fig. 8*B*).

As to the directional tuning of the inhibition, an interesting observation was made on an exceptional MT cell that nonselectively responded to any direction of movement. While the center bar movement was fixed in a particular direction, the inhibition from a conjoint surround movement was tuned around this direction: response to a right-directional bar movement, for example, was suppressed by a right-directional surround movement (Fig. 9*B*), but was not changed by an upward or left-directional surround movement (Fig. 9, *C* and *D*). However, response to an upward bar movement was, in turn, suppressed by the upward surround movement (Fig. 9*F*), which had produced no effect when combined with the right-directional bar movement (Fig. 9*C*). These findings indicate that the directional tuning of the inhibition was relative to the direction of the bar movement. This point has not been tested on other cells, since excitatory responses of a great majority of MT cells were sharply tuned to the direction of motion.

The surround inhibition of D cells was also tuned to the speed of movement, although with larger variations among individual cells than with directional tunings. Five of the 20 cells tested showed V-shaped tuning curves: the surround inhibition became less than half of the maximum on both sides in which the speed of the surround movement was increased to four times or decreased to a quarter of the center speed (as illustrated in Fig. 10, *A* and *B*). Inhibition was more than half of the maximum over the range of the surround speed tested (one-quarter to four times the center speed) for five other cells (Fig. 10*C*). The remaining 10 cells were released from inhibition at one of the high and low ends of the surround speed tested (Fig. 10, *D* and *E*). Since the speed of the center movement was not changed, the question of whether the speed-tuning is absolute or relative remains open.

Another important subject in reference to the surround inhibition of MT cells is the direction and extent of the distribution of the inhibitory field. To examine this point, we conducted a series of experiments in which the surround stimuli were presented to a limited part of the surround field. The strength of suppression was almost balanced between the cases where the dot pattern was confined to the half-field that extended along the axis of motion (Fig. 11*B*) and where the stimulation was confined to the complementary half, extending along the orthogonal axis (Fig. 11*C*). This was true for all 15 cells tested (Fig. 12*A*). We conclude that the inhibitory field is evenly distributed along the two axes.

The extent of the inhibitory field was roughly estimated for 16 MT cells that had a long axis of excitatory field, ranging from 4° to 12°. The response to the bar movement was still well suppressed, even when the dot pattern was presented outside a

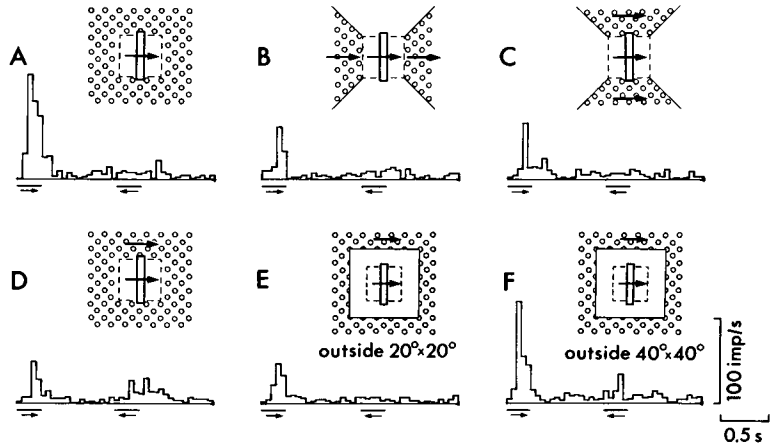

Figure 11. Isotropy and the extent of the inhibitory surround field. *A*, Response of one MT cell to the optimal bar movement. *B–F*, Responses of the same cell to combined movements of the bar and dot pattern. *B*, The moving dot pattern was presented to the half-field, which extended along the axis of the direction of motion; *C*, to the complementary half-field; *D*, to the whole surround field outside the excitatory field (6° × 8°); *E*, to the outside of a 20° × 20° area centered at the excitatory field; *F*, to the outside of a 40° × 40° area. In the control case (*D*), response was reduced by 70%. In both *B* and *C*, where mutually complementary half-field was masked, inhibition of a comparable strength was observed (both 65%). Inhibition was almost unchanged with the 20° × 20° shield (64%), but was decreased considerably by the 40° × 40° shield (to 29%).

20° × 20° area centered at the excitatory field (Fig. 11*E*), although inhibition was less prominent than in the control case, in which only the excitatory field was shielded from the dot pattern (Fig. 11*D*). However, suppression was negligible when a 40° × 40° area was shielded from the dot-pattern stimulation (Fig. 11*F*). The average strength of the surround inhibition on 14 cells tested was 62% of the maximum suppression in the case of a 20° × 20° shield and 23% in the case of a 40° × 40° shield (Fig. 12*B*). We thus conclude that the inhibitory effect is provided mainly by a field that surrounds the excitatory field and is several times as large as the excitatory field.

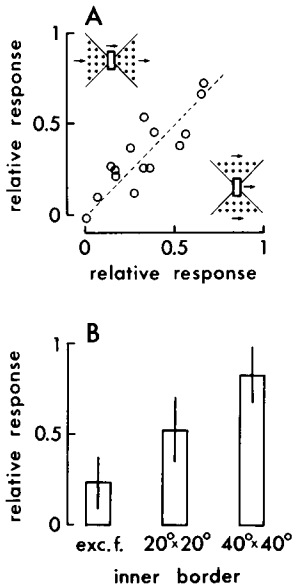

Figure 12. *A*, Scatter diagram of the relationship between the strength of inhibition exerted from the half-field extended along the direction of motion (*ordinate*) and that exerted from the complementary half-field (*abscissa*) for 15 MT cells. The strength of inhibition is given by the relative response magnitude to the combined movements with reference to the response to the bar movement. The *broken line* represents $y = x$. *B*, Mean strength of inhibition of 14 MT cells, with the standard deviation, when the moving dot pattern was presented to the area just outside of the excitatory field, to the outside of a 20° × 20° area, and to the outside of a 40° × 40° area, respectively.

The pattern selectivity of the inhibitory surround field was examined for several cells using random dot patterns and striped patterns as well as dot patterns of different spatial properties. Except for those which were exclusively composed of very small elements (for example, a dot pattern composed of 0.18° spots with 0.5° interval), all patterns tested gave rise to similar strengths of surround inhibition. The structure of the patterns does not seem to be crucial for the strength of the surround inhibition.

Distribution of SI⁺ and SI⁻ types

To facilitate further investigation and discussion, MT cells have been divided into two groups according to the strength of the surround inhibition. A line of demarcation between the two groups was arbitrarily drawn at 50% suppression (0.5 in the ordinate of Fig. 7). Cells showing more than 50% suppression will be referred to as SI⁺-type cells, and those showing less than 50% or no suppression will be referred to as SI⁻-type cells.

SI⁺- and SI⁻-type cells were recorded intermingled within MT. Consequently, the two types did not differ in the distribution of the eccentricity of the receptive field. No systematic difference was noted between them in the physiological properties of the excitatory field, such as the size, speed preference, and sharpness of the directional tuning. However, they seemed to differ in layer distribution. From the reading of the scale on the micromanipulator, we noticed a tendency for the proportion of SI⁺-type cells to be higher in the superficial quarter of the cortical depth (63%) than in the other part (34%).

Three types of D cells in MST

In view of the fact that D cells in MST have large excitatory fields, we first expected that they would prefer movement of a large field. However, this was not necessarily true. They were divided into three types. The first type of cell responded well to a single bar movement anywhere within its large excitatory field (Fig. 13*A*), but showed little excitatory response to a movement of a wide-field dot pattern (Fig. 13*B*). The response to the bar movement was suppressed when the background dot pattern moved together with the bar in the same direction (Fig. 13*C*), and the response was not suppressed when the two patterns moved in opposite directions (Fig. 13*D*). These cells will be referred to as "Figure type." Since they did not respond to the dot-pattern movement even when the stimulus did not extend beyond the excitatory field, the effective area for the inhibition

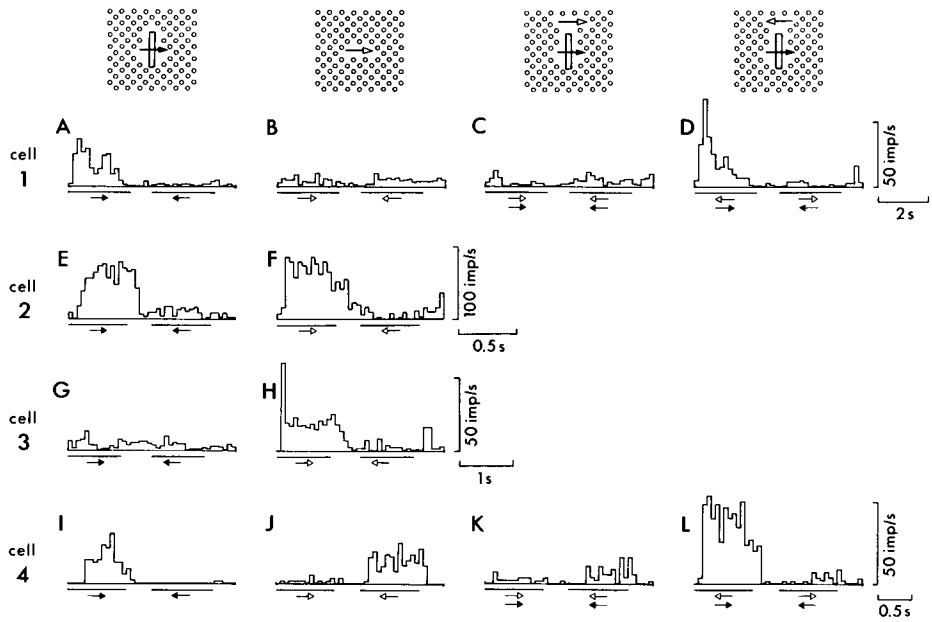

Figure 13. Responses of four D cells in MST to movements of a bar, of a wide-dot pattern, and combined movements of these two. *A–D, Cell 1* preferred a bar (*A*) to a dot-pattern movement (*B*). The response to the bar movement was suppressed when the dot pattern moved concurrently in the same direction (*C*), but was slightly facilitated when the dot pattern moved in the opposite direction (*D*). Stimulated area by the dot pattern was a 55° × 55° square, including the excitatory field. Field size, 45° × 39°, bar size, 3° × 10°, amplitude of movement, 40°. *E* and *F, Cell 2* responded equally well to a bar (*E*) and dot-pattern movements (*F*). Field size, 40° × 55°, bar size, 1° × 25°, amplitude, 20°. *G* and *H, Cell 3* preferred a dot-pattern movement (*H*) to a bar movement (*G*). Field size, 17° × 21°; bar size, 1° × 25°; amplitude, 20°. *I–L, Cell 4* responded equally well to bar (*I*) and dot-pattern (*J*) movements, but the preferred directions were opposite for the two stimuli. The responses were suppressed when the bar and dot pattern moved in the same direction (*K*), but were facilitated when they moved in the opposite direction (*L*). Field size, 19° × 25°; bar size, 1° × 3°; amplitude, 20°.

may coexist with the excitatory field. The inhibition of Figure-type cells is better referred to as "background inhibition."

The second type of cell responded equally well to a single bar movement and a wide-field movement (Fig. 13, *E* and *F*; Non-selective type), as did SI^--type MT cells. The third type of cell preferred a wide-field movement and hardly responded to a movement of a single object (Fig. 13, *G* and *H*). In these experiments, we took special care that the fringe of the dot pattern should not appear on the screen. The last group, which will be referred to as "Field type," is unique to MST: such cells were scarcely encountered in MT. Figure 14 quantifies this point by comparing the distribution of the ratio of the magnitude of the response elicited by a wide-field movement to that elicited by a single bar movement for 42 cells in MST (*A*) and for 130 cells in MT (*B*). Cells that showed a ratio larger than 1.5 constituted 26% in the former area (11/42), but only 5% in MT (6/130). For quantitative criteria of the classification, we tentatively draw the line of demarcation between Field and Nonselective types at 1.5, and between the latter and Figure types at 0.5. The 42 cells tested quantitatively were then divided into the three types with a proportion of about 2:3:2 (Field : Nonselective : Figure). As to the distribution of the eccentricity and size of the excitatory field, the three types of cells showed no systematic difference.

Nonselective-type cells preferred the same direction of motion for the movement of a bar and that of a wide dot pattern. However, there was an exception: one cell in MST responded well to both stimuli, but the preferred directions for the two stimuli were the opposite of each other (Fig. 13, *I* and *J*). The responses were suppressed when the two patterns moved in the same direction (Fig. 13*K*), and were prominently facilitated when they moved in their respective preferred and mutually opposing directions (Fig. 13*L*).

To examine the pattern selectivity of the D cells in MST, we replaced the wide-dot pattern by wide-striped patterns (half-period, 1°–4°). The wide-striped patterns were just as effective as the wide-dot pattern in suppressing Figure-type cells and in activating Field- and Nonselective-type cells. As for selectivity to spatial frequency components of patterns, the majority of Field- and Nonselective-type cells responded strongly to any of the dot patterns used (dot diameter, 0.7–4°), although a few cells showed a preference for patterns composed of large dots (2°–4° in diameter). Therefore, most D cells in MST do not have a clear preference for particular shape or spatial-frequency components of patterns.

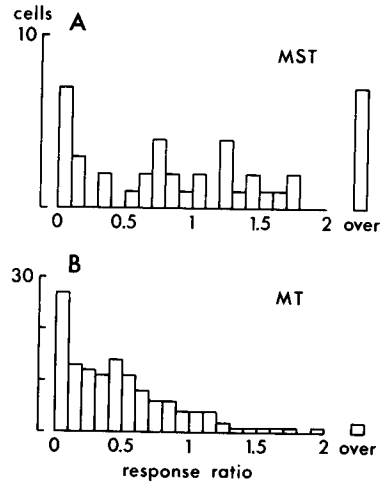

Figure 14. Comparison of response strength to a wide-dot-pattern movement and a bar movement. *A*, Distribution histogram for 42 D cells in MST of the ratio, (response magnitude to movement of a wide-dot pattern)/(response magnitude to movement of a single bar), where the response magnitude is given by the mean firing rate for the period during which the pattern moved over the excitatory field in the optimal direction, subtracted by the spontaneous firing level. *B*, Same histogram for 130 MT cells.

Discussion

The variety of responses to the two kinds of movements

The present study examined response properties of D cells in MT and the area that adjoins it anteriorly. The latter area, in which D cells are dominant, had a mediolateral width of about 4 mm and extended throughout the dorsoventral levels within which MT existed. Therefore, the area was assumed to correspond to a large part of MST (Maunsell and Van Essen, 1983b; Ungerleider et al., 1982; Yukie et al., unpublished observations).

Our main finding was that there was a great variety in the responses of D cells to the movements of a single bar and of a wide-field dot pattern. In MT, SI^+-type cells gave much larger responses to a bar movement than to a wide-field movement, and SI^--type cells responded nonselectively to both stimuli. In MST, Figure-type cells preferred movements of a single bar, Field-type preferred those of a wide-dot pattern, and Nonselective-type cells responded equally well to both stimuli. This variety seems to be a good tool for the discrimination of a local movement of an object relative to the background and of a conjoint movement of a wide visual field, as will be discussed later.

In MT. Since most MT cells were comparably activated by movements of a bar and a dot pattern when the stimuli were confined within the excitatory field, we believe that the magnitude of their responses to the movements of a wide-dot pattern was determined by the strength of the inhibitory field. Cells with strong inhibitory fields were named SI^+-type, while those with weak or no inhibitory field were called SI^--type. However, it should be noted that the distribution of the strength of inhibition was continuous and the borderline between the two types was determined arbitrarily for a heuristic purpose.

The inhibitory field of SI^+-type MT cells extends widely in all radial directions. This is different from the case of the end-stop inhibition of hypercomplex cells: the inhibitory field of hypercomplex cells in the visual cortex of the cat is concentrated in an expanded area along the axis of the preferred orientation (Hubel and Wiesel, 1965; Orban et al., 1979), and therefore it has been assumed that the inhibition is designed to detect a corner of an object, or to scale the length of the object. In MT, the strength of the surround inhibition was changed considerably by the direction and speed of the surround stimuli, while the structure of moving patterns was not crucial. On the basis of the above characteristics of the surround inhibition in MT, we think that it plays a major role in the comparison between movements within the excitatory field and those in the surrounding wide area.

Surround inhibition from outside the central discharge field has been found in several other visual areas (see the review by Allman et al., 1985). However, it seems that the features of inhibition are different in different areas. The strength of the surround inhibition in the macaque V4 area, for instance, depends on the color and spatial-frequency components of patterns in the surround field (Desimone et al., 1985; Schein et al., 1983; M. Tanaka et al., 1984; Zeki, 1980c). Directionally selective surround inhibition, similar to that of the macaque MT cells, was previously reported in the tectum of the pigeon (Frost, 1978; Frost and Nakayama, 1983), the Clare-Bishop area of the cat (Grünau and Frost, 1983), and the MT area of the owl monkey (Allman et al., 1986, in press). The latter two areas are often assumed to be analogous to the macaque MT, in the sense that most cells in these three prestriate areas respond to moving objects with directional selectivity (Baker et al., 1981; Hubel and Wiesel, 1969; Spear and Baumann, 1975; Zeki, 1980b). All these directionally selective cells respond to the movement of nonoriented patterns (spot or array of spots), as well as to that of oriented contours (Albright, 1984; Baker et al., 1981; Spear and Baumann, 1975). A sharp selectivity of the speed of motion has been also found in the macaque and owl monkey's MT (Felleman and Kaas, 1984; Maunsell and Van Essen, 1983b). Now it appears that the macaque MT, the owl monkey MT, and the cat's Clare-Bishop area share another common feature, i.e., the directionally selective surround inhibition. Results similar to ours have been obtained in the owl monkey MT with regard to the direction- and speed-tuning of the inhibition. However, there is a difference between the two areas in the population of cells that have no, or a weak, inhibitory surround field (SI^--type in our terminology). The owl monkey MT has fewer SI^--type cells.

One of the possible structural bases of the surround inhibition is the intrinsic connections within MT. A previous anatomical study showed that there are extensive connections between distant parts within the macaque MT (Maunsell and Van Essen, 1983b). Many SI^--type cells that have different field positions may converge and form inhibitory synapses on each SI^+-type cell. In this case, the preferred direction of motion of the SI^--type cells should be the same as that of the target cell. An alternative possibility is feedback inhibition from cells in MST, especially from Field-type cells. Convergence is not required in this case, since cells in MST have excitatory fields as extensive as the inhibitory fields of SI^+-type MT cells. The anatomical connections from MST to MT were revealed previously (Maunsell and Van Essen, 1983b; Yukie et al., 1983), although it is not known whether they are inhibitory or excitatory. Two other possibilities are that afferent cells to MT already possess directionally selective surround inhibition and that the convergence of afferent connections subserves the surround effect.

In MST. The excitatory fields of D cells in MST were much larger than those in MT. In addition, the variety of responses to local and wide-field movements was augmented in MST. Although Figure and Nonselective types resemble SI^+ and SI^- types in MT, respectively, the Field type is unique to this area.

What is the structural basis of the variety of D cells in MST? Since this area receives fiber projections from MT (Maunsell and Van Essen, 1983b; Ungerleider et al., 1982), we assume that receptive fields of cells in MST are constructed by the convergence of excitatory inputs from MT. A Figure-type cell may receive converging inputs from many SI^+-type cells that have excitatory fields with the same preferred direction of motion, but at various field positions. This is consistent with the fact that the effective area for the inhibition coexists with the excitatory field. A Field-type cell may receive converging inputs from SI^--type cells. A single moving bar simultaneously activates only part of the input, whereas a wide-field movement brings about a volley of inputs from a wide field. Therefore, Field-type cells respond to wide-field movement much more strongly than to the single bar movement. A cell of the Nonselective type may receive inputs from both SI^+- and SI^--type cells. These connections have not yet been directly found, but this is the simplest model that does not conflict with the previous anatomical results. To examine the connections directly, the cross-correlation technique, i.e., simultaneous recordings from two cells and analysis of their connectivity by cross-correlation of their impulse activities (K. Tanaka, 1983; Toyama et al., 1981) would be helpful.

Discrimination of a local movement of an object relative to the background

The utility of relative movements on the retina has been considered thoroughly in the field of psychology (for a review, see Nakayama, 1985). First, a movement of an object relative to the background is an essential cue for extracting the movement of the object in physical space. Even when an object is stationary in physical space, an animal's positional shift causes relative motion between the object and background, if the object is

located at a different depth from the background. Therefore, relative motion can have a second use, to gain awareness of the three-dimensional configuration of the environment. The third use, which is another aspect of the former two, is in perceiving the coherent entity of an object ("figure–ground discrimination").

SI$^+$-type MT cells have an excitatory response to the movement of an object within the excitatory field, and the response is suppressed when the surrounding field concurrently moves with the object in the same direction at the same speed. As the movement of the surrounding field deviates from the movement of the object in direction or speed, the strength of inhibition decreases and the excitatory response to the object's movement recovers. From these facts, one may be tempted to conclude that SI$^+$-type MT cells respond to a relative movement between the object and background. However, the following consideration of the two situations makes it clear that this is not true. When the background moves in the same direction as that of the bar movement, but more quickly, the movement of the bar in relation to the background is directly opposite to the movement of the bar on the retina (Fig. 15*C*). Therefore, if response magnitude had been determined by relative movement, the directional selectivity should have been reversed. There were no cells for which such a reversal was observed. Another fatal inconsistency is in the case where the bar stands stationary while the background moves in the opposite direction to that preferred by the excitatory field (Fig. 15*D*). Although the relative movement is directed to the optimal, no cells in MT yielded excitatory responses in this situation. Thus, we conclude that the response magnitude of SI$^+$-type MT cells does not express the vector of the relative movement directly. It seems that the direction- and speed-tuning of the excitatory responses of SI$^+$-type cells are primarily determined on the retinal basis by comparing the vector of the center movement with the cells' preference; then the scale of the response curve as a whole is adjusted by seeing the difference between center and surround movements (i.e., the size of the relative movement). What SI$^+$-type cells can do with relative movement is to point out the presence of a difference between center and surround movements and to analyze the center movement on the retinal basis.

Properties of the MT cell shown in Figure 9 should be discussed in relation to the detection of relative movements. While the background was stationary, the cell did not seem to be selective to the direction of motion: its responses were delivered to any direction of an object's movement. When examined with a moving background, however, the cell was selective to the direction of an object's movement relative to the background movement. These properties can be explained by converging excitatory input from many SI$^+$-type D cells that shared the same field position but preferred different directions of motion. It was previously reported that cells in the tectum of the pigeon had similar features (Frost and Nakayama, 1983). These cells could detect a difference between directions of center and surround movements regardless of the absolute direction of the center movement.

Figure-type cells in MST receive directionally selective inhibition from the background movement, as do SI$^+$-type MT cells. Since the excitatory fields of Figure-type cells are very large, and their responses are delivered to an object moving anywhere within the large excitatory field, they can detect a difference between the movements of an object and the background regardless of the exact position of the object.

The relative motion between a stationary slit and a moving background never elicited responses in Figure-type MST cells either. Only one cell in MST (cell 4 in Fig. 13) had an excitatory response in this situation. However, since we did not examine whether the reversal of the preferred direction occurred in this cell when the background moved faster than the bar in the same direction, we do not know how perfect the cell is in representing the vector of the relative movement.

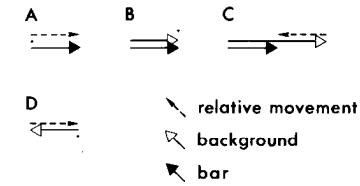

Figure 15. Movements illustrated in vector form. Vectors of bar movement on the retina (*filled arrows*), of background movement on the retina (*open arrows*), and of movement of the bar with reference to the background (*arrows with broken lines*). *A*, When the background is stationary. *B*, When the background moves with the bar in the same direction and at the same speed. *C*, When the background moves in the same direction, but at a speed twice as fast as that of the bar movement. *D*, When only the background moves, while a bar remains stationary.

Discrimination of a wide-field movement

Information about wide-field movement is important not only in ground perception, but for motor control as well (Lee and Aronson, 1974; Lee and Lishman, 1975; see also the review by Nakayama, 1985). In fact, one may experience great difficulty in performing some skilled body movements with the eyelids closed, although corollary signals of motor commands, proprioceptive signals of muscles, and vestibular input are also useful in perceiving one's own movement.

In MT, there are cells that respond to a conjoint movement of a wide field (SI$^-$-type cells). However, their responses are not specific to wide-field movements, for they respond to small moving objects as well. Only Field-type cells in MST can perform the selective analysis of a wide-field movement. They are insensitive to the movements of a single object unless the object is very large and has a clearly textured surface. As discussed above, it is plausible that many SI$^-$-type cells in MT converge to make Field-type cells in MST. If this is true, the variety in the strength of the surround inhibition allows the macaque MT to handle both local and wide-field movements in parallel. SI$^+$-type cells analyze the local movement of an object, whereas SI$^-$-type cells provide Field-type cells in MST with elementary information on wide-field movements.

The perception of the animal's own movement on the basis of retinal signals is never perfect. For example, in order to know whether the visual environment or oneself is moving, vestibular input or corollary signals of motor commands are indispensable. Such a convergence of retinal and nonretinal signals has been reported in the parietal association cortex (for a review, see Hyvärinen, 1982), to which MST sends fibers (Mesulam et al., 1977). In addition, it was briefly reported that some MST cells received signals of smooth-pursuit eye movements (Wurtz et al., 1984). How extensively the convergence occurs on the level of MST remains to be studied.

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