JOURNAL OF NEUROPHYSIOLOGY
Vol. 60, No. 2, August 1988. *Printed in U.S.A.*

Relation of Cortical Areas MT and MST to Pursuit Eye Movements. III. Interaction With Full-Field Visual Stimulation

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SUMMARY AND CONCLUSIONS

1. Pursuit eye movements are usually made against a visual background that is moved across the retina by the pursuit movement. We have investigated the effect of this visual stimulation on the response of pursuit cells that lie within the superior temporal sulcus (STS) of the monkey.

2. We assigned these pursuit cells to one of two groups depending on the nature of their preferred visual stimulus. One group of cells, comprising all cells located in the dorsal-medial region of the medial superior temporal area (MSTd) and some cells in lateral-anterior MST (MSTl), responded to the motion of a large patterned field but showed little or no response to small spots or slits. The other group, consisting of all foveal middle temporal area (MTf) cells and many MSTl cells, responded preferentially to small spot motion or equally well to small spot motion or large field.

3. For many pursuit cells that preferred large-field stimuli, the visual response showed a reversal of the preferred direction of motion as the size of the stimulus field increased. The reversal usually occurred as the size of the moving random-dot field used as a stimulus increased in size from 20 x 20° to 30 x 30° for motion at ~10°/s. The size of the field stimulus leading to reversal of preferred direction depended on the speed of stimulus motion. Higher speeds of motion required larger stimulus fields to produce a reversal of preferred direction. This reversal (of preferred direction) did not reflect a center-surround organization of the receptive field but seemed to reflect the spatial summation properties of these cells.

4. For three-quarters of the cells that preferred large-field stimulation, the preferred direction of motion for the large field was opposite to the preferred direction of the pursuit response. The remaining cells showed either the same preferred directions for large-field visual stimulation and the pursuit response or had bidirectional visual responses. If we consider only the cells that show a reversal of preferred direction for large- and small-field stimuli, the preferred direction for the large field was always the opposite to that of pursuit, and the preferred direction for the small field was always the same.

5. During pursuit against a lighted background, the cells that showed opposite preferred directions for large-field stimulation and pursuit had synergistic responses—a facilitation of the pursuit response over the response during pursuit in the dark. Slow pursuit speeds (<20°/s) produced the greatest facilitation. For those cells with the same preferred directions, some showed an increase in the response in the light compared with the dark, and some showed a decrease.

6. Those pursuit cells that preferred small spots of light showed no reversal of the preferred direction of visual motion with increasing stimulus size. The preferred direction for visual stimulation and for the pursuit response was always the same. The response during pursuit in the light was usually slightly weaker than pursuit in the dark.

7. Large-field stimulation often produced a slight optokinetic nystagmus with a drift of less than a few degrees per second even in the

presence of the fixation spot. The presence or absence of this nystagmus seemed to have minimal effect on the visual response of cells preferring large-field stimulation except for an interruption of discharge during the reset saccade. For cells that preferred small spots, however, the nystagmus generated by the large-field visual stimulation, in the direction opposite to the preferred direction to a spot, produced discharge because of the retinal slip of the fixation point in the receptive field. This response could be eliminated by stabilizing the fixation spot on the retina.

8. These experiments show that pursuit cells within the STS have different visual characteristics and can be regarded as serving different functions. Those pursuit cells that respond preferentially to small spots are appropriate for providing a signal required to maintain pursuit. Those cells that prefer large-field visual stimulation and that tend to show a synergistic effect between visual and pursuit-related responses, seem most appropriate for indicating the perceptual consequences of pursuit.

INTRODUCTION

We have identified the location of pursuit cells within the superior temporal sulcus (STS) of the monkey (12) and have shown that many of these cells have an extraretinal input (17). We also know that these pursuit cells, those that discharge during pursuit of a target moving in an otherwise dark room, almost all have a visual response. In this paper we investigate the visual characteristics of pursuit cells and determine how the pursuit and visual characteristics of the cells are interrelated.

We have already shown that cells in the dorsal-medial region of the medial superior temporal area (MSTd) and some in lateral-anterior MST (MSTl) are more sensitive to motion of large fields than to individual spots, whereas cells in the foveal region of the middle temporal area (MTf) and many in MSTl respond preferentially to small spot motion as opposed to large-field motion. Furthermore, an interaction of the response to a visual background and the response during pursuit has already been demonstrated by Sakata and his collaborators (21). In the present experiments we will show that the visual response of pursuit cells interacts with the pursuit response in systematic ways that are different for different groups of cells. We think that the combination of characteristics for these cell groups make it possible to refine hypotheses about their function. We will suggest that some interactions are appropriate for the maintenance of pursuit, others for indicating the perceptual consequences of pursuit, and that these functions may be related to separate anatomical areas.

A brief report of some of these results has appeared previously (11).

METHODS

The general methods we used for recording cells in these experiments were the same as those described in the previous reports (12, 17). Two added methodological points were the use of a large-field stimulus and analysis of cell discharge using spike density displays.

Large-field random-dot stimuli were generated by an IBM PC/XT microcomputer and then back projected onto a tangent screen using a TV projector (SONY). The largest stimulus field used was 80 × 66° (40° left and right, 40° up, and 26° down). The stimulus consisted of spatially separated small dots ($0.2\ cd/m^2$; 0.2° diam) on a dark background. Each dot moved linearly with the same speed and direction in an imaginary rectangular field, one with no visible boundary. This imaginary rectangular field was stationary on the visual field, and each dot, therefore, appeared at one side of the field and disappeared at the opposite boundary of the field. Parameters of the stimulus, such as direction, speed, number of dots, field size, and the location of the stimulus in the visual field could be changed independently from other parameters. The entire behavioral paradigm was controlled by a real-time experimental system (7) running on a PDP 11/34 computer, and the PC used for random-dot generation was under the control of this system.

When we used a large moving random-dot field (80 × 66°), we used a low-density field of 120 dots, $0.02\ dots/deg^2$. One of eight directions (0, 52, 90, 127, 180, 232, 270, 307°) was chosen as a direction of motion in each trial, and a fixed speed was usually used (9°/s for 0 and 180°, 11°/s for 90 and 270°, and 14°/s for other directions). After the preferred direction for large-field moving dots was determined, we tested the response to four smaller random-dot fields (9 × 11°, 20 × 20°, 30 × 30°, and 40 × 40°). The density of dots usually used was $0.4/deg^2$ for horizontal and vertical motion, $0.2/deg^2$ for other directions. The directions and speeds of the smaller dot fields were the same as for the large fields. Other variations in these parameters are explained with the results.

The discharge of cells on individual trials was represented by raster displays, but the average of these responses was represented by a spike density function rather than by a histogram as in the preceding two papers. The spike density is a smoother and less biased estimate of the probability of cell discharge than is the conventional histogram (18). The estimate is produced by replacing the millisecond wide square pulse that represents each spike with a Gaussian pulse. The pulse had a width corresponding to a standard deviation of 20 ms.

RESULTS

Three monkeys were used for a quantitative analysis of the visual response to small spots and random-dot stimuli, and the present report concentrates on 128 pursuit-related single cells recorded from these monkeys. As we described in the preceding papers (12, 17), these pursuit cells can be classified into two groups in terms of their pursuit and visual properties. One group of cells responded to the motion of large moving patterns but showed weak or no response to small spots or slits, frequently received an extraretinal input, and was located in MSTd (49 cells) and MSTl (31 cells). Another group of cells responded preferentially to small spot motion or responded equally well to both large-field and small spot motion or received an extraretinal input infrequently and was located in MTf (14 cells) and MSTl (34 cells). We have now found that the organization of the receptive fields of these two groups of cells also differs. In the following sections we will first describe the visual responses of the group of cells preferring large-field motion and then consider how this visual response interacts with pursuit eye movements. We will then do the same for the group of cells preferring motion of small spots.

Cells preferring large-field motion

Figure 1 shows an example of a cell that preferred random dots as a visual stimulus. Moving random dots (80 × 66°) were presented while the monkey fixated a stationary spot, and Fig. 1*A* shows a strong directional response to random dots moving upward and to the left, (Fig. 1*A, left*) but only a slight response in the opposite direction of motion (Fig. 1*A, right*). In the preferred direction (Fig. 1*A, left*), a strong phasic increase in discharge with a latency of ~100 ms was followed by a tonic discharge for the duration of stimulus presentation. When the stimulus was turned off, the discharge returned to the spontaneous level in ~200 ms. The phasic and tonic pattern of excitation in the preferred direction was the most common one observed, but in the null direction there was a marked difference of response patterns among cells as we will consider later (Fig. 16). In contrast, this cell responded poorly to spots of light moving in any direction across any area of the visual field. Figure 1*B* shows an example of the lack of response of the cell to a 0.6° spot moved obliquely across the center of the visual field in the same direction that was effective for the large-field stimulus. Although this lack of response to small moving spots was typical of these cells, a few cells did give a slight response to such moving spots.

INDEPENDENCE FROM OPTOKINETIC DRIFT. One of the problems with this comparison of large-field and small spot stimulation was the very different effect these stimuli have on oculomotor control. Even though the monkey was fixating on a small spot of light in these experiments, the motion of the large-field stimulus was so powerful that it frequently produced slight optokinetic nystagmus. This consisted of a slow drift in the direction of the large-field stimulus motion followed by a saccade in the opposite direction, presumably to bring the fovea back onto the fixation point. One possible explanation of the response of the cell to the large-field motion is that it results not from visual stimulation, but from the generation of the optokinetic response. Figure 2 illustrates vertical eye movements and the discharge of a cell preferring large-field stimulation moving upward and shows why we think the response of the cell is a visual one. In each of these trials (numbered 1–6) after the fixation point (FP) came on the monkey made a saccade to it, and then a large-field random-dot stimulus came on moving upward. On the first trial, for example, the large-field stimulation produced an upward drift of the eye of ~1.0° followed by a corrective saccade downward, and then further drift upward. Subsequently, there was minimal drift. The response of the cell, except for the pause after saccades, was similar dur-

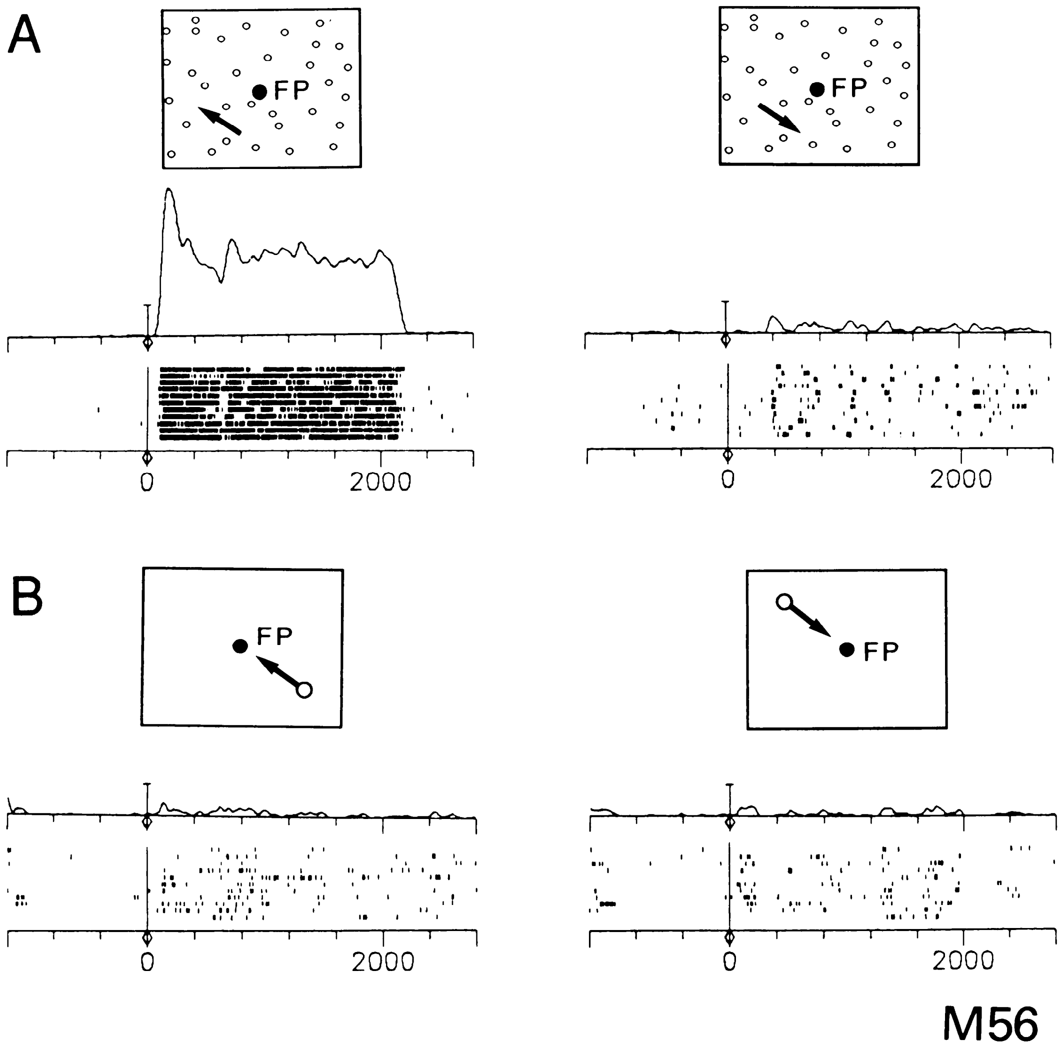

FIG. 1. Stimulation of a cell in the lateral-anterior region of the medial superior temporal area (MSTl) by moving random dots and small spots. The monkey looked at the fixation point (FP) during the period of stimulation, and direction of stimulus motion is indicated by the arrows. *A*: response was vigorous to motion of a field (80 × 66°) of random dots moving up and to the left at 14°/s, but the response was weak for motion of the same pattern moving downward and to the right. *B*: response was slight to a small 0.6° spot moving at 16°/s in the center of the visual field. The spot first appeared 20° away from the fixation spot and then moved toward it for 2 s. In this and subsequent figures, responses are shown as raster patterns described in a previous paper (12) and by spike density computed as described in METHODS. Both are aligned on stimulus onset. The numbers below the abscissa of each raster are time (ms) from stimulus onset. Presentation of random dots lasted 2 s. Vertical bar in each histogram is 50 spikes$\cdot$s$^{-1}\cdot$ trial^{-1}. Cell number is given in *bottom right* corner.

ing periods of both clear and minimal drift, indicating that such a small amount of drift during fixation was not necessary to produce the cell discharge. Instead, it is more likely that this increase in cell discharge is a response to visual stimulation.

REVERSAL OF PREFERRED DIRECTION. The most striking feature of many of these cells that preferred large-field stimulation was that the preferred direction of motion reversed as the size of the stimulus changed. Figure 3 shows an example of this reversal by showing the response of a cell to motion of progressively larger fields of random dots centered on the fixation spot (Fig. 3*A*). The *top* set of records in Fig. 3*B* shows that when a pattern

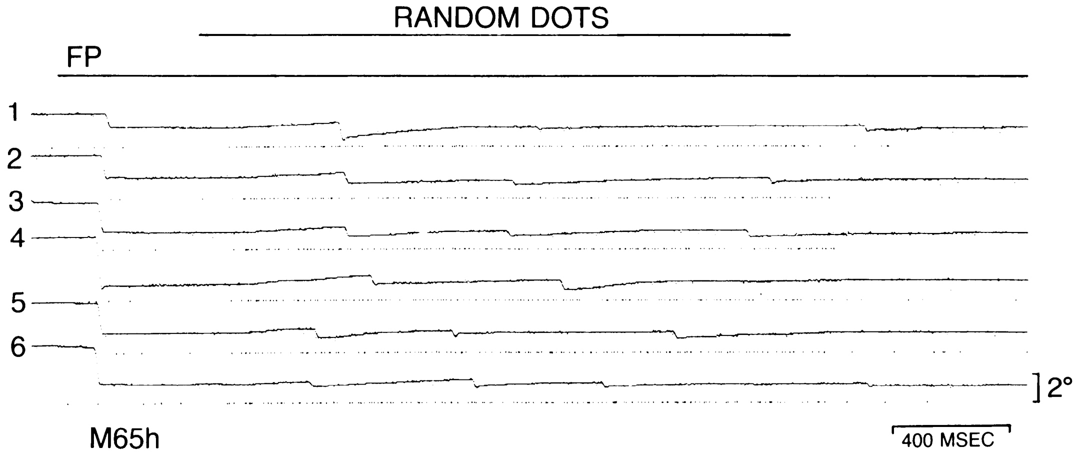

FIG. 2. Eye movement during fixation in the presence of large-field random-dot motion. After the fixation point (FP) came on, the monkey fixated, and then the large pattern came on (80 × 66° field of random dots) and moved upward at 11°/s. Six separate trials are shown. Calibration bar for the vertical eye movement was 2°. Cell discharge occurred with and without vertical drift of the eyes.

of random dots 10° on a side moved downward across the center of the visual field, the discharge rate of the cell increased. The response was directional, since upward movement reduced the discharge rate. For a stimulus 20° on a side, the response to downward motion still predominated, but there was also an increase in response for upward motion. For a 30° stimulus, the response in the two directions appeared to be about equal but with that to upward motion somewhat stronger. For larger fields, upward motion produced a larger response, until for the largest field (73°) the response was the reverse of that for a 10° stimulus—an increase in discharge rate for upward motion, a decrease for downward. Figure 3*C* shows quantification of the same visual responses shown in Fig. 3*B* and confirms that the reversal of direction occurs between field sizes of 20 and 30°. Another example of such a reversal is shown in Fig. 5.

We tested 30 cells (19 MSTl, 11 MSTd) using more than two different sizes of dot fields, and found such a reversal of the preferred direction in 20 (66%) of the cells (12 MSTl, 8 MSTd). In 12 of the 20 cells with the reversal, we determined the field size where the reversal occurred. Four cells reversed between 10 and 20°, five between 20 and 30°, one between 30 and 40°, and two with larger field sizes. The other 10 cells [34% (7 MSTl, 3 MSTd)] that preferred large-field stimulation showed no reversal of preferred direction with change in stimulus size. Of these cells, two did not respond at all to smaller fields of dots, and two became bidirectional with change in field size.

RECEPTIVE-FIELD ORGANIZATION. One type of receptive-field organization that might explain the reversal of preferred direction is a center-surround organization with opposite preferred directions in the two subregions. In this case, the reversal of direction seen in Fig. 3 would result from the increased size of the moving random-dot pattern invading areas of the peripheral visual field not stimulated by the smaller fields of dots. If this were the case, an adequately placed field of dots in the peripheral visual field should produce a response opposite to that of the same size in the center of the field. To test this possibility, we positioned small fields of moving random dots at several locations in the periphery of the visual field, and Fig. 4 shows the results obtained for the same cell shown in Fig. 3. The preferred direction was downward for a small dot field moving across the center of the visual field (Fig. 4, *stimulus 1*) but upward for motion of a large (40 × 40°) field centered on the fixation point (Fig. 4, *stimulus 6*). Stimulus loci 2–5 in Fig. 4 were at visual field locations away from the fixation point but still within the area of the large stimulus. These stimuli produced stronger responses for

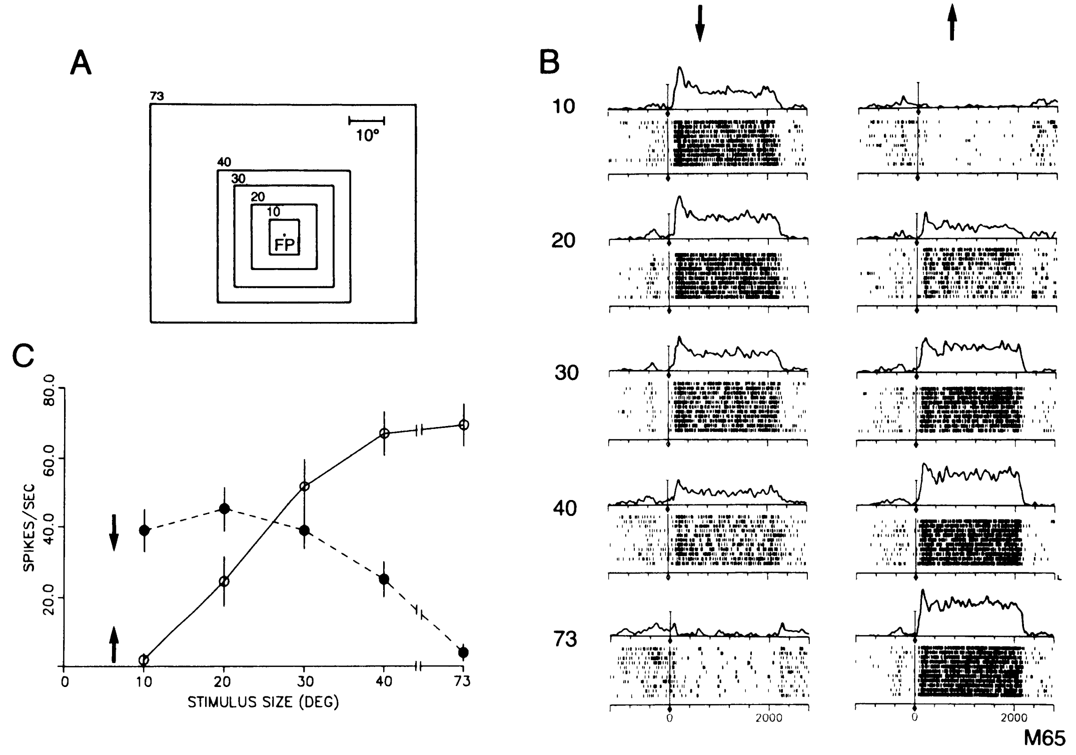

FIG. 3. Reversal of preferred direction of stimulus motion with increase in stimulus size. The receptive field of this cell in the lateral-anterior region of the medial superior temporal area (MSTl) extended over the entire screen (80 × 80°) with the strongest response in the center and progressively weaker responses toward the periphery. *A*: schematic illustration of the 5 sizes of random-dot fields used. The number above each rectangle indicates the square root of the area of the random-dot field (the 10° size was actually 9 × 11°; 73° was 80 × 66°). All sizes of fields were centered on the fixation point (FP) except the largest which stimulated an area 40° above but only 26° below the FP. *B*: responses to random-dot fields whose size is indicated on the *left* side of each row. The speed of the stimulus motion was 11°/s, and the direction was downward in the *left* column and upward in the *right* column. Responses are aligned on stimulus onset. *C*: graph of the relationship between size of dot field and magnitude of response. In this and subsequent figures where quantification of response magnitude to random-dot motion is shown, each point indicates the mean and standard deviation of the number of spikes per second calculated during a 1- to 1.5-s period after stimulus onset. The same time period was used to calculate the response magnitude for bar graphs. Directions of stimulus motion are indicated by arrows on the *left* side of each graph. This cell showed weak responses to small spots moving downward.

downward motion than for upward motion just as did the motion of the same size stimulus in the visual field center. This is not what would be expected from stimulation of a spatially separated center and surround that have opposite preferred directions. Instead, the response is dependent on spatial summation over the total area of the field stimulated, and the difference in spatial summation for the two directions is likely to be responsible for the reversal of the preferred directions with change in stimulus size.

As shown above, spatial summation was important for the reversal of the preferred direction. However, in the random-dot stimulus we used, the number of dots included in the stimuli was proportional to stimulus area because the density of dots was constant (for stimuli between 10 and 40°). This raised the possibility that an important factor for the reversal was actually not the area of moving random dots but the number of moving dots. This would happen if the spatial summation were independent of the distance between dots. If so, we would expect that with an increase in the number of dots in the small-field stimulus, the spatially summed effect would become strong enough to yield an observable response in the null direction of small stimulus motion. We tested this possibility in the

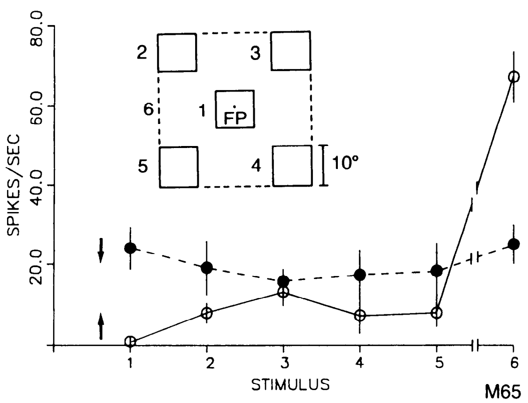

FIG. 4. Effect of motion of a random-dot pattern at different locations within the visual field. Same cell as in Fig. 3. In the *inset, squares 1–5* indicate the location and extent of a 9 × 11° field of random dots. *Square 1* is on the fixation point (FP), *squares 2–5* are 15° up/down and right/left from the FP. *Square 6* indicated by dashed lines is a 40 × 40° field centered on FP. The direction of stimulus motion is indicated by the arrows on the graph. The different positions of the small stimulus (*1–5*) did not lead to a reversal of the response, only the larger stimulus (*6*) did so.

same cell as in Fig. 4. We increased the density from 0.4 dots/deg^2 used in Fig. 4 to 6.4 dots/deg^2 while keeping the field size at 9 × 11°. The total number of dots in the latter stimulus was the same as that in a 40 × 40° stimulus with a density of 0.4 dots/deg^2. We observed no significant change for either direction of motion indicating that any spatial summation effect had already reached saturation with 0.4 dots/deg^2 for this area of the visual field. A low-density large-field stimulus was therefore much more efficient than a small dense field. We obtained the same results in three other cells tested under similar conditions.

The response to large-field stimuli was influenced by the speed of motion, and Fig. 5 shows an example of this interaction. In Fig. 5*A*, when the random-dot fields were moving at 14°/s, a reversal of preferred direction occurred for stimuli between 20 and 30° on a side as shown both by the response on the rasters and on the graph below. However, when the random dots were moved at 28°/s (Fig. 5*B*), only the largest stimulus (73°) led to a reversal. We have studied the size and speed interaction in only a few cells, but we obtained the same result; a larger stimulus field was required to produce the reversal at higher speeds of stimulus motion.

These results showed that pursuit cells preferring large-field visual stimulation generally had several visual properties in common. They were directionally selective, and the preferred direction often reversed as stimulus size increased. The reversal was not due to a simple center-surround organization, and the reversal occurred with smaller stimulus fields at lower speeds of stimulus motion.

DIRECTION OF VISUAL AND PURSUIT RESPONSES. Since most pursuit eye movements are made in the light against a contoured background, this background motion must have consequences for the response of these pursuit cells that preferred large-field stimulation. The first issue was the relation between the preferred direction of visual stimulation and the preferred direction of the pursuit response. To see if there was any relation between these two directional preferences, we took the direction of pursuit as the standard and compared the response to visual motion in that direction to the response to visual motion in the null pursuit direction. Our comparison was the ratio of the visual response to large-field stimulation during fixation for one direction of motion to the response in the opposite direction, with the first direction always being that of the preferred direction of pursuit. Figure 6 shows the results of 48 MST cells preferring large-field stimulation that were quantitatively analyzed. The abscissa in Fig. 6 shows this ratio obtained using the largest field of random dots. A value <1 on the abscissa means that the preferred direction of the visual response was opposite to that for the pursuit response. A value >1 means the visual and pursuit responses had the same preferred direction. A majority of the cells [37/48 (77%)] had ratios <1 indicating *opposite* preferred directions for visual stimulation and pursuit. This tendency to have the opposite preferred directions for large-field visual and pursuit-related discharge was true for both MSTd cells [20/27 (74%)] and MSTl cells [17/21 (80%)]. Therefore, a substantial majority of cells showed stronger responses to a large-field stimulus moving in the direction opposite to the preferred direction of the pursuit response. The remaining cells (23% in the en-

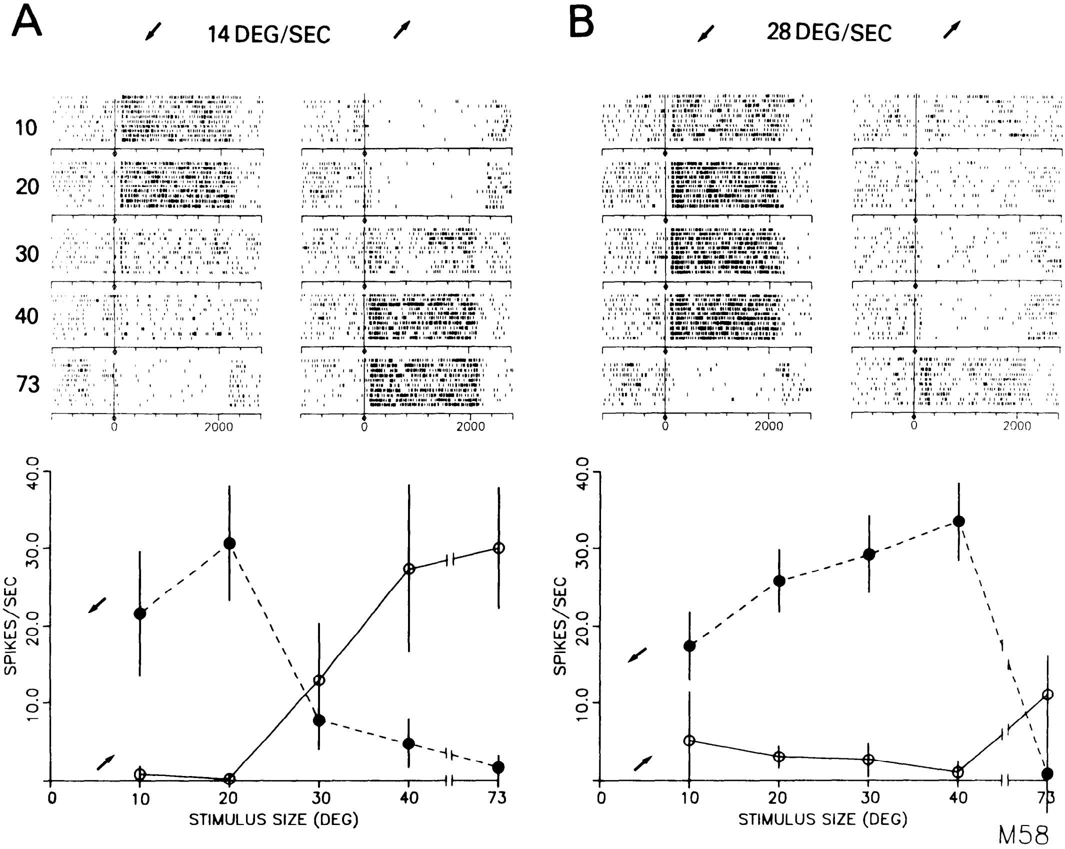

FIG. 5. Interaction of speed of motion and size of stimulus from MSTl cell. The effect of stimulus size (10–73° on a side) and stimulus speeds (*A*, 14°/s; *B*, 28°/s) is illustrated in the rasters (*top*) and graphs (*bottom*). For each speed of random-dot motion, the *left* column of rasters shows the responses to the random dots moving downward and to the *left* and opposite in the *right* column. The size of dot fields are indicated on the *left* side of each row of rasters. Reversal of preferred direction of motion occurred at smaller stimulus sizes at lower speeds of stimulus motion.

tire sample) showed a ratio >1 indicating the same preferred direction between the visual and the pursuit response.

This relationship between preferred directions of the visual and the pursuit response did not hold when the stimulus size was reduced, as would be expected knowing the reversal of the visual response seen in Fig. 3. Figure 7 compares preferred directions for visual motion and pursuit in a manner identical to that used in Fig. 6 but for four smaller sizes of random-dot fields (from *top* to *bottom*, 40, 30, 20, and 10° on a side). For the 40 or 30° fields, a majority of the cells tested [10/14 (71%) and 11/17 (65%), respectively] had preferred directions opposite that of the pursuit response as was the case in Fig. 6. In contrast, for a 20° field, only 7 out of 22 cells (32%) had opposite preferred directions, and in a 10° field, only 4 out of 28 cells (14%) had opposite preferred directions. The crossover between 30 and 20° was what would be expected knowing that the reversal of the preferred direction most frequently occurred between field stimuli of these sizes.

In net, there was a strong tendency for large-field stimuli to drive these cells when visual motion was in the direction opposite to the preferred direction of the pursuit response of the cell. In contrast, small fields of moving dots tend to drive these cells when they were moving in the preferred direction of pursuit. The cells that showed this effect most clearly were those that showed a reversal of preferred direction with increasing size of the moving dot field (the 20 cells, 12 MSTl and 8 MSTd,

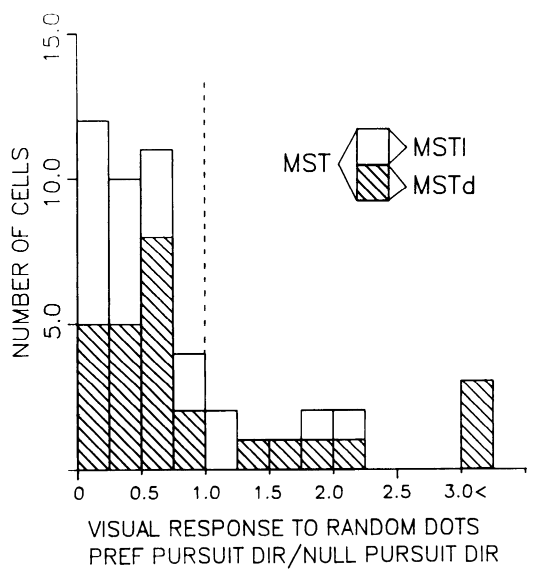

FIG. 6. Relative magnitude of response to large-field (80 × 66°) stimulus moving in the same direction of the preferred direction of pursuit compared with that moving in the opposite direction. The abscissa indicates the relative response magnitude between 2 directions, and the ordinate the number of cells. A value <1 on the abscissa means a stronger response in the direction opposite to that of pursuit, and a value >1, the same preferred direction. This reversed point (1) is indicated by the vertical dashed line. $n = 48$. MSTl, lateral-anterior region of medial superior temporal area; MSTd, dorsal-medial region of MST.

cited earlier). In all of the 20 cells, the preferred direction of motion for the smallest visual field tested was the same as that for pursuit, whereas the preferred direction of motion for the largest field tested was opposite to that of pursuit.

EFFECT OF VISUAL BACKGROUND ON PURSUIT. Since these pursuit cells respond to large-field motion, we can expect the visual response to background motion during pursuit to interact with the pursuit response. If a cell preferred a direction of visual motion opposite to the preferred direction of pursuit, the two responses should be synergistic, and the response in the light should be better than that in the dark. Figure 8*A*, shows an example of such a synergistic interaction. The preferred direction of the pursuit-related response in the dark (Fig. 8*A1*) was a movement down and to the right, while that for the visual response to field motion during fixation (Fig. 8*A3*) was upward and to the left. The two were combined during pursuit in the light (Fig. 8*A2*) to produce a facilitation of the response during pursuit downward and to the right. The graph to the *right* shows the quantified response to motion for each of these three test conditions.

We tested the visual pursuit interaction in the same way as shown in Fig. 8*A* for 39 MST cells (24 MSTd and 15 MSTl) that had opposite preferred directions of response to large-field visual motion and to pursuit, and Fig. 9*A* summarizes the results. Of these, ~85% (33 out of 39) of the cells showed stronger dis-

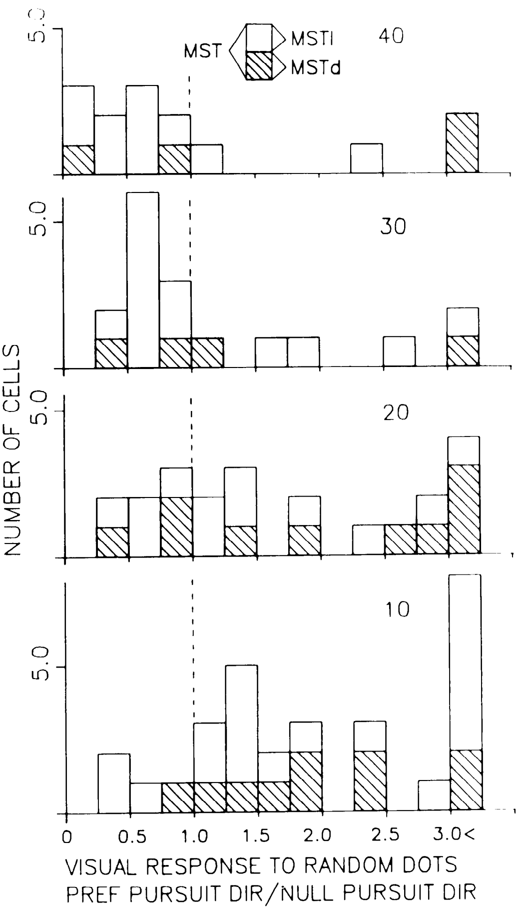

FIG. 7. Relative magnitude of responses to 4 different sizes of fields moving in the same and the opposite direction to the preferred direction of pursuit (as in Fig. 6). Numbers in *top right* corner of each graph indicate the length of 1 side of the random-dot field used. Dot fields were centered on the fixation point. Included in this figure are all cells in which the pursuit response and the response to 1 or more field sizes were tested. See Fig. 6 legend for definitions of abbreviations.

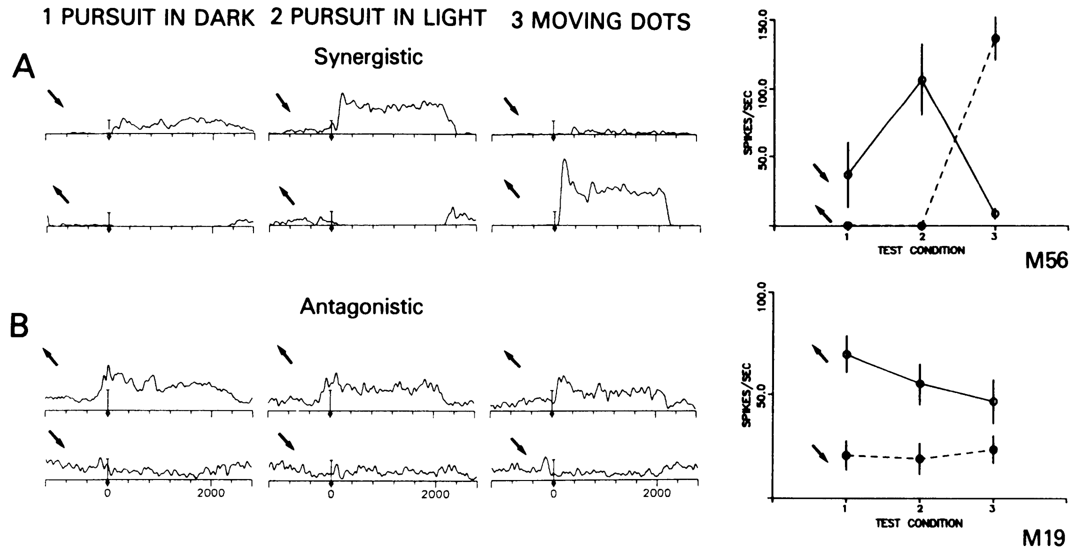

FIG. 8. Example of a synergistic (*A*) and antagonistic (*B*) effect of a lighted background on the pursuit-related response. *A* is an MSTl cell, and *B* is an MSTd cell. Spike density curves in *1* and *2* are for pursuit aligned on the end of the saccade made to acquire the target. Spike density curves in *3* are aligned on the onset of a moving field of random dots (80 × 66°, 14°/s) while the monkey fixated. Direction of pursuit (16°/s) and random-dot motion is indicated by the arrows. Magnitude of response in these 3 conditions are summarized in the graph on the *right*. Each test condition (*1*, *2*, or *3*) is a point on the abscissa. In this and subsequent figures where quantification of pursuit response is shown, each point indicates the mean and standard deviation of the number of spikes per second calculated during a 0.6–1.1 s after a saccade to the pursuit target, unless otherwise noted. The same time period was used to calculate the response magnitude for bar graphs.

charge during pursuit in diffuse light than in the dark, and even the remaining cells (6 of 39) were close to giving the same response in the light and the dark. This basic tendency was the same in MSTd and MSTl. We also found, however, that MSTd cells tended to show a greater facilitation of discharge in the light compared with MSTl cells.

There were also cells that did not show a response during pursuit in the dark (nonpursuit cells) but showed a clear response during pursuit in a diffusely lighted background. These cells were concentrated in MSTd and intermingled with cells that had pursuit-related response. Fourteen of such cells were examined. Twelve responded to moving large-field stimuli, and all of them had opposite preferred directions between pursuit in the light and large-field motion during fixation. Thus even cells in MSTd that did not show a pursuit response responded during pursuit in the light due to visual stimulation from the background.

Other cells in MST had preferred directions for visual stimulation and pursuit that were the same, and Fig. 8*B* shows an example of one of these cells. There was a response with pursuit to the upper left in the dark (Fig. 8*B1*), with motion of the random-dot field in the same direction during fixation (Fig. 8*B3*), and with pursuit to the upper left in the light (Fig. 8*B2*). As expected from the slight inhibition in response with the downward motion of the field stimulus (Fig. 8*B3*), the discharge during pursuit in the light was slightly weaker than in the dark. This weak interaction was seen in other cells that had the same preferred direction to a moving visual field and pursuit in the dark (Fig. 9*B*), but no clear tendency was observed.

Given the relation between speed of motion and the strength of the visual response shown in Fig. 5, we would also expect that the effect of the background during pursuit should be larger at lower pursuit speeds. We tested this by comparing the effect of target speed on the pursuit response in two different background conditions; one in total darkness and the other in the presence of a large stationary random-dot pattern. Figure 10*A*

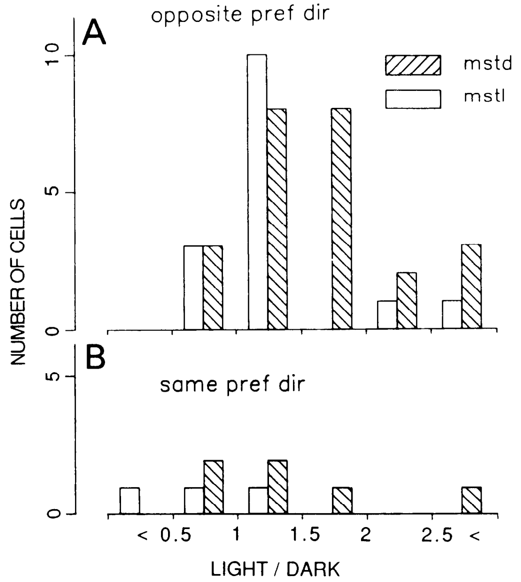

FIG. 9. Summary of the effect of a lighted background on pursuit responses. Abscissa is the ratio of the response during pursuit in the light to that in the dark. A number >1 indicates facilitation of responses during pursuit in a lighted background compared with that in the dark. *A*: cells whose preferred directions to large dot field (80 × 66°) motion and pursuit were the opposite. A facilitation of response (values >1) was evident particularly for MSTd cells, *n* = 39. *B*: cells with the same preferred directions of visual stimulation and pursuit. Interaction was varied but generally weak, *n* = 9.

shows the discharge during pursuit at different speeds in the light (solid line) compared with that in the dark (dashed line). With a dark background, a gradual increase in discharge occurred as pursuit speed increased from 1°/s to 32°/s then saturated. Against a stationary random-dot background, a comparatively stronger pursuit response developed even at low pursuit speeds (1°/s), reaching a peak at ~16°/s. Figure 10*B* shows the difference of response in the light and dark and emphasizes the facilitation of the pursuit response in the light at the lower speeds.

We have tested this speed-related facilitation of response during pursuit on a lighted background on only a few cells, but the response was consistently larger at lower pursuit speeds. These results are consistent with the results obtained when speed of random-dot motion and size of the field were changed when the monkey was fixating (Fig. 5). The results from both experiments (Fig. 5 and Fig. 10) indicate a high sensitivity to large moving backgrounds with speeds at least as low as 1°/s and relatively low sensitivity to background motion greater than ~20°/s.

In summary, for many MST cells that respond preferentially to large-field visual stimulation, we find that there is a substantial facilitation of the pursuit-related response by visual stimulation during pursuit when the preferred direction of stimulus motion and pursuit are the opposite. The facilitation is greatest in certain MST cells (MSTd), with large visual field stimuli (>30° judging by the reversal point), and slow pursuit speeds (<20°/s). In contrast, when the preferred direction of stimulus motion and pursuit are the same, interaction between the pursuit-related response and the visual stimulation

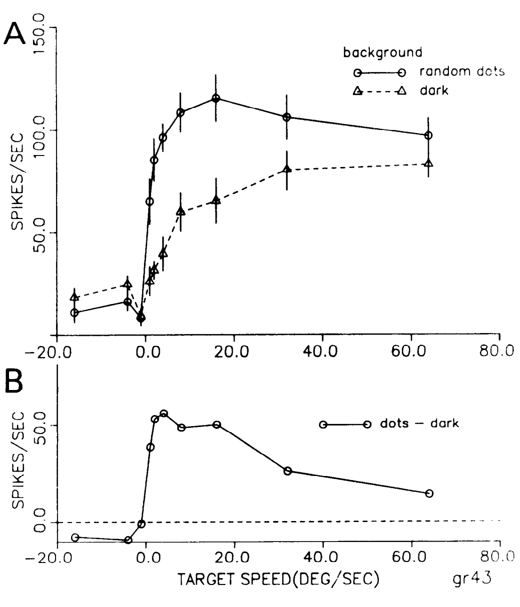

FIG. 10. Effects of target speed on discharge during pursuit eye movement under different background conditions. *A*: responses of an MSTl cell with pursuit of target in the dark are shown by triangles connected by dashed lines, those with pursuit across stationary random-dot fields (80 × 66°) are shown by circles connected by solid lines. The response magnitude for this figure was obtained from the number of spikes during 0.1–0.6 s after a saccade to the pursuit target. Abscissa indicates the target speed toward the left, preferred direction; negative values are for target motion to the right. *B*: difference in the response for the 2 conditions shown in *A* (dots-dark). The facilitation of the pursuit-related response was greatest at speeds <20°/s. Also shown is a weak inhibitory effect observed at 4°/s and 16°/s for pursuit in the opposite direction.

show no clear tendency; some have an increase in the pursuit-related response in the light, and some, a decrease.

Cells preferring small spot motion

The second type of cells we studied were those that preferred moving spots of light to random-dot patterns. We found these cells in both MSTl and MTf, and Fig. 11 shows an example of this type of cell. The cell showed a clear response when spots moved downward through the receptive field of the cell in the upper visual field (Fig. 11*A*, *left*), whereas when the spot moved upward in the same part of the visual field, no response was evident (Fig. 11*A*, *right*). This cell also responded to moving random dots (Fig. 11*B*) but never as strongly as to a spot. When a large random-dot field moved downward, phasic excitation was followed by tonic excitation, but with upward motion phasic excitation was followed by very slight tonic inhibition.

RECEPTIVE-FIELD ORGANIZATION. Of 24 of these cells preferring small spot stimuli, for which we have quantitative data, 20 cells responded somewhat to the motion of a large random-dot stimulus (as in Fig. 11) and all

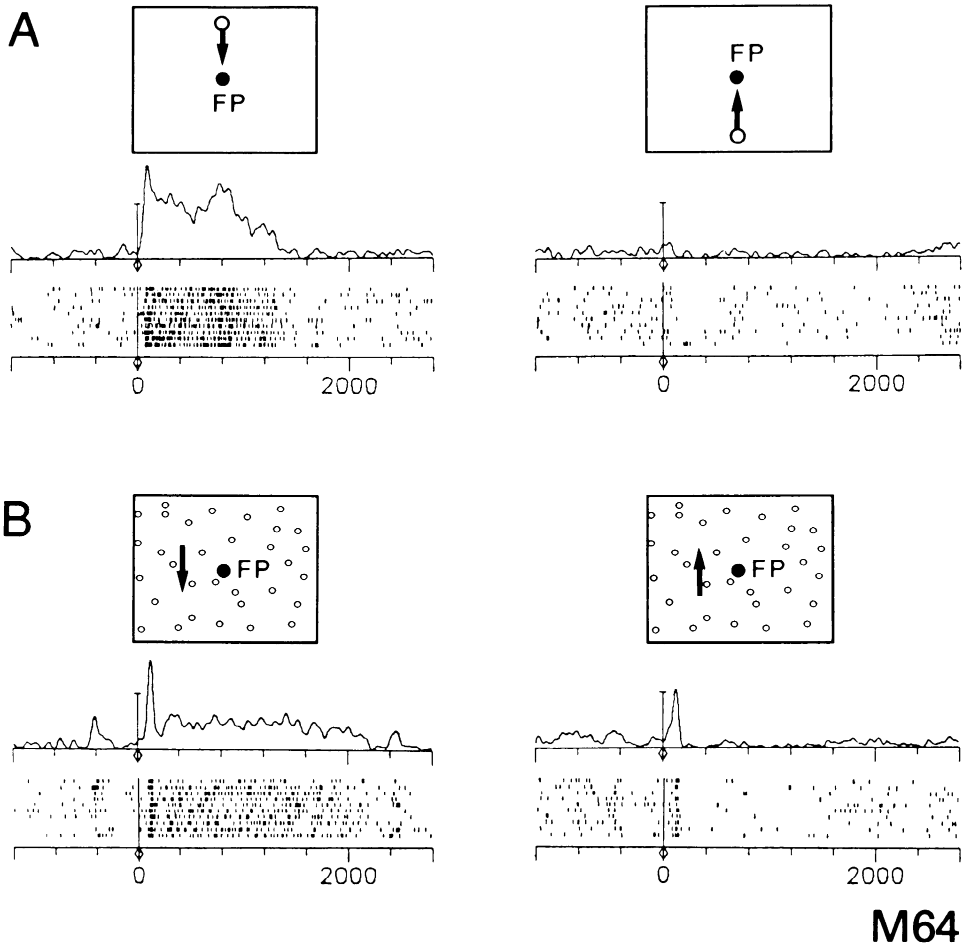

FIG. 11. Response of a cell that preferred small spots to random-dot fields as a visual stimulus. The receptive field of this MSTl cell covered the entire upper half of the screen when mapped using small spots of light with a weak fringe extending into the lower visual field. *A*: responses to a small spot moving in the center of the visual field (0.6° diam). Direction is downward in the *left* figure and upward in the *right* figure. The spot first appeared 20° up or down from fixation point (FP), then moved downward or upward at 16°/s for 2 s. *B*: less vigorous response of the same cell to moving random dots (80 × 66°, 11°/s).

were directionally selective. Figure 12 shows an example of the analysis of the organization of the receptive field for the same cell as in Fig. 11. For every size stimulus used (Fig. 12*A*), the preferred direction was always downward, and the response magnitude did not vary substantially as indicated by the graph.

Figure 12*B* shows the response of the same cell when a 9 × 11° field of random dots was presented in different locations in the visual field. When the dot field was placed in the upper portion of the cell's receptive field (*locations 1–3*), the cell responded to downward but not upward motion at all three points. With motion of the dots in a fringe area of the receptive field in the lower visual field (*locations 4* and *5*), only very weak responses were observed. All these responses are what would be expected from a receptive field with no ap-

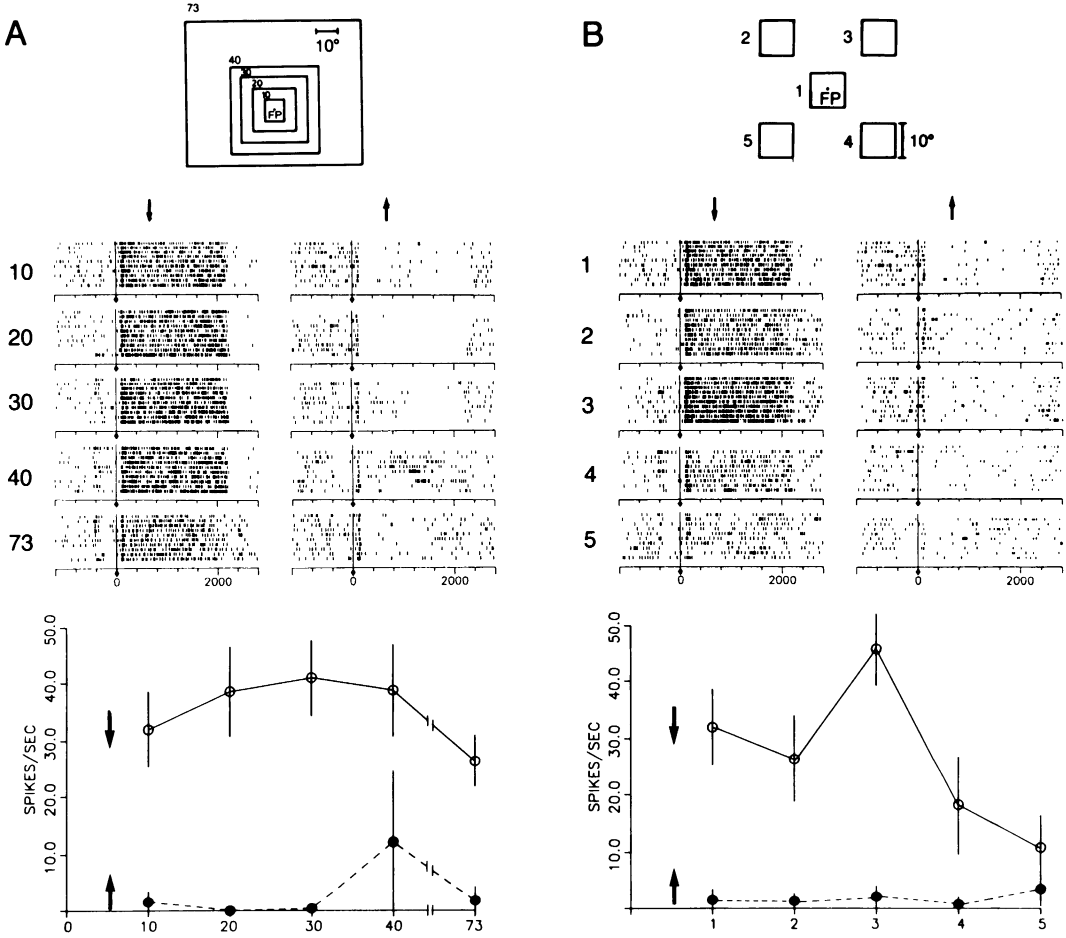

FIG. 12. Organization of receptive fields of a cell that responded preferentially to small spots. Same cell as in Fig. 11. *A*: effect of field sizes of random-dot stimuli. *Top*: schematic illustration of various sizes of random-dot fields used. *Middle*: raster display of responses to random-dot fields whose sizes are indicated on the *left* side. Direction of stimulus motion is indicated by arrows. Responses are aligned on stimulus onset. *Bottom*: graph of the relationship between dot field size and magnitude of response. *B*: response of the same cell as that shown in *A* when a small field of moving random dots (9 × 11°) was presented in 1 of the 5 locations indicated in the drawing at the *top*. Response is shown by rasters in the *middle* and by the graph at the *bottom*. The cell showed no reversal of preferred direction of stimulus motion with increasing size of the stimulus field, and no structure within the field that would suggest such a reversal.

parent center-surround or apparent spatial summation. This organization is clearly different from the cells that preferred large-field stimulation. Of the 20 cells that responded somewhat to large-field motion, six had the same preferred direction for moving spots and large random-dot patterns (as in Fig. 12). The remaining 14 cells appeared to have opposite preferred directions for these stimuli.

REVERSAL OF DIRECTION AND OPTOKINETIC DRIFT. We think the reversal in these 14 cells was, however, a consequence of the weak optokinetic nystagmus illustrated in Fig. 2 and does not reflect the receptive-field organization of the cell. Figure 13 shows an example of the visual response and the results of our analysis for one of these cells. This cell showed a leftward directional preference for small spots moving to the left. The receptive field plotted using the motion of small spots included the fovea and was restricted to within 3° from the center of the visual field. When a small-to-medium field of dots (10 to 40° on a side) moved across the center of the visual field (Fig. 13*A*), this cell continued to show a stronger response to leftward motion. However when motion was over a larger area (80 x 66°) this cell showed a reversal of the preferred direction and gave a stronger response with rightward motion of the dots. This looks similar to the reversal of the preferred direction observed in the pursuit cells that responded preferentially to random dots (Fig. 3).

However, we think the source of the reversal was the weak nystagmus occurring during fixation. The eye tended to move with a low velocity (<3°/s) in the direction of the motion of the field stimulus, and this eye movement could produce a retinal slip of the stationary fixation spot during this nystagmus. This slip could cause a discharge because these cells had receptive fields that included the fovea, preferred small well-localized visual stimuli like the fixation spot, and responded to the motion of such a spot. In addition, for these cells, the direction of the moving field stimulus that produced adequate retinal slip was opposite to the preferred direction for motion of the small spot. To test this possibility, we reduced the motion of the fixation spot by stabilizing it on the retina during the presentation of the random-dot stimulus, and Fig.

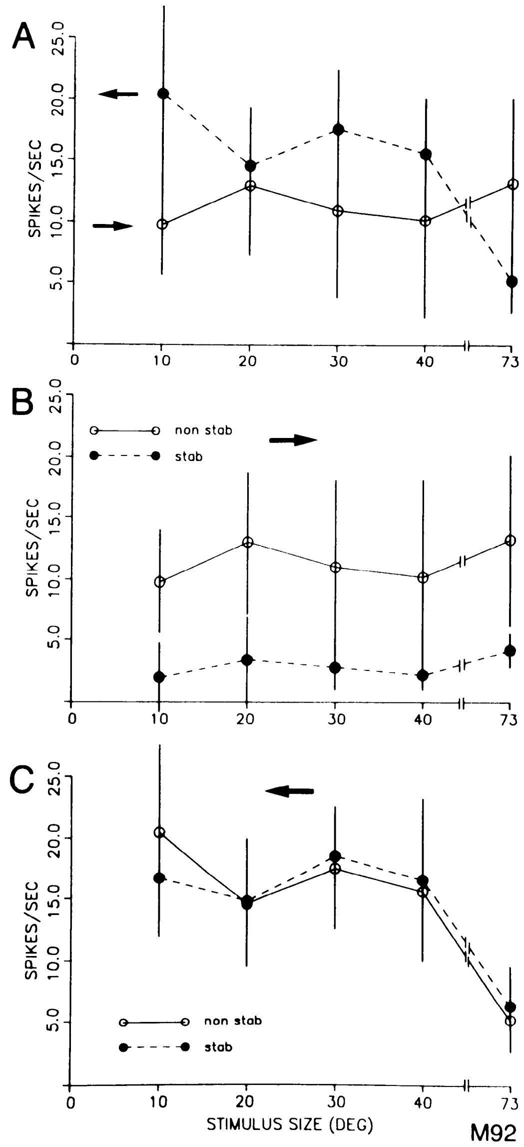

FIG. 13. Reversal of preferred stimulus direction eliminated by stabilization (STAB) of the fixation spot on the retina during presentation of moving random dots. This MSTl cell preferred small spots as a visual stimulus and showed a reversal of preferred direction when the area of the random-dot field was increased. *A*: graph of the relationship between field size and magnitude of responses. *B*: effects of stabilization of the fixation spot when the dots were moving to the right in the null direction for the visual response to spots. Graphs for the response of various sizes of dot fields during stabilization (●) and nonstabilization (○) are shown. Each circle represents the mean number of spikes per second for the period of 100–600 ms after the start of stabilization or at the same time in the case of nonstabilization. *C*: effects of stabilization of fixation spot when the dots are moving to the left, in the preferred direction for motion of spots. Stabilization did not affect the response.

13, *B* and *C*, show the results of such stabilization. Stabilization produced a clear decrease in the response to the dot field moving rightward (Fig. 13*B*) in the null direction for small spots, indicating that the response for this direction of motion was likely to result from motion of the fixation point. No clear change was evident in the response to dots moving leftward (Fig. 13*C*), in the preferred direction for small spots, indicating that this response was due to the visual motion stimulation by the random-dot field itself. We conclude that the reversal of preferred direction for these cells preferring small spots is not a property of the visual receptive field but results from the retinal slip of fixation-point spot caused by nystagmus. This slip of the fixation point is unlikely to be a factor for cells that preferred large-field stimuli, since they are frequently insensitive to motion of small spots such as the fixation point.

The effect of removal of retinal slip by stabilization of the fixation spot is summarized for 33 MSTl and MTf cells in Fig. 14. Stabilization was done during presentation of a large field of random dots (80 × 66°) moving in the preferred direction. The ratio of the responses during stabilization and nonstabilization was close to one for cells that preferred random dots (>0.8 in 14/18 cells), indicating that retinal slip of the fixation point had little effect. The ratio was small for cells that preferred small spots (<0.8 in 11/15 cells), indicating that retinal slip of the fixation point did contribute strongly to the response of these cells.

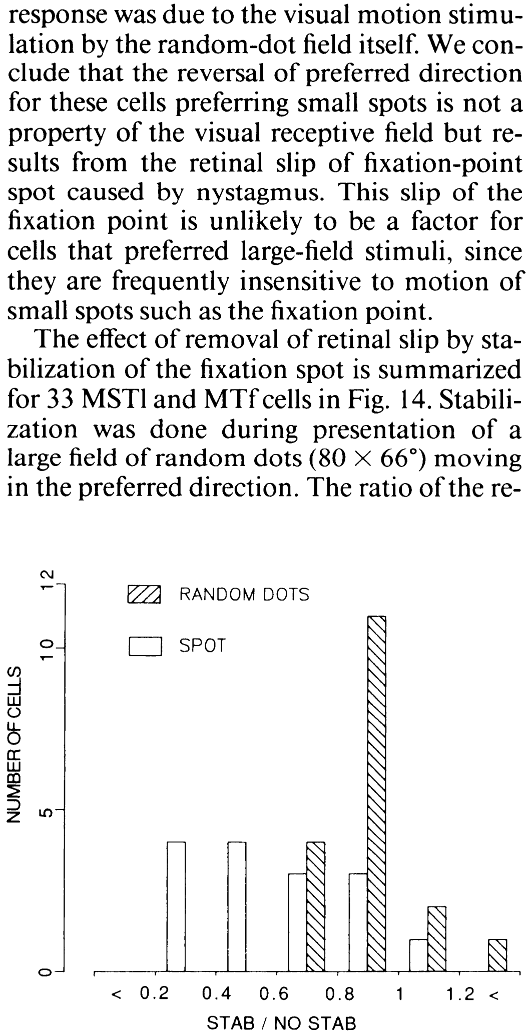

FIG. 14. Effect of stabilization (STAB) of the fixation spot during movement of the random-dot field (80 × 66°) in the preferred direction for MSTl and foveal region of middle temporal area (MTf) cells. Abscissa indicates the ratio of the response during stabilization to the response in the nonstabilized conditions. Values <1 indicate a decrease in response during stabilization of the fixation point. ▨, effects of stabilization on cells that preferred random dots as visual stimuli; □, cells that preferred small spots. *n* = 33.

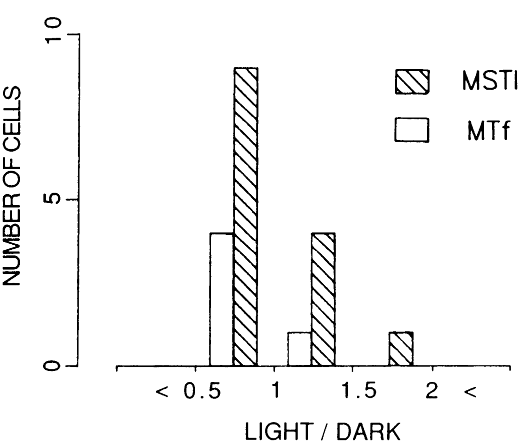

FIG. 15. Summary of the effect of a lighted background on pursuit-related responses of MSTl and MTf cells that preferred small spots as visual stimuli. The abscissa shows the ratio of the response during pursuit in the light to that in the dark. A number <1 indicates decreased response during pursuit in the light, *n* = 19.

In summary, these experiments confirmed the idea that the reversal of the preferred direction in the group of cells preferring large-field stimulation resulted from the structure within the receptive field of the cells. The reversal observed in the cells preferring small spots is just an apparent one due to the presence of a fixation point, and there is actually no evidence for such structure in their receptive fields. We conclude that these cells preferring small spots respond to random dots only when they are moving in the same direction as small spots.

EFFECT OF VISUAL BACKGROUND ON PURSUIT. For the cells preferring small spots, the relationship between the preferred direction of the pursuit response and the visual response to small spots is simple; the directions were the same. We tested the effect of diffuse illumination of the background on the pursuit-related response of 19 cells that preferred small spots as a visual stimulus. The result shown in Fig. 15 is considerably different

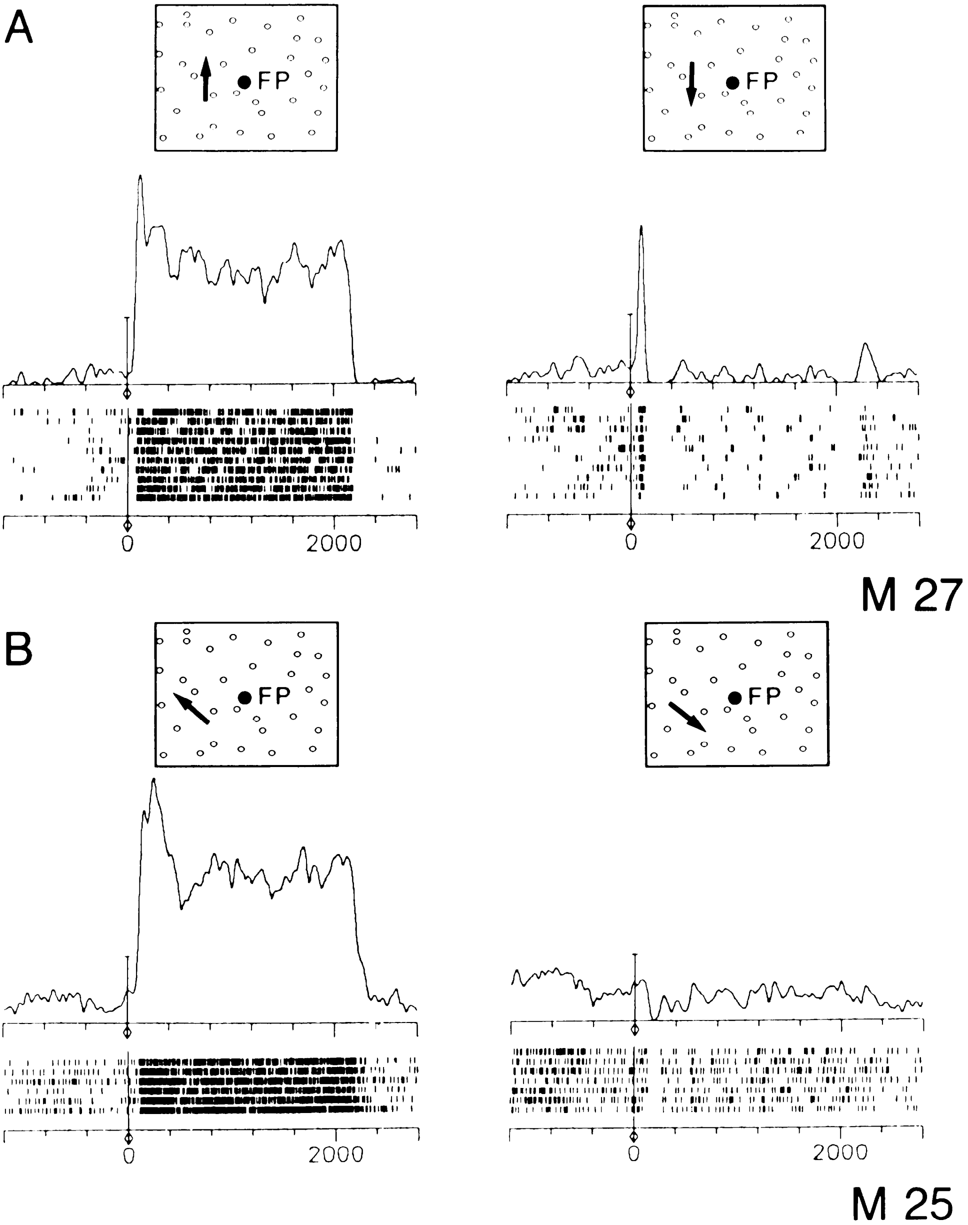

FIG. 16. Two different types of phasic response to a large field of moving dots (80 × 66°) in 2 cells in MSTd that preferred large-field motion. Both cells showed phasic and tonic activity in the preferred direction but a phasic increase of activity (*A*) or a decrease of activity (*B*) in the null direction. FP, fixation point.

from that obtained from cells that preferred random-dot stimuli (Fig. 9). Less than one-third of the cells (6/19) showed an increased response in the light compared with dark, and the increase was slight. In contrast, for cells that preferred random dots, nearly 80% showed stronger response with pursuit in the light (Fig. 9). A weak inhibitory effect observed in a majority of cells can be explained by the background movement that is in the null direction of the visual response. These results support the notion that the cells preferring small spots have no structure within their receptive fields that contributes significantly to the response during pursuit in the light.

It should be noted, however, that a small number of cells that preferred motion of small spots did show a stronger response during pursuit in a lighted background and/or responded to large fields of moving dots and continued to do so during stabilization of the fixation spot. These cells were few in number, but their presence suggests that some of the cells in MST have properties that combine some of the characteristics of both types of cells that we have considered separately in this study.

Phasic responses

We have concentrated on the tonic response of cells to stimulus motion, but there were also phasic responses of many cells to the same stimulus motion. Figure 16 shows examples of the response of two cells that responded preferentially to the motion of moving random dots. In both cells, the response to random dots moving in the preferred direction (*left* column) had a phasic and tonic pattern comparable to that seen in Fig. 1. However, when the random dots were moving in the null direction (*right* column) there was a marked difference in the phasic response of the cells. For the cell shown in Fig. 16*A*, a phasic increase in discharge occurred with a similar latency and a somewhat smaller magnitude than the corresponding peak in the preferred direction. In contrast, for the cell in Fig. 16*B* the discharge in the null direction decreased for ~150–200 ms with a latency similar to that for the increase of discharge in the preferred direction. In either case, no tonic response was observed in the null direction.

One plausible interpretation of this phasic component of the response in either the preferred or null direction is that the response might be due to a change of luminance at stimulus onset. In this case the same luminance change should occur regardless of the direction of motion and should produce similar phasic responses. We found this to be the case for the cell shown in Fig. 16*A*, and others like it, and for these cells we also found similar phasic responses to the onset of stationary random dots. The phasic responses of these cells were clearly due to the luminance change. In the cell shown in Fig. 16*B*, however, a phasic increase in discharge followed one direction of motion; a decrease followed the other direction of motion. This phasic response therefore did not result from a luminance change. One possible interpretation of this phasic response is that it reflects sensitivity to the acceleration of the stimulus as well as the velocity. The onset of the moving random dots then might give rise to a stronger directionally selective response than would continuous presentation because of this acceleration component.

The two types of phasic activity were also observed in the cells that preferred motion of small spots of light rather than large-field movement.

That the phasic discharge is related to acceleration requires further verification, such as determining the response of a cell to change in speed of an already moving stimulus. One observation consistent with this idea is that "jerky" stimulus motion is frequently more effective than smooth motion in activating the MST cells. Such movement essentially provides a strong acceleration component to stimulus motion.

DISCUSSION

In the present set of experiments, we have found that the response of pursuit cells to motion of the visual background is striking in some cells but nearly absent in others. We think that the sensitivity to background stimulation is another in a series of visual and pursuit characteristics of these cells that allows us to identify groups of neurons within the STS extending from MT into MST. We will first summarize our understanding of these groups of cells based on what we have observed, and consider what the connections between the cells might be. Based on these observations we will then consider the possible contributions that these cells make to several behavioral functions dependent on visual motion processing.

Characteristics of MTf, MSTl, and MSTd cells

Table 1 summarizes our salient observations on the pursuit cells we have studied in this and the preceding two papers (12, 17). The areas considered are MTf, MSTl, and MSTd, since pursuit cells were located in

TABLE 1. *Summary of pursuit cells*

		MSTl		
	MTf	MTf-like	MSTd-like	MSTd
1. Visual: directional	Yes	Yes		Yes
2. RF including fovea	Yes	Yes		Yes
3. RF size	Small	Small	Large	Large
4. Preferred stimulus	Spot	Spot	Field	Field
5. Pursuit: directional	Yes	Yes		Yes
6. Pursuit: in dark	Yes	Yes		Yes
7. Extraretinal input	No	No/Yes	No/Yes	Yes
8. Direction: spot and pursuit	Same	Same	Same	Same
9. Direction: field and pursuit		Same	Opposite*	Opposite*
10. Pursuit light/pursuit dark	Lt ≤ Dk	Lt ≤ Dk	Lt > Dk	Lt ≫ Dk

MTf, foveal region of middle temporal area; MSTl, lateral-anterior region of medial superior temporal area; MSTd, dorsal-medial region of medial superior temporal area; RF, receptive field; Lt, light; Dk, dark. *Most but not all respond in this way.

these areas. If we consider the visual responses first, then all pursuit cells have at least two characteristics in common; they all have directionally selective responses, and the receptive field of all include or are near the fovea (Table 1, *entries 1* and *2*). Beyond these, the characteristics diverge; cells in MTf have small receptive fields, in MSTd large fields (12), and in MSTl some cells are found with each of these receptive-field sizes. Similarly, cells in MTf prefer small spots to large-field stimuli, cells in MSTd prefer large-field stimuli, and examples of each type of cell were found in MSTl (Table 1, *entries 3* and *4*). These visual characteristics illustrate an observation made repeatedly in these experiments. MTf and MSTd appear to represent homogeneous populations of cell types, MSTl a mixture of at least two cell types (indicated by the division of MSTl into 2 columns in Table 1).

Two of the major characteristics of the pursuit response of these cells are the same for all cells. The pursuit response was directional (with a few exceptions) (12), and the response was clear with pursuit in the dark except for the target (Table 1, *entries 5* and *6*). In our experiments, what distinguishes the pursuit cells of MST from those in MTf is the presence of an extraretinal input into many MST cells—all those in MSTd and many in MSTl (Table 1, *entry 7*).

Probably the most significant interaction of visual and pursuit responses in these pursuit cells are those related to motion of the background (Table 1, *entries 8, 9,* and *10*). For MTf cells we found that the preferred direction for motion of a spot was the same as the preferred direction of pursuit. These MTf cells had minimal sensitivity to background motion, although if they did respond it was still with the same direction of motion as pursuit. In so far as the background had any effect, it reduced the response with pursuit in the light compared with the dark because the motion of the background during pursuit was in the null direction for these cells. We found the same characteristics in general for those MSTl cells that responded to small spots.

These cells with the same preferred direction for the visual and the pursuit response are similar to the cells Sakata et al. (21) referred to as "isodirectional" cells. Our finding here is that these cells are localized in MTf and MSTl and that the lack of sensitivity to large-field motion makes the effect of background rather small. The problem of distinguishing background motion from target motion is solved by the visual sensitivity of these cells—response to small spots coupled with insensitivity to large-field stimuli, including background motion. In contrast, the cells that prefer large-field stimuli in MSTl and MSTd usually show facilitation with movement of the background during pursuit. Most of these pursuit cells have *opposite* preferred directions for pursuit and visual motion. This opposite preferred direction produces a *synergistic* response during pursuit in the light compared with that in the dark and emphasizes the importance of background motion for these cells. These latter cells are almost certainly the "antidirectional" cells of Sakata et al. (21) who also emphasized the role of the background during pursuit.

Our most striking observation on many (but not all) of these MSTl and MSTd cells that preferred large-field stimuli was that they reversed their preferred direction for visual motion when the stimulus size was reduced. In this case then the pursuit response and the visual response were in the same direction, just like the other cells that responded preferentially to motion of small spots. The reversal of preferred direction between a slit stimulus and a patterned stimulus has been reported in MST by Tanaka et al. in an anesthetized monkey (24). Although they found only one such cell (their Fig. 13 *cell 4*), the visual characteristics seem to be identical to the cells we have studied. We do not know the reason for the small number of this type of cell in their sample, but there are several possibilities. One is the influence of anesthesia, one is the difference in visual stimuli used, and another is the area in MST where recording was done. We have concentrated on subregions of MST (MSTl and MSTd) where pursuit cells were located. Although Sakata et al. (21) did not observe the reversal of the preferred direction of the visual response, probably because large-field stimuli were not used in their analysis, they discussed such a possibility based on the observation that some of their isodirectional cells, which have the same preferred direction between the visual and pursuit response, frequently showed a facilitation of the pursuit response in the light in spite of the antagonistic interaction expected from the visual response to small stimuli and the pursuit response. However, the lack of information about the recording sites of cells in relation to area MT and MST in their study make further comparison to our study difficult.

It is important to distinguish the reversal of preferred direction with change in stimulus size of these MSTl and MSTd cells from such a reversal in direction reported in MT cells (1, 24), pigeon tectal neurons (5), and cells in the lateral suprasylvian area of cat cortex (26). In these areas, large-field motion *modulates* the response of cells to motion of smaller stimuli moving in the center of the field; these cells do not respond to motion of the large field by itself as is the case in the MST cells that we have described. The preferred direction for small stimulus motion of cells in these areas is often opposite to the effective direction for large-field motion. Cells in these areas seem appropriate to discriminate figure from ground or to discriminate object motion from self motion, since many cells respond optimally when an object moves in a direction opposite to the background but not when both the object and background move in the same direction (1, 5, 24). In contrast, for the MST cells we have found that stimulation of the background produces a response in itself and does not just modulate the response to object motion. Because the MST cells respond to background motion, they seem to be inappropriate for these two functions.

Possible connections between MTf, MSTl, and MSTd

Having considered how the visual and pursuit functions of MT and MST cells are organized, we can now consider how these elements might be functionally connected. Figure 17 outlines the relationships between the types of cells we have summarized in Table 1. Velocity of a visual stimulus on the retina is determined by the difference between stimulus velocity and eye velocity as indicated at summing *junction 1*. MT cells are activated by visual stimuli moving with direction and speed within a specific range and in a specific area of the visual field. MTf indicates MT cells with foveal receptive fields, and MTe those with extrafoveal receptive fields. All the information processing between retina and MT is simply represented by the "visual delay." Summing *junctions 2* and *3* produce different kinds of visual cells in MST. Cells after *junction 2* prefer large-field stimulation and cells after *junction 3* prefer well-localized stimuli such as spots or slits. In this schema, which highlights the relationship between visual and pursuit responses, summing *junction 3* also produces one type of pursuit cell carrying retinal slip information (17). An-

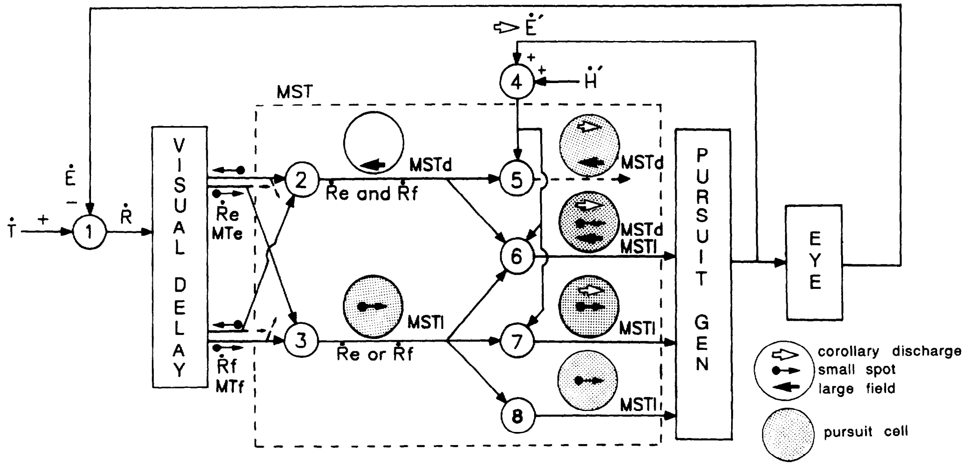

FIG. 17. Schematic diagram of the functional connections of medial superior temporal (MST) cells with different visual and pursuit-related properties and the signals carried by these cells. Circles with numbers indicate summing junctions. The dashed line encloses processing occurring in MST. Circles after each summing junction in MST show the organization of the receptive field that results from the output of the summing junction. Each circle represents a different cell type, and subareas (MSTd or MSTl) where we found each cell type are indicated next to each circle. The shaded circles represent pursuit cells (which would remain active during pursuit in the dark). In each circle, the open arrow (placed at the *top*) represents a corollary discharge of the pursuit eye movement, the thin arrow with a dot (*middle*) represents the visual response to a small spot, and a thick solid arrow (*bottom*) represents the visual response to large-field motion. The direction of the arrows in each circle indicates the preferred direction of each cell type that, in this example, is activated during rightward pursuit. See text of discussion for further explanation. MTf, MT fovea; MTe, MT extrafovea; MSTl, lateral MST; MSTd, dorsal MST; $\dot{T}$, target velocity; $\dot{E}$, eye velocity; $\dot{R}f$, retinal slip error in the foveal field; $\dot{R}e$, retinal slip error in the extrafoveal field; $\dot{E}'$, corollary of eye velocity; $\dot{H}'$, corollary of head velocity; GEN, generator.

other input into MST cells is a corollary discharge from the oculomotor command generator as indicated at *junction 4* (or might be proprioceptive as we discussed in the preceding paper) (17). Head movement related input might also be included in this corollary discharge (9). This eye and head movement related input interacts with the visual input in MST at *junctions 5, 6*, and *7*, all of which represent ways in which these interactions take place.

Figure 17 also shows the frequently observed combinations of preferred direction between visual and extraretinal responses and between different types of visual responses. Preferred directions for visual stimuli are indicated with filled arrows, and pursuit direction with open arrows. To distinguish the visual response to motion of small spots and large fields, the preferred direction for spots is represented by a thin arrow with a dot and that for the field stimuli by a thick arrow. Summing *junction 5* represents a convergence of visual input produced by wide-field stimulation and the eye movement signal, and in most cases, these two signals have the opposite preferred direction. In addition to the above interactions, that at *junction 6* is activated by visual motion in a restricted area of visual field; the preferred direction is the same as that of pursuit and opposite to that for wide-field stimulation. Summing *junction 7* indicates a small group of cells with a convergence of an eye movement signal and a retinal slip signal for motion of small targets. Summing *junction 8* is the same as *junction 3*, indicating that no interaction with the extraretinal input occurs, and that this pathway carries only retinal slip signal for motion of small targets.

Functional roles of MT and MST cells in pursuit

In the preceding paper (17), we considered what the presence or absence of an extraretinal signal suggested about the function of these pursuit cells. With the added information about the effect of the visual background on these cells and the cluster of characteristics summarized in Table 1 and Fig. 17, we can now extend our hypotheses about the roles of these cells. We will do this by comparing the characteristics of the cells that we have observed to the characteristics that would seem to be required of cells contributing to a given function.

We would expect cells related to the maintenance of pursuit to have the following cluster of characteristics. The receptive field of the relevant cells should include the fovea, and these cells should show directionally selective responses in order to provide information about retinal slip. The cells should be sensitive to the motion of small spots, since pursuit of such targets is routine, and the preferred direction should be the same as the direction of pursuit in which these cells have a role. This latter requirement results from the repeated observation that in pursuit, at least by the monkeys in our experiments, the speed of eye movement is usually lower than that of the target, so that the slip motion is in the same direction as the eye movement. Responsiveness to motion of larger stimuli might also be expected, since pursuit need not only be for small objects. For the maintenance of pursuit in the absence of any visual slip signal, other signals related to eye velocity are required. Such an extraretinal signal should carry a velocity signal for the same direction of movement as the pursuit movement itself. This signal might be carried by the same cells as those carrying retinal slip or by a different group of cells.

We think that the cells in MSTl that respond to small spots of light (summing *junctions 3, 7,* and *8* in Fig. 17) clearly carry such retinal slip information. These cells have directionally selective responses and prefer small spots of light. The fact that these cells respond only poorly to large-field stimuli allows them *on the basis of their visual properties alone* to respond to motion of a target against the moving visual background swept over the retina during pursuit. The absence of a substantial contribution from motion of the visual background to the response of these cells is also consistent with the slight change observed in pursuit performance when a target moves over a lighted as opposed to a dark background (2, 10). Some cells in MSTl that prefer small spots as visual stimuli also have an extraretinal input (summing *junction 7* in Fig. 17). In these cells the direction of the visual motion of the small stimulus and that of the extraretinal input is almost always the same. This isodirectional aspect of these cells would provide the same directional signal whether pursuit was maintained by retinal slip or an extraretinal signal. Furthermore, a recent study that made punctate chemical lesions within STS (4) showed that the most pronounced directional pursuit deficit followed lesions of the area most closely associated with MSTl, not the other areas of MST. For these reasons, we think that the most reasonable interpretation of these MSTl cells that respond to spots, that have an extraretinal input, and that have the same preferred direction for visual stimuli and pursuit eye movements, is that they function during pursuit eye movements as an input to the pursuit system, as diagrammed in the preceding paper (17).

The cells in MST that prefer large-field stimulation (Table 1, and summing *junction 5* in Fig. 17) have only a slight response to small spots, which we used as pursuit targets in our experiments, and which monkeys and humans pursue very readily. Because of the clear lack of a retinal slip signal from the moving target in these cells, their role in the maintenance of pursuit (if any) is restricted to a pathway that is independent of that for retinal slip. In addition the synergistic response between the visual background stimulation and the pursuit in these cells also has no demonstrated correlate in pursuit performance as we have already indicated. However, the fact the performance is not substantially degraded when pursuit is made over a background may indicate that the synergistic response of these cells may in fact play a key role in pursuit generation. The background motion would be expected to produce an optokinetic response in the direction opposite to pursuit and therefore to compete with the pursuit response. One possible function of the synergistic response of these cells might be to increase the pursuit response of these cells to compensate for the optokinetic nystagmus (OKN). Both the synergy in pursuit and the OKN would be generated by the same stimulus, but the effects might functionally cancel.

Functional roles of MT and MST cells in perception

Another function that cells discharging in relation to pursuit eye movements might perform is more closely related to the consequences of pursuit eye movements rather than their generation. During pursuit eye movement, even if there is no retinal slip as is the case in afterimage tracking, we still clearly perceive motion of the target. The perceived direction of motion is the same as that of the pursuit eye movement. Large-field stimulation also has significant influence on the motion perception, the phenomenon being known as induced motion (3). When a large field is moving and a central spot is stationary, the perception is that the spot is moving in the opposite direction. Therefore, perception of motion of a small spot can occur as a result of at least three different retinal events as mentioned above—one with the motion of the spot on the retina, the other during pursuit of the spot, and another by moving a large stimulus with the spot being stationary.

At the cellular level, one would have several expectations for cells that were related to such perception of motion that is independent of the retinal event. The first is that the cells respond to large-field stimulation as well as to small spots. The second is that the preferred direction for large-field visual stimulation be the opposite to that for small spots. Finally, the extraretinal input related to pursuit is required, and the preferred direction of pursuit is the same as the motion of the small spot used as the target.

The cells most appropriate for these perceptual functions are those that respond to large-field stimulation in MSTd and MSTl. All of the pursuit cells we observed in MSTd and some we observed in MSTl prefer large-field visual stimuli to small spots of light (summing *junctions 5* and *6* in Fig. 17). Many did respond to small spots of light, however, and when they did so the preferred directions for the large and small stimuli were in the opposite direction (summing *junction 6*, Fig. 17). The preferred direction for the large-field stimulus was also opposite that of the pursuit response. The preferred direction for large visual field motion in over three-fourths of the cells was opposite to that for pursuit. Put another way, the response of these cells to small stimuli and during pursuit had the same preferred direction. These cells would therefore seem to be reasonable candidates for indicating the direction of perceived motion. They would indicate by their increased discharge pursuit in a given direction and motion of small spots in that same direction. In contrast, the response of these cells to motion of a large visual field would be in the opposite direction to that for the motion of small spots or for pursuit eye movements. This is exactly what would be expected if these cells were relevant to perception rather than to pursuit.

A similar perceptual function was first proposed by Sakata et al. (20) for cells in the posterior parietal cortex that were activated by motion of a frame of light (in an otherwise darkened room) in one direction but to pursuit eye movements in the opposite direction. Although we do not know whether we are sampling from the same population of cells they studied, the visual properties and pursuit responses suggest the similarity to the cells at summing *junction 5* in Fig. 17. In these cells, however, the lack of any response to small spots makes them less appropriate for the perception of the motion we have just described. Instead, we might regard these cells as related to the orientation in space based on the flow of the visual field as proposed by Gibson (6).

In net, many of these cells provide an excellent signal for analyzing the consequences of pursuit rather than for the generation of the pursuit. One possible reason for bringing the extraretinal input through the cerebral cortex might be the benefit this brings to the integration of the perception of motion with the generation of motion. The combining of visual motion and eye movement information provides a coherent report of perceived visual motion to the next levels of visual processing.

Another effect of large-field motion in the oculomotor control system is related to the short-latency ocular following response recently demonstrated by Miles and his collaborators (13). The visual characteristic relevant to the current discussion is that this response also shows a modulatory effect of large-field stimulation similar to that of the figure-ground discrimination. The peripheral visual field does not in itself have substantial effects on the following response but instead modulates the effectiveness of a stimulus falling in the central visual field. The cells in MST would seem inappropriate for this function whereas those in MT would seem particularly appropriate. It is interesting to note, however, that the effective central stimulus for ocular following is not a small spot but rather a stimulus as large as 40° in the central part of the visual field. This fact might be relevant to our observations that in a reversal of preferred direction in MST cells, a relatively large size was required before reversal of direction occurred. Reversal of the preferred direction with increase in the field size did not occur for many MSTd and MSTl cells until the stimulus was near 30° on a side.

Transition in cortical organization from MT to MST

MST probably represents at least the third of three sequential cortical areas related to visual motion processing. It receives a direct input from area MT that in turn receives input from the primary visual cortex (25, 27). Primary visual cortex is the first cortical area in the primate to show a directionally selective response to moving visual stimuli (8), but there is no indication that these cells discharge during pursuit or respond preferentially to large-field stimulation. Cells in MT also do not respond with pursuit movements in the absence of visual stimulation (17), and do not prefer large-field stimulation (1, 24). Of these motion-related areas, MST appears to be the first where the interactions between retinal and nonretinal inputs occur. This interaction suggests that a divergence of function takes place in the population of MST cells. As discussed above, some cells are particularly suited for the generation of pursuit eye movement, whereas others seem to be particularly important for motion perception that is independent of retinal events. The divergence of function in the population of MST cells may correspond to two of the output pathways from this area, one to the posterior parietal cortex and the other to the dorsolateral pons. Cells in the dorsolateral pontine area have recently been shown to respond during pursuit (14, 23). In contrast, in MT, a major source of visual input to MST, visual motion information appears to be available for both generation of pursuit and motion perception (15, 16, 22). This transition from a functionally more general purpose MT to a functionally divergent MST may be correlated with the different organization of these two visual areas. The retinotopic organization covering the contralateral visual field is relatively clear in MT, whereas this is less clear in the lateral subdivision of MST, and we have found no such organization in the medial subdivision of MST (12). To know how these cortical areas are organized to analyze higher order motion information, we need to know the way different cell types are distributed in each subdivision; MSTl includes different types of pursuit cells, and MSTd probably includes Saito et al.'s R cells or S cells (19). Such information may reveal a higher level of cortical organization based on the representation of specific functions, not on the representation of the visual field.

ACKNOWLEDGMENTS

We thank G. Creswell and L. Cooper for histological assistance, A. Ziminsky, C. Crist, and T. Ruffner for technical assistance, and J. Steinberg for typing the manuscript. We are particularly grateful to Max R. Dürsteler for designing the computer programs for the generation of the moving random-dot fields and the system for synchronizing the PC and the PDP-11 computers.

Received 29 June 1987; accepted in final form 14 March 1988.

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