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Relation of Cortical Areas MT and MST to Pursuit Eye Movements. II. Differentiation of Retinal From Extraretinal Inputs

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SUMMARY AND CONCLUSIONS

1. We investigated cells in the middle temporal visual area (MT) and the medial superior temporal area (MST) that discharged during smooth pursuit of a dim target in an otherwise dark room. For each of these pursuit cells we determined whether the response during pursuit originated from visual stimulation of the retina by the pursuit target or from an extraretinal input related to the pursuit movement itself. We distinguished between these alternatives by removing the visual motion stimulus during pursuit either by blinking off the visual target briefly or by stabilizing the target on the retina.

2. In the foveal representation of MT (MTf), we found that pursuit cells usually decreased their rate of discharge during a blink or during stabilization of the visual target. The pursuit response of these cells depends on visual stimulation of the retina by the pursuit target.

3. In a dorsal-medial region of MST (MSTd), cells continued to respond during pursuit despite a blink or stabilization of the pursuit target. The pursuit response of these cells is dependent on an extraretinal input.

4. In a lateral-anterior region of MST (MSTl), we found both types of pursuit cells; some, like those in MTf, were dependent on visual inputs whereas others, like those in MSTd, received an extraretinal input.

5. We observed a relationship between pursuit responses and passive visual responses. MST cells whose pursuit responses were attributable to extraretinal inputs tended to respond preferentially to large-field random-dot patterns. Some cells that preferred small spots also had an extraretinal input.

6. For 92% of the pursuit cells we studied, the pursuit response began *after* onset of the pursuit eye movement. A visual response preceding onset of the eye movement could be observed in many of these cells if the initial motion of the target occurred within the visual receptive field of the cell and in its preferred direction. In contrast to the pursuit response, however, this visual response was not dependent on execution of the pursuit movement.

7. For the remaining 8% of the pursuit cells, the pursuit discharge began before initiation of the pursuit eye movement. This occurred even though the initial motion of the target was outside the receptive field as mapped during fixation trials. Our data suggest, however, that such responses may be attributable to an expansion of the receptive field that accompanies enhanced visual responses. We observed enhancement effects in several MST cells when the monkey used the visual stimulus as a pursuit target. We have not, therefore, obtained unequivocal evidence that the pursuit response proper can commence before onset of pursuit eye movements.

8. We conclude that one class of pursuit cells (in MTf and MSTl) provides visual motion information to the pursuit system. These cells may play a role in pursuit initiation by providing information about the motion of potential pursuit targets. They also appear to encode the slip of a visual target on the retina during ongoing pursuit. A second class of pursuit cells (in MSTd and MSTl) receives an additional extraretinal input related to the execution of pursuit eye movements. This input may derive from corollary discharge mechanisms or from proprioceptive sources.

INTRODUCTION

In the preceding paper (6), we found that neurons with pursuit responses were localized to specific regions within the superior temporal sulcus (STS). In this paper we analyze the inputs that are responsible for the pursuit responses, with particular emphasis on differentiating inputs of retinal and extraretinal origin. Pursuit cells respond when a monkey pursues a dim visual target in an otherwise dark room. The dark room ensures that the pursuit response does not result from visual stimulation of the receptive field by extraneous background contours. Even this reduced visual environment does not, however, eliminate the possibility that the pursuit response is visual (retinal) in origin; the response could result from motion on the retina of the image of the target itself. Such "retinal slip" is an inevitable concomitant of imperfect pursuit performance. Because we have found that most pursuit cells in the STS have visual receptive fields that include the fovea (6), a visual origin for the pursuit response is entirely plausible. Alternatively, the pursuit response may result from some nonvisual aspect of pursuit performance (an extraretinal signal). This possibility is supported by the results of Sakata and his collaborators (19) who showed that some pursuit cells in the STS continued to respond during pursuit in total darkness when the pursuit target was briefly turned off. A similar observation was made for cells in the dorsolateral pontine nucleus (17).

Precise characterization of the inputs responsible for the pursuit response is critical for understanding the functional role of these neurons. In the present experiments we have differentiated between pursuit inputs of retinal and extraretinal origin by eliminating or greatly reducing motion of the visual target on the retina (retinal slip) during pursuit. We accomplished this in two ways—by blinking the target briefly during pursuit (19) or by stabilizing the image of the pursuit target on the retina. We found that the pursuit inputs to one class of cells were unambiguously visual, whereas those to another class were characterized by an extraretinal input in addition to the visual input. We were also able to localize these classes of cells with respect to regions of the middle temporal visual area (MT) and the medial superior temporal area (MST) that we have identified (6). Pursuit cells in foveal MT (MTf) received visual pursuit inputs whereas cells in a dorsal-medial subdivision of MST (MSTd) (6) received extraretinal pursuit inputs. Both types of response were observed in a lateral-anterior subdivision of MST (MSTl).

A brief report of these results has appeared previously (24).

METHODS

The procedures for monkey training, electrophysiological recording, and data analysis were described in the preceding paper (6). Our methods for determining receptive-field boundaries, assessing direction selectivity, and localizing recording sites were also identical to those employed in the previous experiment.

An additional procedure used in these experiments required the stabilization of the visual image on the retina during smooth-pursuit eye movements. To accomplish this, we replaced the normal voltage-ramp input to the mirror galvanometers with a voltage input that corresponded to the monkey's current eye position. Under these conditions the motion of the pursuit target "mimicked" each movement of the eyes, and the image was therefore "stabilized" at a predetermined location on the retina. Each of these trials began with a brief interval of normal pursuit, followed by a 700- to 1,000-ms interval of pursuit with the image stabilized. A second interval of normal pursuit terminated each trial. The monkey was rewarded for detecting the dimming of the pursuit target during the final interval of normal pursuit. We have previously provided a detailed account of our methods for calibrating the equipment and assessing the efficacy of our stabilization procedure (2).

In other experiments we turned off the pursuit target for 150–200 ms after the monkey had established pursuit. This interval was sufficiently short so that the monkey continued to pursue the target during the "blink"; significantly longer intervals resulted in a drop in pursuit velocity. This blink of the visual target was instantaneous, since the target was the projected image of a light-emitting diode (LED) controlled by solid state switches.

We quantified the responses of individual cells by means of an off-line computer program that calculated total spikes and average firing rate during preset time windows. We measured the average discharge rate beginning 100 ms after onset of the blink or stabilization. This 100-ms delay allowed the visual latency period to pass before responses were measured. The interval during which the discharge rate was measured was 100 ms for the blink and 500 ms for the stabilization trials. In most cases, the effect of target blink or stabilization on the pursuit response was assessed by comparing the response in the test interval with the response of the cell during an identical interval in control trials of normal pursuit. In some cases, however, the response during the blink or stabilization interval was compared with the response in the same trials during a 100-ms interval that began 50 ms before onset of the blink or stabilization.

RESULTS

We identified a total of 165 pursuit-related single cells in four monkeys. In addition to measuring the response of these cells during pursuit, we assessed passive visual properties such as direction selectivity and size of the receptive field. We also localized each neuron with respect to regions we identified within the STS—MTf, MSTd, and MSTl. As described in the preceding paper (6), we employed several physiological and histological criteria to assign a neuron to the appropriate area.

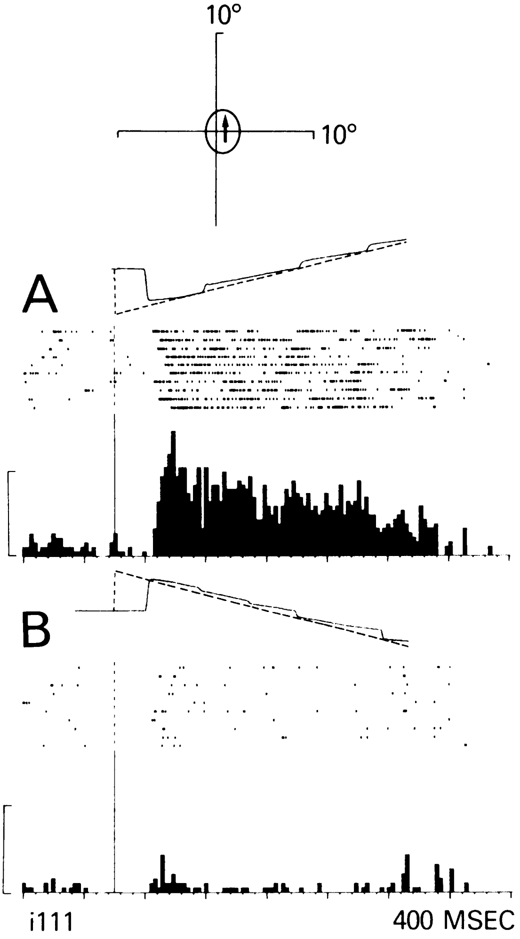

FIG. 1. Discharge of a middle temporal area (MT) neuron with a foveal receptive field (MTf) during pursuit eye movements. The schematic drawing at the *top* of the figure shows the visual receptive field as mapped with a hand-held stimulus while the monkey fixated. ↑, upward-preferred direction for stimulus motion. *A*: response during upward pursuit. The target stepped downward 20° and then moved upward at 15°/s. Individual trials are aligned on the onset of the target step. The position traces above the raster illustrate vertical target position (– – –) and vertical eye position (——) for 1 trial. The monkey made a saccade to the target and pursued the target with pursuit eye movements and small amplitude saccades for the duration of the trial. *B*: response of the same cell during downward pursuit. In this and subsequent figures, the dots on the raster display indicate cell discharge, and successive lines represent successive trials. The peristimulus time histogram is the sum of a series of trials. The larger tick marks on the abscissa are 400 ms apart; binwidth is 20 ms. The ordinate scale on the histogram is 250 spikes$\cdot$s$^{-1}\cdot$trial^{-1}. The cell number is in the *bottom left* corner.

Effect of visual inputs on pursuit responses

The pursuit cells that we identified in MT were all located within the foveal representation of the visual field. All of these cells had small receptive fields within 2° of the fovea, and we refer to this region as MTf (6). We did not observe pursuit cells in MT outside this region. Figure 1 illustrates the responses of one such cell. This cell had a small visual receptive field that included the fovea and an upward direction of preferred motion as shown in the schematic diagram of Fig. 1. This cell also responded during upward pursuit as shown in the raster and histogram of Fig. 1*A*. In this paradigm, the monkey fixated the central target for a variable period of time. The target then disappeared and reappeared 20° below the fixation point, moving upward at 15°/s. The monkey made a saccadic eye movement to the moving target and then tracked the target with smooth-pursuit eye movements for the duration of the trial. The position traces above the raster illustrate target position and vertical eye movements for one such trial. In our experience, vertical pursuit is less accurate than horizontal pursuit, and this fact is reflected in the numerous "catch-up" saccades made by the monkey in pursuing the target. The raster and histogram in Fig. 1*B* show that the pursuit response was directionally selective; the cell did not discharge during downward pursuit.

We then determined whether the pursuit response resulted from visual stimulation of the retina by the pursuit target or from some aspect of the pursuit eye movement itself. We first extinguished the visual target briefly as the monkey pursued in the upward direction (Fig. 2, same cell as in Fig. 1). The monkey therefore executed pursuit eye movements during a 150-ms interval of total darkness as indicated by the short solid line above the target position trace in Fig. 2. The 150-ms blink of the target was sufficiently short that the monkey maintained smooth pursuit throughout the interval of darkness (see eye position trace in Fig. 2). A clear interruption of the response accompanied the blink of the pursuit target even though the monkey continued to pursue during the interval of complete darkness. The ratio of discharge during the blink period to the discharge during normal pursuit was 0.25. The cell resumed its normal pursuit response on reappearance of the visual target.

The results illustrated in Fig. 2 suggest that the pursuit response of this MTf neuron resulted from stimulation of the visual receptive field by the target motion during pursuit.

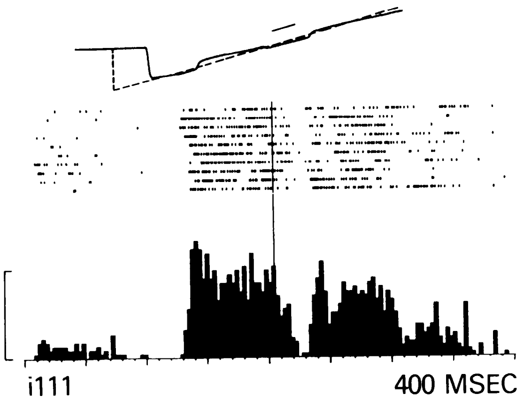

FIG. 2. Decrease in discharge of a foveal MT (MTf) cell after blink of the target during pursuit. Responses are from the same cell, and pursuit is in the same direction as shown in Fig. 1*A*. The blink of the target for 150 ms is indicated by the solid line above the position trace; the raster is aligned on the blink.

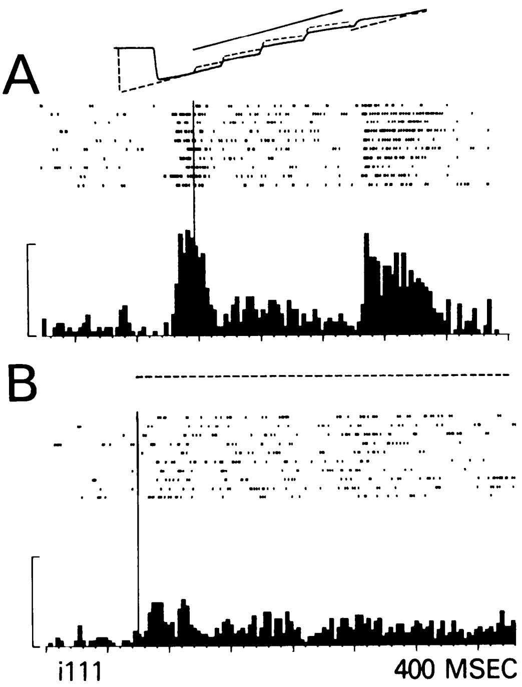

FIG. 3. Decrease in discharge of a foveal MT (MTf) cell during pursuit of a stabilized image. Recordings were from the same cell and for pursuit in the same direction as that in Fig. 1*A*. *A*: interval of stabilization is indicated by the solid line above the position traces. The raster is aligned on onset of stabilization. *B*: responses to a stationary stimulus (- - -) falling on the receptive field while the monkey fixated. The low-level response in *B* is comparable to that seen during stabilization of the stimulus on the receptive field during pursuit (as in *A*).

We confirmed this result by having the monkey pursue a target that was stabilized on the retina (see METHODS). In this task the monkey initiated pursuit under normal conditions, and we then stabilized the target for a 1-s interval as indicated by the solid line above the position traces in Fig. 3*A*. We provided a small (1°) offset to keep the stabilized target ahead of the fovea, thus ensuring continued pursuit throughout the period of stabilization. This offset in the vertical direction still kept the target within the visual receptive field of the cell (see field illustration in Fig. 1). Thus the visual target was present in the receptive field during the interval of stabilization, but *motion* of the target on the retina (retinal slip) was greatly reduced. The record of the eye movement at the *top* of Fig. 3*A* shows that pursuit continued during the period of stabilization. During the stabilization interval, however, the response of the cell decreased dramatically. The ratio of the response during the stabilization interval to that of the response during an equivalent interval of pursuit under normal conditions was 0.32 (Fig. 3*A*). Thus the bulk of the pursuit response for this MTf neuron is attributable to slip of the target on the retina that results from imperfect pursuit.

We suspected that the residual response during the stabilization interval resulted from a tonic visual response to the stabilized target. We tested this notion by presenting a stationary stimulus at the same location in the receptive field while the monkey fixated a stationary target. Figure 3*B* illustrates the response of this cell under this condition. The small tonic response obtained was roughly equal in amplitude to the residual response during the interval of stabilization in Fig. 3*A*. This observation suggests that the entire pursuit response of this neuron can be accounted for by visual inputs from the pursuit target. This pattern of responses was characteristic of the pursuit cells we studied in MTf.

Pursuit cells in MSTd yielded a strikingly different pattern of responses, and Figs. 4 and 5 illustrate the results from one such cell. As indicated in the schematic drawing at the *top* of Fig. 4, the receptive field of this cell included the fovea and covered a large portion of the visual hemifield. The passive visual response of this cell was directionally selective, and the preferred direction was to the left. In addition, the cell yielded a robust directionally selective response during pursuit. The cell responded strongly during leftward pursuit (Fig. 4*A*) but was inhibited during rightward pursuit (Fig. 4*B*).

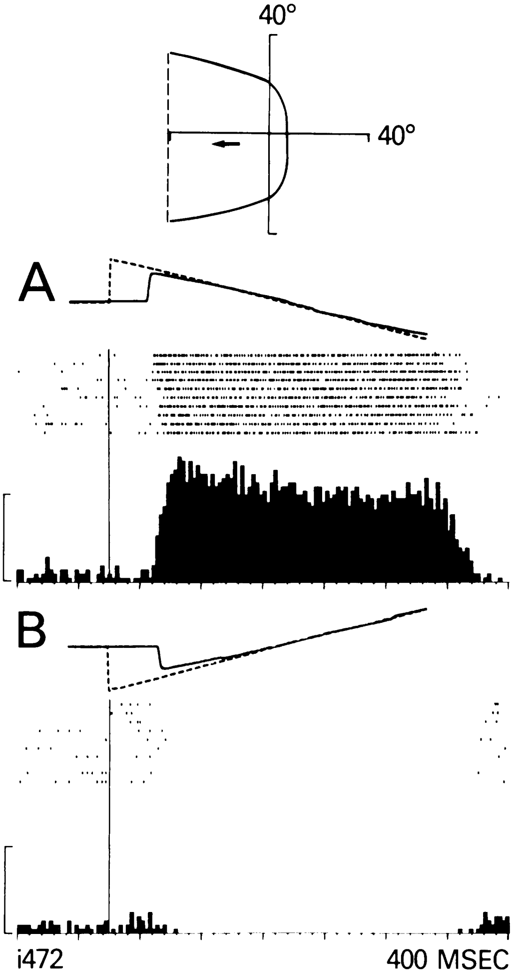

FIG. 4. Discharge of a dorsal-medial MST (MSTd) cell during pursuit eye movements. The schematic drawing shows receptive-field boundaries; the lateral edge (– – –) was in the far periphery and was not localized. ←, leftward-preferred direction of motion. The raster lines are aligned on the onset of target motion. *A*: neuronal response during pursuit of a target moving leftward at 15°/s. *B*: response during rightward pursuit.

Figure 5 depicts the pursuit responses of this cell during manipulation of the visual input. In the experiment illustrated in Fig. 5*B*, we "blinked" the pursuit target for 200 ms as indicated by the solid line segment below the eye movement record. In contrast to the MTf neuron described previously, this MSTd neuron continued its discharge throughout the blink period (compare Fig. 5, *A* and *B*). Quantitative measurement of the discharge rate indicated that the ratio of response during the blink to that during the preceding time interval was 0.91. Similarly, Fig. 5*C* shows that removal of retinal slip by target stabilization had no effect on the pursuit response of this cell. The ratio of the response during stabilization to that during the preceding period was 0.82. Because neither of these manipulations of visual input substantially affected the pursuit response of this neuron, we think that the pursuit response is likely to result from an extraretinal input.

Alternatively, the continued discharge of these MST cells during blink or stabilization of the target may represent a persistence of the visual response after removal of the stimulus. We think this is unlikely, however, because a persistent visual response should also be evident after turning off a visual stimulus during fixation of a stationary target. We did

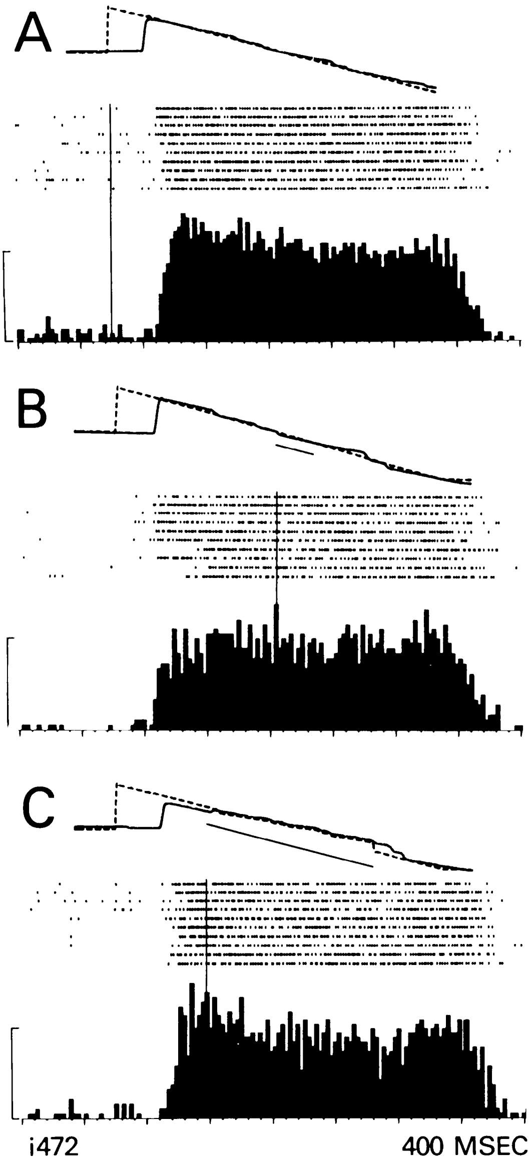

FIG. 5. Effect of target blink and stabilization on the pursuit response of the same dorsal-medial MST (MSTd) cell as in Fig. 4. *A*: normal pursuit in the preferred direction (as in Fig. 4*A*). *B*: effect of target blink (short line beneath the position traces). Raster lines are aligned on blink onset (vertical line). *C*: effect of target stabilization (line beneath position traces). Raster lines are aligned on the onset of stabilization (vertical line). The effect of both manipulations was minimal indicating that the pursuit response was largely independent of visual inputs.

not observe such persistence of the visual response in the cells that continued to respond during blink and stabilization. We conclude that an extraretinal input is the most likely basis for the pursuit responses such as those in Fig. 5 that are independent of the visual stimulus.

We quantitatively measured the responses of each pursuit neuron in both the blink and stabilization experiments, and the results are illustrated in Fig. 6. Figure 6*A* shows the ratio of responses during blink and "no blink" periods for all cells from which we obtained adequate data. The number of cells falling in each bin is illustrated separately for each of three cortical visual areas—MTf, MSTd, and MSTl. The data obtained from MTf and MSTd differed along the lines illustrated in Figs. 2–5; the blink interval resulted in a significant reduction of the responses of most MTf cells but had little or no effect on the responses of most MSTd cells. Although there is some overlap in the ratio of response in the two areas, the distributions are clearly skewed

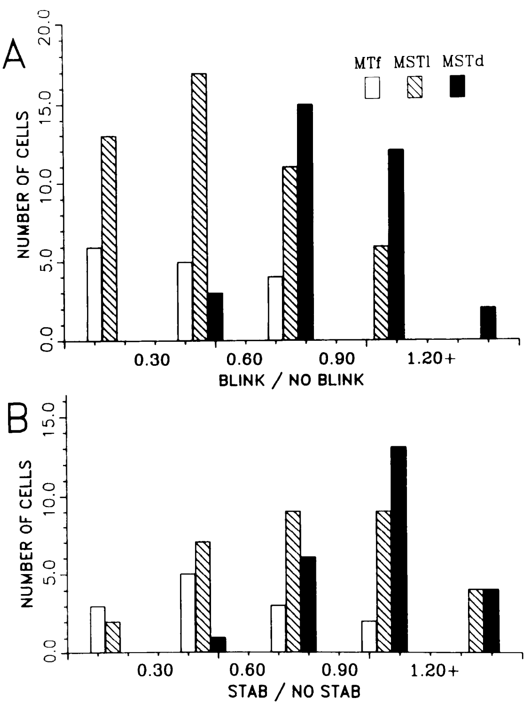

FIG. 6. *A*: ratio of the pursuit response during target blink to the response without a target blink. *B*: ratio of the pursuit response during target stabilization to the response without stabilization. Cells are in the following bins 0.30 units wide: 0–0.29, 0.3–0.59, 0.6–0.89, 0.9–1.19, 1.20+. Foveal MT (MTf) cells exhibited the greatest response reduction during blink and stabilization intervals; dorsal-medial MST (MSTd) cells showed the least reduction and occasionally even an increased response (>1.0); both types of responses were present in lateral-anterior MST (MSTl). STAB, stabilization.

in opposite directions. We observed both types of response in MSTl; the response ratios in Fig. 6*A* are more evenly distributed through the observed range. The same pattern of results emerged from the stabilization data illustrated in Fig. 6*B*. Pursuit responses in MTf tended to be reduced by the stabilization interval, whereas responses in MSTd were frequently unaffected. Again, we found a broad range of responses in MSTl with cells being distributed across the entire range of ratios in Fig. 6*B*. In general, then, manipulations of the visual input during pursuit had strong effects on the responses of cells in MTf, weak effects on cells in MSTd, and varied effects on cells in MSTl.

As expected from the results shown in Fig. 6, cells whose responses were affected by one of these manipulations tended to be affected by the other as well. Figure 7 is a scatter plot of the response ratios obtained for each cell in the blink and stabilization experiments. The two measures were clearly related, but a majority of the cells fell above the 45° line suggesting that many cells were more strongly affected by the blink than by stabilization. We believe that this phenomenon is attributable to the fact that a stationary stimulus continued to be present in the receptive field of most neurons during the stabilization interval.

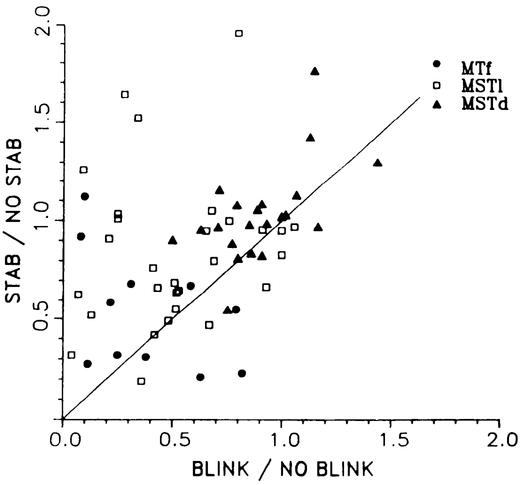

FIG. 7. Scatter plot of response ratios for the blink and stabilization experiments. Cells whose responses were affected equally by both manipulations fall on the diagonal line. There is a tendency for points to fall above the line indicating less reduction during stabilization than during blink of the target. STAB, stabilization.

Preferred visual stimuli

As illustrated in Fig. 6, manipulation of the visual inputs during pursuit had differing effects on the responses of pursuit cells in MTf, MSTd, and MSTl. Interestingly, the distribution of responses in Fig. 6 resembles the distribution of preferred visual stimuli depicted in Fig. 11 of the preceding paper (6). Komatsu and Wurtz reported that MSTd neurons responded optimally to full-field texture stimuli as opposed to geometric stimuli such as spots and bars. MTf neurons, on the other hand, preferred spots of light to the full-field textures employed in their study. A similar dichotomy was evident in the present experiments; the pursuit responses of MSTd neurons depended heavily on extraretinal inputs, whereas those of MTf neurons were generally attributable to visual inputs. For both the visual and pursuit responses, cells of each response type can be found in MSTl. It is interesting to ask whether this apparent correlation between preferred visual stimuli and the origin of pursuit inputs actually holds on a cell-by-cell basis.

The results of such a comparison are shown in Fig. 8. Figure 8*A* shows the effects of the blink experiment on pursuit responses, whereas Figure 8*B* illustrates the effects of target stabilization. The abscissa indicates ratios of responses in the same manner as for Fig. 6. The ordinate denotes the number of cells in each bin, with upward bars depicting data from MSTd and downward bars illustrating results from MSTl. In each bin, the dark bars indicate cells that responded preferentially to random-dot fields, whereas the light bars denote cells that preferred small spots or that showed a similar preference for each. Of the cells that preferred large-field random-dot patterns, the large majority received substantial pursuit inputs from extraretinal sources (as indicated by continued pursuit responses during manipulation of the visual inputs). These properties seem to be tightly coupled, and they were characteristic of almost all MSTd cells. Cells that responded well to small spots, as expected, were found exclusively in MSTl (6). During the blink of the target the response of these cells tended to decrease (Fig. 8*A*), whereas during stabilization they were more evenly distributed along the abscissa (Fig. 8*B*). Although this sample of cells is small, it is clear that some of the cells

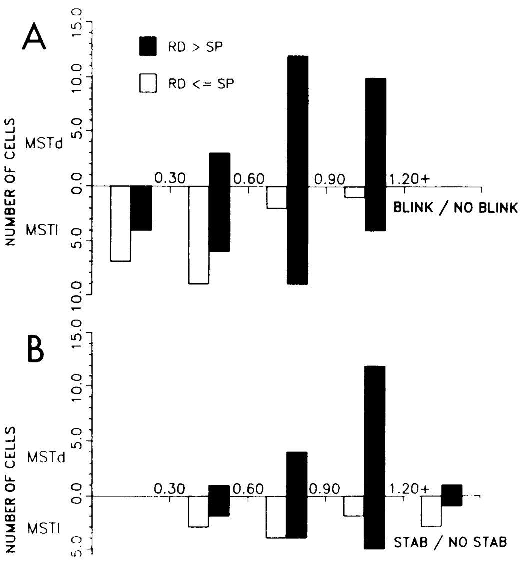

FIG. 8. Relation of preferred visual stimulus and subdivision of MST to responses during blink (*A*) and stabilization (STAB) (*B*) experiments. Dark bars show cells that preferred large-field random-dot stimuli (RD) to small spots of light (SP); light bars indicate those cells in which the response to spots was greater than or equal to that to random dots. Upward bars are for cells in MSTd, downward for cells in MSTl. Cells are those shown in Fig. 6 (from monkeys *M1* and *C1*) for which the visual stimulus requirements were adequately determined. The majority of cells that preferred random dots tended to show little change during blink and stabilization; all cells in MSTd were of this type. Cells in MSTl that preferred spots showed a decrease of response during blink but a range of changes during stabilization. See Fig. 4 and 6 legends for definitions of abbreviations.

in MSTl that prefer spots also receive an extraretinal input.

Response during pursuit initiation

During maintenance of pursuit, we have observed both a retinal and an extraretinal input to the pursuit cells. We next determined whether an extraretinal input was active during pursuit initiation. If the extraretinal input was active *before* the onset of eye movement, this input could represent a motor signal for the initiation of pursuit. If, on the other hand, the extraretinal input commenced *after* the onset of eye movement, this input would more likely be involved in the maintenance of ongoing pursuit.

We employed the same strategy of manipulating the visual stimulation in order to reveal an extraretinal input. For the cells that yielded no visual response to motion of the small spots used as pursuit targets, any discharge that preceded pursuit initiation must have resulted from an extraretinal source. However, for cells that were visually responsive to spots of light, it was necessary to place the target outside of the receptive field in order to determine whether an extraretinal input was active during pursuit initiation.

The responses shown in Fig. 9 illustrate the discharge of two cells during pursuit initiation. Figure 9, *A* and *B*, depicts data obtained from an MTf cell during upward pursuit. This neuron had a small perifoveal receptive field (illustrated in the schematic drawing at the *top* of the figure) that responded selectively to upward motion. In the trial illustrated in Fig. 9*A*, the monkey fixated a stationary spot of light that then began to move upward (dashed line, vertical target position; solid line, vertical eye position). The monkey responded with a short interval of presaccadic pursuit followed by a saccade to the moving target. The monkey then pursued the target with smooth eye movements for the duration of the trial. The neuron responded with a burst of spikes immediately before initiation of the pursuit eye movement and continued responding in a bursty manner for the duration of the trial. The initial burst of spikes that preceded onset of the eye movement may be obligately related to pursuit initiation, or it may simply result from the initial target motion through the receptive field of the neuron. To distinguish between these alternatives, we repeated the experiment with a single difference; the fixation target was displaced downward outside of the receptive field of the cell immediately before being set in motion. As shown in Fig. 9*B*, the cell continued to respond robustly during smooth pursuit, but the burst of spikes preceding pursuit initiation was eliminated.

The results in Figs. 9, *C* and *D*, show that the same observations hold true for pursuit cells in MST as well. This MSTl cell had a visual receptive field that included a portion of the inferior vertical meridian (see schematic drawing), and it responded selectively to upward motion. In Fig. 9*C* the fixation target was displaced into the receptive field of the neuron (*point C* in the schematic drawing) before moving upward. The monkey responded with a brief interval of presaccadic pursuit followed by a saccade to the moving target and then continued pursuit for the duration of the trial. The neuron began to re-

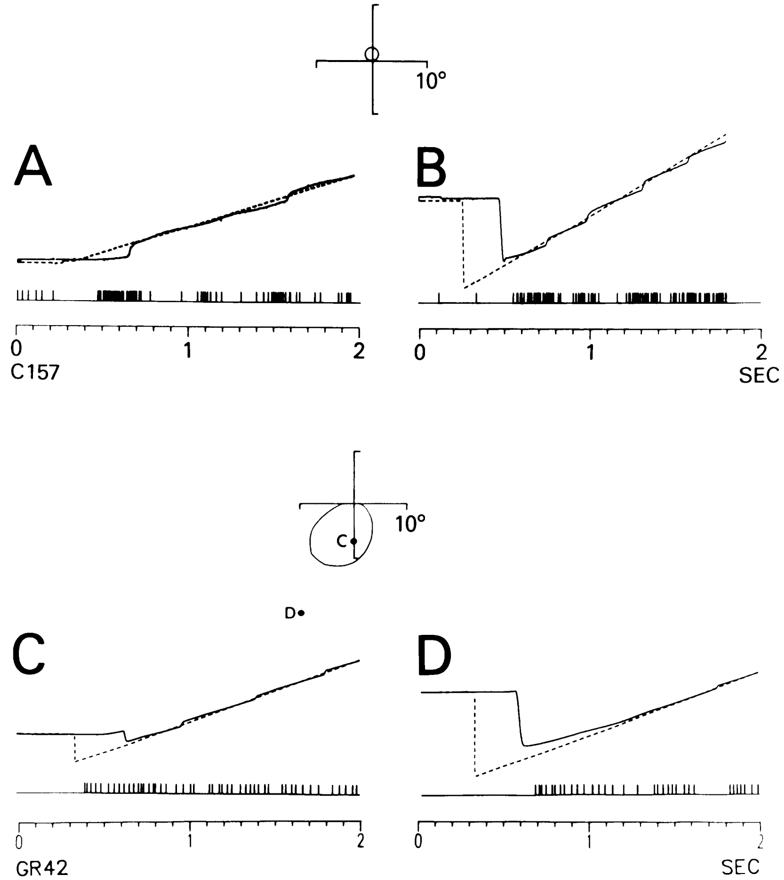

FIG. 9. Temporal relation of neuronal discharge of an MTf cell (*A* and *B*) and an MSTl cell (*C* and *D*) to pursuit eye movements. The schematic drawing above *A* and *B* shows the receptive field of the MTf cell that included and extended above the fovea. *A*: vertical target position (- - -), vertical eye position (——), and discharge of the MTf cell as the target moved from its initial position upward at 8°/s. *B*: cell response for a trial in which the initial step placed the target outside of the receptive field of the cell (20° down) with target motion upward at 25°/s. The drawing above *C* and *D* illustrates the receptive field of an MSTl cell. *C*: pursuit of a target that stepped down 7° into the receptive field of the cell (*point C*) and then moved upward at 16°/s. *D*: upward pursuit after a step 20° down and 10° left that is outside of the field (*point D*). In both the MTf and the MSTl cells, the pursuit response commenced before the onset of eye movement when the initial motion of the target was in the visual receptive field (*A* and *C*). When, however, the target fell outside of the receptive field (*B* and *D*), there was no response preceding pursuit onset. We therefore consider the early response in *A* and *C* to be a visual response that is not a necessary component of the pursuit response. The small tick marks on the abscissa indicate 100-ms intervals. See Fig. 6 legend for definitions of abbreviations.

spond well before pursuit initiation and continued responding throughout the trial. In the control experiment illustrated in Fig. 9*D*, the target was displaced to a point outside the receptive field of the neuron (*point D*). Again, the neuron responded during the interval of smooth pursuit, but the response that had preceded eye movement onset in Fig. 9*C* was abolished.

We examined the time of onset of the pursuit response for cells in MTf, MSTd, and MSTl. Figure 10 shows the latency of this response for 48 cells in which we were certain that the initial response was not a visual one produced by the target motion within the receptive field of the cell. Zero on the abscissa indicates onset of the pursuit movement, and 44 of 48 cells began to discharge at least 50 ms after pursuit onset. This is consistent with the examples shown in Fig. 9 and with the notion that the pursuit response in the vast majority of cells follows, rather than precedes, pursuit onset. In these cells, the "early" response that sometimes precedes pursuit on-

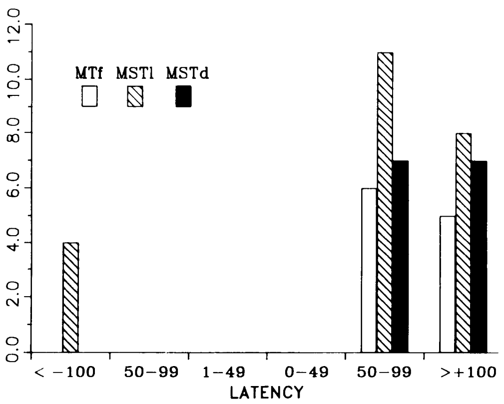

FIG. 10. Latency of pursuit response with respect to the onset of pursuit eye movements. Zero on the abscissa indicates the initiation of pursuit as judged by the end of the saccade to the target in a step-ramp pursuit task. The increase in discharge for most cells followed the onset of pursuit by at least 50 ms. Cells in the >100-ms bin had latencies of 200 ms or less except for one at 270 ms. Cells in the <−100-ms bin preceded pursuit onset by 130–160 ms. Any presaccadic pursuit would slightly change these latencies. However, since the size of the target steps in these experiments were large (usually at least 20°), and since our experience and that of others (10) indicates that such large target steps have the least presaccadic pursuit initiation, the error introduced by this measure is small.

set is not an obligatory component of the pursuit response. It is a separate response that may, or may not, be present depending on the spatial geometry of the pursuit target relative to the visual receptive field. We conclude, therefore, that these cells were only involved in pursuit initiation via their visual response to target motion in their receptive field and that an extraretinal input does not play a role in initiation of pursuit eye movements; it is more likely to be involved in the maintenance of ongoing pursuit eye movements (see DISCUSSION).

Figure 10 also shows, however, that four cells in MSTl began to discharge before the onset of pursuit. In each of these cases, the initial motion of the target occurred near the edge of, but clearly outside the receptive field as mapped during trials in which the monkey maintained fixation on a stationary target. For these cells, the early response might reflect a motor signal that is necessarily related to occurrence of the pursuit movement. An alternative explanation, however, is that the early response might simply reflect an enhancement of the normal visual response that has the effect of enlarging the receptive field by a small amount. If so, the early response is still visual in origin and is not qualitatively different from those discussed above. We therefore investigated this visual enhancement further.

Enhanced visual responses

Figure 11 illustrates data from a nonpursuit cell in MST whose visual response was enhanced when the monkey used the stimulus as a target for pursuit eye movements. As shown in the schematic drawing at the *top* of the figure, the visual receptive field of this cell was located in the upper field and included the fovea. The visual response to upward motion of the target was greater when the animal used the stimulus as a pursuit target (Fig. 11*A*) than when he maintained fixation during presentation of the same moving stimulus (Fig. 11*B*). The drawing at the bottom of Fig. 11*A* shows target position, vertical eye position, and cell response for a single trial in the pursuit task. The visual response of the cell occurred during the fixation period, before the saccade to the moving target. Stimulation of the retina by the moving target during this period is therefore identical in the paradigms of Fig. 11, *A* and *B*, but the monkey's use of the target is different in the two situations. The cell responded more vigorously when the monkey used the stimulus as a pursuit target. Enhancement effects have been observed in other brain structures when a stationary stimulus is used as a target for saccadic eye movements (22, 23), but Fig. 11, *C* and *D*, show that enhancement in this MST cell differs from that observed in other brain structures. The response obtained when the monkey used a stationary spot of light as the target for a saccade (Fig. 11*C*) was indistinguishable from the visual response obtained in the absence of the saccade (Fig. 11*D*). These observations indicate that the enhancement illustrated in Fig. 11*A* cannot be attributed to a generalized "use" of the target by the monkey. Rather, the enhancement in this MST cell was specifically related to use of a *moving* target for *pursuit* initiation.

To quantify the enhancement effect, we calculated the ratio of responses when the stimulus was, and was not, used as a pursuit target. Of 21 MST cells for which we performed the experiment outlined in Fig. 11*A* and *B*, six yielded a ratio of 1.5 or greater. In contrast, only one of nine MT cells reached this level of enhancement. This experiment

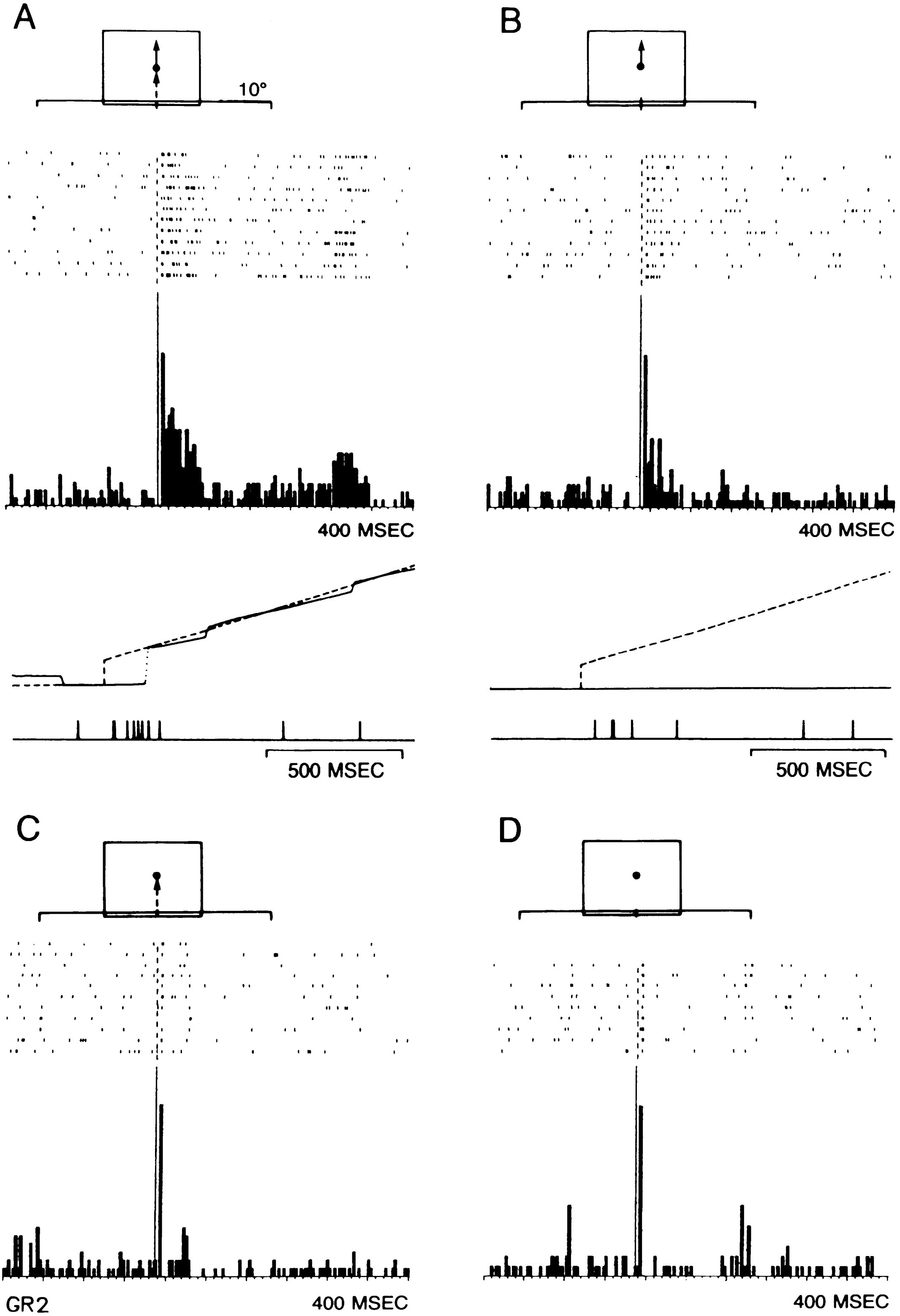

FIG. 11. Enhanced visual response of a medial superior temporal area (MST) cell when a moving stimulus was used as the target for a saccade. The receptive-field outline indicates its location in the upper visual field; the preferred

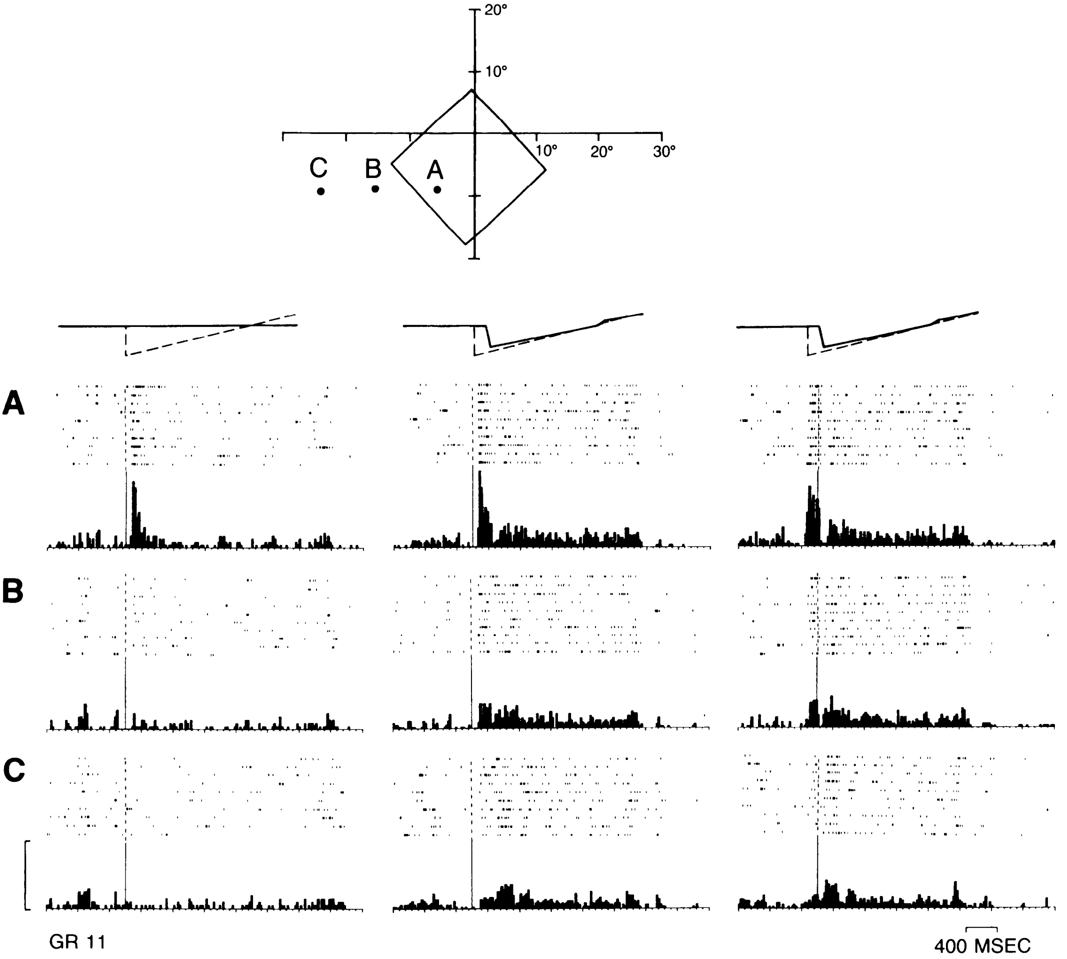

FIG. 12. Expansion of the visual receptive field of a lateral-anterior MST (MSTl) cell. The drawing shows the receptive field determined with moving spots of light while the monkey was looking at the fixation point in the center of the visual field. Rows labeled *A*, *B*, and *C* show cell discharge for the points labeled *A* (in the receptive field), *B*, and *C* (outside the receptive field). The *left* column shows the response of the cell to rightward motion of the spot after the stimulus stepped to *point A*, *B*, or *C* while the monkey fixated. The response of the cell is aligned on the step (as shown schematically at the *top* of the column). The *middle* column shows the response of the cell aligned on the same stimulus motion but for blocks of trials in which the monkey used the stimulus as a pursuit target (as indicated in the schematic illustration of target and eye position). The *right* column shows the same response as in the *middle* column but aligned on the end of the saccade to the moving stimulus rather than the step of the stimulus. The cell responded to target motion slightly at *B* but only when the monkey used the moving stimulus as the target for pursuit. There was no such response at *C*. Calibration line for the histograms is 250 spikes$\cdot$s$^{-1}\cdot$trial^{-1}.

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direction of motion was upward. On the drawing the 10° calibration is from the middle to the end of the horizontal line. The rasters show the response of the cell aligned on the onset of a spot of light at the same part of the visual field but under different behavioral conditions. In *A*, a moving spot of light came on, and the monkey made a saccade to the target and then pursued it. In *B*, the same moving spot came on, but in this series of trials the monkey continued to fixate rather than make a saccade to the target. Comparison of the responses in *A* and *B* shows that the response was enhanced when the monkey used the stimulus as a pursuit target. Single-trial records for each case are shown below *A* and *B*. The vertical eye position (——), the target position (– – –) with a 3° upward step, and cell discharge are shown on an expanded time base. In *C*, the monkey made a saccade to the same spot of light that came on but remained stationary, and in *D* the same stationary spot came on, but the monkey continued to fixate. Comparison of *A* and *C* shows that the enhancement is related to use of the stimulus as a target for pursuit, but not to its use as a target for saccades.

was only performed for those cells in MST that responded to small spots, all of which were located in MSTl. Although our sample of cells is small, this visual enhancement indicates the existence of an additional extraretinal signal that may also be localized to MST.

Figure 12 illustrates the responses of a pursuit cell in MST for which enhancement had the net effect of expanding the receptive field. The rasters in 12, *A*, *B*, and *C*, depict responses obtained with moving visual stimuli at *points A*, *B*, and *C*, in the schematic diagram at the *top* of the figure. The *left* column of rasters shows responses for trials in which the monkey maintained fixation during motion of the stimulus, and the *middle* and *right* columns illustrate responses when the monkey used the moving stimulus as a pursuit target. The individual trials in the *left* and *middle* columns are aligned on the onset of the visual stimulus. The *right* column depicts the same responses as the *middle* column, but the trials are aligned on the saccade to the visual target. The *middle* and *right* columns of rasters show that the neuron responded weakly during steady pursuit of the target, but we are particularly interested in the early visual response evident in several of the rasters. The cell responded well to motion within the receptive field at *point A* during fixation trials (Fig. 12*A*, *left* column), and the response was enhanced when the monkey used the stimulus as a pursuit target (Fig. 12*A*, *middle* column). The raster in the *right* column in Fig. 12*A* shows that the enhanced visual response preceded the saccade to the target. *Point C* was well outside the receptive field as mapped during fixation trials (see schematic drawing, Fig. 12), and the rasters in Fig. 12*C* show that visual responses were not observed at *point C* on fixation trials or on pursuit trials. *Point B* was also outside the receptive field as originally mapped, and the *left* raster in Fig. 12*B* confirms that no visual responses were obtained at this point during fixation trials. However, the *right* raster in Fig. 12*B* shows that a visual response preceded the saccade when the monkey used the stimulus as a pursuit target. Because we did not observe a similar early response at *point C* (*right* raster, Fig. 12*C*), we consider the early response at *point B* to be an enhanced visual response rather than a necessary component of the pursuit response. Therefore, the enhancement effect in this MST cell appears to expand the boundaries of the visual receptive field. Similar instances of receptive-field expansion are associated with saccade-related enhancement in a number of brain structures including the superior colliculus and substantia nigra (22, 23).

These observations on visual enhancement are important for interpreting the small number of instances in which the pursuit responses of individual cells appeared to commence before onset of pursuit eye movements (Fig. 10). For each of these cells, initial motion of the visual stimulus occurred outside, but close to, the receptive-field boundary as mapped during fixation trials. Although detailed controls were not performed for these cells, it is clearly possible that the early component of the pursuit response (that which immediately follows target presentation and precedes pursuit initiation) results from enhanced visual responses such as those demonstrated for the cell in Fig. 12. In short, then, we have no firm evidence that the early response reflects a genuine extraretinal input that is involved in generating the command to initiate pursuit, as has been suggested by other investigators (3, 16).

DISCUSSION

We have manipulated visual inputs during pursuit eye movements in order to determine whether the pursuit responses of neurons in the superior temporal sulcus are of retinal or extraretinal origin. Specifically, we removed retinal slip stimulation by blinking the target briefly during pursuit and by stabilizing the target on the retina during pursuit. We found that the pursuit responses of some cells are completely dependent on visual stimulation of the retina by the pursuit target, whereas the responses of other cells result from an extraretinal signal. Many cells receive both retinal and extraretinal inputs. Furthermore, the presence or absence of an extraretinal input was correlated with the anatomical location of the cell and, in some cases, with its visual properties as well. Pursuit cells in MTf rarely showed any indication of an extraretinal input and responded best to small visual stimuli. Pursuit cells in MSTd frequently received an extraretinal input and responded optimally to large-field visual stimulation. We observed a broad range of pursuit cells in MSTl, including all types observed in MTf and MSTd. Although much remains to be learned about these cells, the present data suggest several behavioral functions in which they may participate. We will briefly discuss three of these functions in light of our current knowledge of the physiology of these cells.

MTf and retinal slip

Manipulation of the visual inputs reduced the pursuit responses of the large majority of foveal MT cells in our sample. Response rates decreased when all visual stimulation was eliminated by a brief blink of the pursuit target and when visual motion was eliminated by target stabilization. These observations indicate that the pursuit responses of most MTf cells were dependent on visual motion stimulation or retinal slip, during pursuit. In support of this interpretation, the pursuit response of MTf cells always followed onset of the eye movement if the initial motion of the target was *outside* the visual receptive field of the cell. The pursuit response could commence *before* onset of the eye movement only if the initial motion of the target was inside the receptive field and in the cell's preferred direction. In net, our observations are consistent with the view that the pursuit responses of MTf cells are visual in origin and heavily dependent on motion of the target image on the retina during pursuit.

These cells are ideal candidates to convey a retinal slip signal to the pursuit system; they have visual receptive fields that include the fovea, and their pursuit responses appear to encode slip of the target on the retina. Such slip signals (or retinal velocity error signals) are known to be important for correcting errors in performance during the maintenance of ongoing pursuit eye movements (9). This hypothesis would be on firmer ground, however, if it were demonstrated that MTf cells faithfully encoded the retinal slip of the pursuit target during pursuit over a lighted background. In the present experiments, the experimental room was completely darkened in order to reduce the number of possible inputs to the cells. Under illuminated conditions, however, extraneous visual contours might affect the response of MTf cells during pursuit. Data presented in the following paper (7) suggest that the pursuit responses of some MTf cells are affected only weakly, if at all, by illumination of the background.

Previous behavioral experiments from this laboratory indicated that MT provides visual inputs for the *initiation* of pursuit eye movements (18). There is, however, no contradiction between the previous result and the present suggestion that MTf neurons may provide important visual signals for pursuit *maintenance.* This difference in functional roles is probably a simple correlate of retinal eccentricity. We would expect that neurons with eccentric receptive fields and relatively high optimal speeds (11, 13) are well suited for detecting the motion of peripheral stimuli that may become targets for pursuit or saccadic eye movements. Such cells are more likely to provide visual inputs for pursuit initiation. On the other hand, neurons with foveal receptive fields and relatively low optimal speeds are better suited for encoding slip signals during ongoing foveal pursuit. Such foveal neurons may also provide visual inputs for pursuit initiation if initial target motion occurs near the fovea. This reasoning is consistent with the results of lesion experiments, since lesions of peripheral MT impair pursuit initiation without affecting pursuit maintenance (18). Lesions of MTf, however, impair both the initiation and maintenance phases of pursuit (2).

MST and pursuit maintenance

MT provides a robust anatomical projection to MST (12, 20), and many pursuit cells in MST exhibited an extraretinal input in addition to the visual signal. In Fig. 13*A*, addition of the extraretinal signal to a retinal slip signal is indicated by a summing junction. One input to this junction is a visual one labeled MTf and MSTl. The other input is the source (as yet unidentified) of the extraretinal signal. The output, labeled MSTd and MSTl, represents pursuit cells in which these two signals are combined.

An attractive hypothesis is that pursuit cells in MST play a role in generating the motor signals responsible for the maintenance of ongoing pursuit. A formal scheme that could encompass our experimental observations has been proposed by Yasui and Young (25), and a variant of this is illustrated in Fig. 13*B*. In this model, a corollary discharge of an eye velocity signal is fed back and summed with

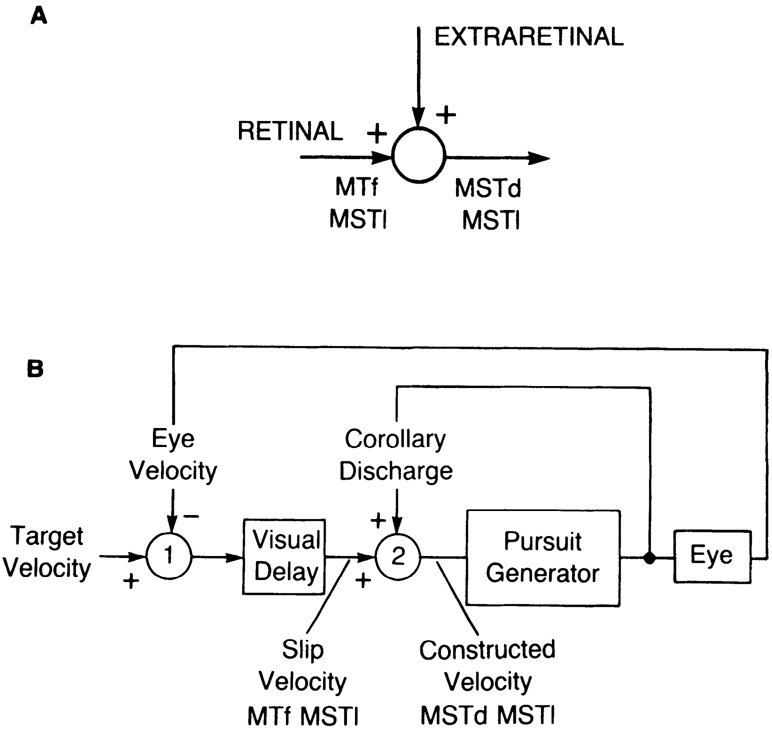

FIG. 13. Block diagram summarizing possible functional relationships between MTf, MSTd, and MSTl cells. *A*: inputs to cells showing an extraretinal input. *B*: possible role of these cells in generation of pursuit. See DISCUSSION for details.

retinal slip velocity to generate a motor command for pursuit maintenance. A significant virtue of this model is that it accounts for the ability of subjects to maintain pursuit in the complete absence of retinal slip signals (4, 8). Under these conditions, the retinal slip input to summing *junction 2* would be 0, but the positive feedback of eye velocity through corollary discharge would provide the necessary signal to maintain pursuit in the absence of retinal slip. With regard to the present experiments, it is plausible that the role of some pursuit cells in MST is to provide the summed slip and eye velocity signal to the oculomotor pursuit generator. In this view, the extraretinal input to pursuit cells in MST represents a corollary discharge of eye velocity that is important for pursuit maintenance.

This hypothesis has several experimental observations in its favor. First, both retinal and extraretinal signals are evident in the responses of many MST pursuit cells. Secondly, identification of the extraretinal input as corollary discharge is consistent with our current observation that this input, in a large majority of MST cells, does not become active until after onset of the eye movement. Finally, lesions that include MSTl are known to impair the maintenance of ongoing pursuit (1).

There are, however, several uncertainties that warrant caution in evaluating this hypothesis. First, we do not know whether the extraretinal input to MST pursuit cells actually reflects eye velocity. We must measure velocity tuning curves of the isolated extraretinal signal (i.e., under stabilized conditions) in order to resolve this question. Second, we have not established that the extraretinal signal is actually a corollary discharge; it might, in fact, reflect proprioceptive feedback from the orbit. It should be noted, however, that it would make no practical difference to the model as long as the proprioceptive signal were sufficiently precise to encode eye velocity. Third, only a minority of MST pursuit cells appears to be appropriate for encoding the summed signal as conceived in Fig. 13*B*. The visual inputs to cells in MSTd respond optimally, or exclusively, to full-field texture patterns, and these cells are therefore ill-suited for encoding the slip velocity of the tracking target. The most likely candidates for performing the motor function illustrated in Fig. 13*B* are the pursuit cells in MSTl that receive extraretinal inputs and whose visual responses are optimal for small spots. Finally, a feedback loop through the cerebral cortex such as that envisaged in Fig. 13*B* might be sufficiently long so as to introduce oscillations into the system.

MST and perception

An alternative role for pursuit cells in MST is that they are important for perceptual rather than motor functions. For example, MST projects directly to the parietal lobe (21), and parietal cortex appears to be crucial for perceiving and attending to the changing relations between the body and objects in surrounding space (14, 15). To accomplish this task, parietal cortex must have access to signals that reflect eye movements, head movements, and limb movements as well as information about the motion of objects in the external world. The extraretinal signal of pursuit eye movements carried by MST pursuit cells might well provide such eye movement information to parietal cortex, and a vestibular input related to head rotation (5) has also been demonstrated for some pursuit cells in the STS. The combination of these extraretinal signals and the visual signal produced by large-field stimulation in many of these cells might provide information about the spatial relationships between the subject and the environment. However, more information concerning the interaction of the visual and extraretinal inputs to these cells is necessary before this possibility can be reasonably evaluated. In the following paper (7), we describe interactions between these inputs, and we consider possible roles of pursuit cells in perception.

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