

Relation of Cortical Areas MT and MST to Pursuit Eye Movements. I. Localization and Visual Properties of Neurons

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SUMMARY AND CONCLUSIONS

1. Among the multiple extrastriate visual areas in monkey cerebral cortex, several areas within the superior temporal sulcus (STS) are selectively related to visual motion processing. In this series of experiments we have attempted to relate this visual motion processing at a neuronal level to a behavior that is dependent on such processing, the generation of smooth-pursuit eye movements.

2. We studied two visual areas within the STS, the middle temporal area (MT) and the medial superior temporal area (MST). For the purposes of this study, MT and MST were defined functionally as those areas within the STS having a high proportion of directionally selective neurons. MST was distinguished from MT by using the established relationship of receptive-field size to eccentricity, with MST having larger receptive fields than MT.

3. A subset of these visually responsive cells within the STS were identified as pursuit cells—those cells that discharge during smooth pursuit of a small target in an otherwise dark room. Pursuit cells were found only in localized regions—in the foveal region of MT (MTf), in a dorsal-medial area of MST on the anterior bank of the STS (MSTd), and in a lateral-anterior area of MST on the floor and the posterior bank of the STS (MSTl).

4. Pursuit cells showed two characteristics in common when their visual properties were studied while the monkey was fixating. Almost all cells showed direction selectivity for moving stimuli and included the fovea within their receptive fields.

5. The visual response of pursuit cells in the several areas differed in two ways. Cells in MTf preferred small moving spots of light, whereas cells in MSTd preferred large moving stimuli, such as a pattern of random dots. Cells in MTf had small receptive fields; those in MSTd usually had large receptive fields. Visual responses of pursuit neurons in MSTl were heterogeneous; some resembled those in MTf, whereas others were similar to those in MSTd. This suggests that the pursuit cells in MSTd and MSTl belong to different subregions of MST.

INTRODUCTION

The superior temporal sulcus (STS) of the macaque monkey contains a series of visual areas that are involved in visual motion processing. The first, the middle temporal area (MT), was identified anatomically (6, 50) on the basis of the direct projection it receives from striate cortex. Dubner and Zeki (8) and Zeki (51) first determined that a large fraction of the cells in this region show a directionally selective response to moving spots of light. MT in turn projects to other areas on the floor and anterior bank of the STS (27, 46). A part of this projection zone we will refer to as the medial superior temporal area (MST—see DISCUSSION for further consideration of this definition). This MST area, like MT, has a preponderance of neurons that show direction selectivity but that differ from MT in the size of their receptive fields and frequently in the size and type of their preferred stimulus (7, 44, 48).

In addition to an analysis of the visual properties of cells in those areas (1, 2, 4, 12, 25, 26, 40, 44, 51–53), recent experiments have attempted to relate this visual motion processing to either the perception of motion or to the initiation of movement dependent on such motion. The relation of MT to the perception of motion of patterns (31), motion aftereffects (38), and apparent motion (28, 29, 33), has been explored, and damage to MT has been shown to elevate the threshold for detection or discrimination of motion (34, 42). Other experiments (9, 10, 36) have attempted to relate MT and MST to the control of smooth-pursuit eye movements that is also the subject of this and the following two papers.

Pursuit eye movements must use motion information in order to match movement of the eyes to motion of a target, thereby reducing the slip of the target image on the retina. Chemical lesions of the extrafoveal region of MT impair a monkey's ability to initiate pursuit eye movements to a moving visual target (36). This deficit is a retinotopic one; pursuit initiation is impaired only for motion in a region of the contralateral visual field whose representation in MT was damaged by the lesion. This impairment is most easily interpreted as a deficit in the visual motion processing on which pursuit depends. Similar chemical lesions of the foveal representation of MT, which probably encroach on MST (9), or lesions of MST itself (10), produce a directional deficit superimposed on the retinotopic pursuit deficit. The directional deficit impairs all pursuit *toward* the side of the brain with the lesion regardless of the region of the visual field in which target motion begins. Whereas the retinotopic deficit reflects impaired visual processing, the directional deficit appears to involve visual-motor mechanisms underlying the generation of pursuit.

Single-cell activity during smooth pursuit has been found within the STS by Sakata, Kawano, and their collaborators (19, 41). They found that cells in the STS show continuous activity during pursuit eye movements even when the eye movement is made in the dark except for the moving target. The localization of these cells with respect to MT and MST and the nature of their inputs were not determined. Erickson (11) identified cells responding during pursuit in foveal MT and an adja-

cent area. His recording was done with a lighted background, and the response of these cells in the dark was not determined. The STS in turn has a direct projection to the dorsolateral pontine nucleus of the brain stem (15), and cells in this pontine region also discharge during pursuit eye movements (32, 43).

In the present set of experiments we have attempted to determine the location, the nature of the inputs, and the functional contribution of these pursuit cells within the STS. We have also attempted to identify which of a number of factors influence the discharge of the cells during pursuit—visual stimulation from slip of the pursuit target on the fovea, generation of the pursuit movement itself, or the sweep of the visual background during pursuit. Although pursuit eye movements are accompanied by motion of the background under natural conditions, previous studies (5, 20) have shown that this does not influence substantially the maintenance of pursuit. Therefore, it is important to distinguish cells discharging during pursuit without background and those whose discharge is due to background motion. We will use the term pursuit cell to designate the former group of cells because these are the cells most likely to be involved in the generation of a pursuit movement. This more stringent definition also makes our pursuit cells comparable to the “true pursuit cells” of Sakata et al. (41). In this paper we will concentrate on the visual characteristics of the pursuit cells and their location within MT and MST. In the next paper (37), we determine how the two other factors listed above, the slip of the target and the generation of pursuit, influence these cells. Finally, in the third paper (22) we have determined the interaction of the pursuit response of these cells with that due to motion of the visual background.

In this paper we have localized pursuit cells to subregions within MT and MST: in foveal MT (MTf), in a dorsal-medial area of MST (MSTd), and a lateral-anterior area of MST near MT fovea (MSTl). We find two visual properties common to nearly all pursuit cells in these regions: direction selectivity and inclusion of the fovea in the visual receptive field of the cells. We also find two differences in the visual properties between the regions. MTf cells differ from MSTd cells in responding to small spots rather than full-field stimuli

and in having small rather than large receptive fields whereas MSTl cells are a mixture of these cell types.

A brief report of these experiments has appeared previously (21).

METHODS

Behavioral paradigms

Four monkeys (*Macaca mulatta*) were used in these experiments. During the experiments, monkeys sat in a plastic primate chair and faced a tangent screen 86 cm away. The field coils of a magnetic search-coil system (used to record eye position) surrounded the chair but allowed an unobstructed view of the screen out to 40° from the center.

Two kinds of visual tasks were employed: a visual fixation task and a visual pursuit task. In either task, a trial started when the monkey touched a bar in front of him that turned on a spot of light (fixation spot) on the tangent screen. In the fixation task, the fixation spot stayed on for ~3 s, then dimmed, and if the monkey released the bar within a brief period of time (usually 600 ms), he received a drop of water as a reward (49). If he released the bar earlier or later, he received neither reward nor punishment. During this fixation period we projected a second visual stimulus onto the screen in order to determine the visual characteristics of the cell under study: the size and location of its receptive field, its preferred visual stimulus (as determined by comparing cell responses to several different stimuli), and whether it was directionally selective. In the pursuit task, the fixation spot was turned off 0.8–1.2 s after its onset, and another spot of light (the pursuit target) appeared at another location on the screen, moved for 1–3 s, and then dimmed. The location of the target, its direction of movement, and its speed were varied, but the target usually appeared 20° in visual angle away from the center of gaze and moved at 16°/s back toward the center of gaze.

During a trial, the monkey was required to keep his eye in a position window centered on the fixation point or on the pursuit target. If the monkey made an eye movement outside of the window, the trial was aborted. In the pursuit task, this window was removed during the initial 400 ms of target motion to allow the monkey to shift his gaze from the fixation spot to the pursuit target.

The fixation spot and the pursuit target were produced by light-emitting diodes (LED) (Stanley H-2K) that were back projected onto the tangent screen using a single lens optical system. The fixation spot was directly projected from the light source onto the center of the screen. The pursuit target was projected via a double galvanometer mirror system, and a smooth linear motion of the

target was obtained by feeding a voltage ramp into the galvanometer. The size of the fixation spot was 0.2° in diameter, the size of the pursuit target was 0.6°, and the luminance of both was 3.7 cd/m².

The entire tangent screen was illuminated by the light from a tungsten filament bulb (0.2 cd/m²). However, when the neuronal response to pursuit eye movements was examined, this background light was turned off, and since light sources such as CRT displays were separated by thick black drapes from the monkey, the monkey was in total darkness except for the fixation spot or pursuit target. Furthermore, to eliminate any increased sensitivity to light by dark adaptation, we turned on the background light during every inter-trial interval.

The behavioral tasks as well as storage and display of digitized data were controlled by a real-time experimental system (REX) developed by Hays, et al. (16), which was run on a PDP 11/34 computer.

Recording and data analysis

After the behavioral training, surgery was performed under general anesthesia (pentobarbital sodium). A stainless steel cylinder for single-cell recording was implanted over a trephine hole in the skull. In four hemispheres, the cylinder was placed vertically over posterior parietal cortex so that electrodes passed through parietal cortex into the cortex of the STS. In the other two hemispheres, the cylinder was tilted ~20° off the horizontal plane and was placed over occipital cortex so that electrodes passed through striate cortex and lunate sulcus in a parasagittal plane. A stainless steel socket for connecting the monkey's head to the primate chair was also implanted. An eye coil was surgically placed under the conjunctiva of one eye using the method of Judge, et al. (18) and was connected to a plug on top of the skull. The recording cylinder, the socket, and the eye coil plug were all embedded in one acrylic cap covering the top of the skull and connected to the skull by implanted bolts and selftapping screws. Recording was started no sooner than 1 wk after the surgery, and the monkey was given analgesia during the postsurgical period.

For cell recording, a hydraulic microdrive (Narishige) was mounted on the recording cylinder, and initial mapping of the STS was done with a glass-coated platinum-iridium electrode. We identified MT by its location within the STS, by the characteristic direction selectivity of its neurons, and by the eccentricity-size relationship of its receptive fields. We were then able to locate MST by virtue of its position adjacent to the border of MT.

We studied the pursuit cells in these areas in one of two ways. In three hemispheres [11, 12, and M2 (the letter designates the monkey and the number indicates the order in which hemispheres in the

same monkey were studied)], we mapped the location of pursuit cells with respect to these areas by using a grid of electrode penetrations. This was done in two hemispheres in one monkey (*I1* and *I2*) by recording from single cells with glass-coated platinum microelectrodes in a near-horizontal approach through the lunate sulcus. In another hemisphere (*M2*) we recorded from single cells and clusters of cells in vertical penetrations. The glass-coated microelectrodes were introduced through a plastic grid (with holes separated 1.5 mm center to center) placed in the recording cylinder. This grid produced more parallel electrode penetrations and facilitated the subsequent histological reconstruction of the electrode tracks. In many penetrations during these experiments, one or more electrolytic lesions (10 μ A for 10–60 s) were made for later identification of the penetration. The second way we studied pursuit cells [in the other 3 hemispheres (*C1*, *M1*, and *G1*)] was by using stainless steel guide tubes directed toward areas in MT and MST. This allowed concentrated sampling in one area rather than mapping of the entire area. The tip of the guide tubes were positioned in the gray or white matter 3–5 mm above the targeted recording sites in the STS. Single cells were recorded on electrode penetrations through these guide tubes using flexible tungsten electrodes (Frederick Haer).

Visual receptive-field mapping was done by projecting visual stimuli onto the tangent screen while the monkey looked at the fixation spot. A spot or slit of light, or a random-dot pattern was used as the visual stimulus. Spots and slits were produced by either the same LED used for generating the pursuit target or by a hand-held projector. For the stimulus produced by a hand-held projector, spots were ~ 1 – 15° in diameter, and slits were ~ 1 – 15° in length and 0.2– 3° in width. Random dots were produced either by a hand-held projector with a dot pattern or by a computer-generated pattern. The area of random dots generated by the hand-held projector was rectangular in shape and ranged from $\sim 30 \times 15^\circ$ to $70 \times 50^\circ$. A random-dot stimulus (static not dynamic) was also produced by a microcomputer and projected onto the screen using a TV projector as described in a following paper (22). In this stimulus, spatially separated small dots (0.2° diam) moved in a rectangular field with one of the following sizes ($80 \times 66^\circ$, $40 \times 40^\circ$, $30 \times 30^\circ$, $20 \times 20^\circ$, and $9 \times 11^\circ$). The stimulus (spot/slit or random dot) that produced the largest response was used in subsequent tests. Cells yielding equal responses to both stimuli were usually studied using spots of light. Neuronal response was judged using the audio monitor and an on-line raster display. The area of the visual receptive field was determined by oscillating the stimulus at successive points away from the center of the recep-

tive field until the cell no longer responded. The edge of the receptive field was recorded as the point where the response was lost. For some cells that were activated only by a large field of random dots, the extent of the receptive field could not be accurately plotted. Cells were classified as directionally selective if they gave a consistent response to motion in one direction but little or none for motion in the opposite direction.

We assessed pursuit-related responses while the monkey pursued targets whose motion was controlled by the computer. A cell was classified as a pursuit cell when it showed clear change of activity from the background activity level and when the change was maintained during the pursuit. The preferred directions of both passive visual responses and the pursuit responses were determined to the nearest 45° .

At the end of an experimental session, the monkey was returned to his home cage. The monkey's weight was monitored daily and supplementary water and fruit given if necessary.

Histology

At the end of the experiments, monkeys were deeply anesthetized with pentobarbital sodium and were perfused through the heart with saline followed by 10% Formalin. The posterior half of the brain was sectioned in the sagittal plane and stained with cresyl violet for cell bodies and with a modified silver stain (13) for myelinated fibers. In each monkey, the STS and surrounding cortex was displayed on "unfolded" maps using the method of Van Essen and Maunsell (47).

For the hemispheres in which mapping was done by a series of penetrations, electrode tracks were identified on the basis of the relative location of the penetration to the entire recording area, the spatial relationship to other tracks, marking lesions, and the depth profile during a penetration. The approximate location of each recording site on the track was determined based on the distance from landmarks such as appearance and disappearance of gray matter or marking lesions. The results were plotted on the unfolded map by projecting each recording site onto layer IV.

For the hemispheres in which recording was through guide tubes, each guide tube was identified in the same way as described above. Although we can often see a spray of electrode tracks emanating from the guide tube in histological sections, it was not possible to identify each track. Instead, we made an estimate of the extent of the recording site based on the size of the spray.

RESULTS

We recorded neuronal activity in the STS in six hemispheres of four awake, behaving

monkeys. Our sample includes 525 single cells from five hemispheres (*I1*, *I2*, *C1*, *M1*, *G1*) and 373 multiple cell recordings from one hemisphere (*M2*). Of these, 165 single cells and 21 multiple cell recordings were classified as pursuit related.

We considered a cell to be pursuit related (a pursuit cell) if it responded continuously

during smooth pursuit of a small target in an otherwise dark room, and Fig. 1 shows an example of such a cell. Fig. 1*A* illustrates the activity of the cell during pursuit of a moving target. As depicted on the schematic drawing (*left*, Fig. 1*A*), the target stepped 20° down from the fixation spot and then moved upward at 16°/s. The adjacent histogram and

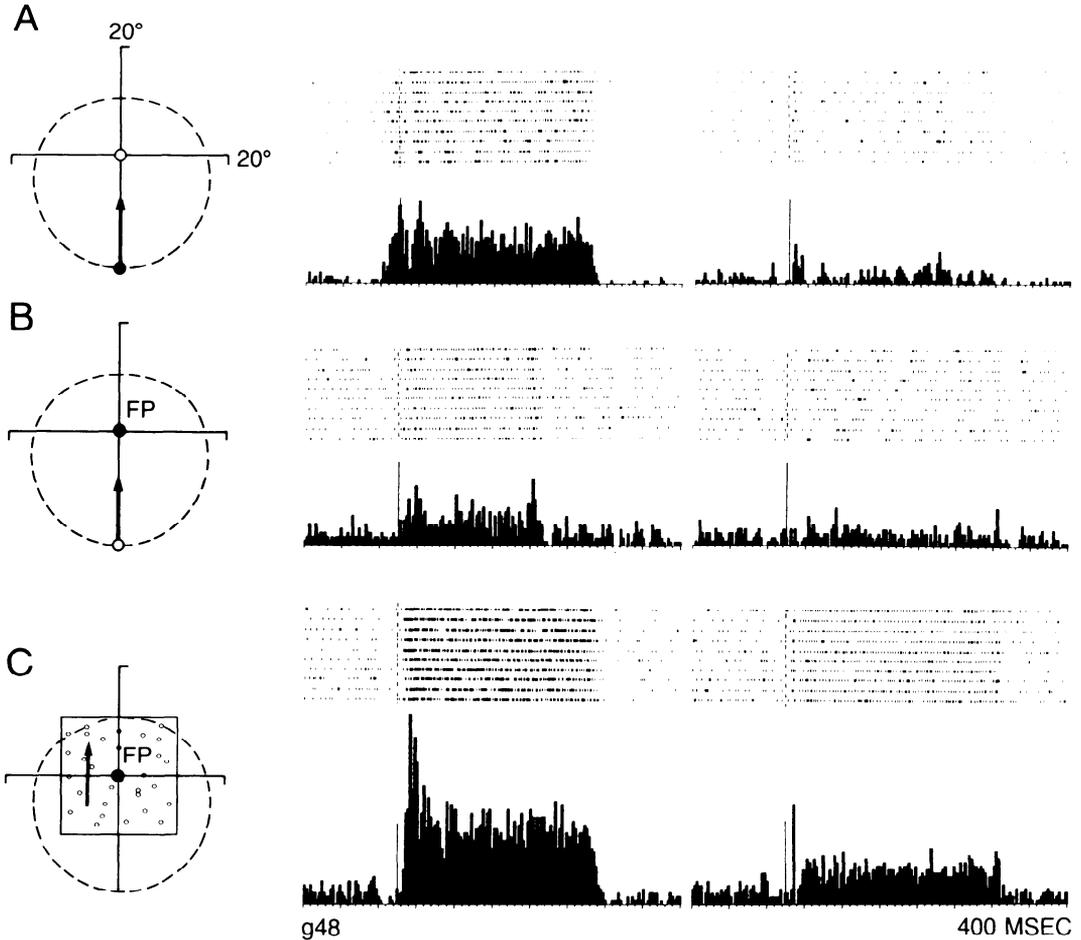


FIG. 1. Discharge of a pursuit cell during smooth-pursuit eye movements (*A*) and visual stimulation (*B* and *C*). In *A*, the drawing on the *left* shows the visual receptive field (\circ) and target motion (\uparrow). When the fixation spot disappeared, the target appeared 20° below it and moved upward at 16°/s. Histograms and rasters show the response of the cell during the pursuit eye movement made to this upward target motion (*middle*) or comparable downward motion [*right*, (Following an upward step)]. Vertical lines are aligned on the initiation of pursuit. In this and subsequent histograms, binwidth is 10 ms, and the height of the vertical bar indicates 250 spikes \cdot s $^{-1}$ \cdot trial $^{-1}$. *B*: visual response to a moving small spot. As shown on the drawing, a small spot (0.6° diam) appeared 20° below the fixation spot (FP) and moved upward at 16°/s while the fixation spot remained on. Histograms and rasters are for upward movement of the spot (*middle*) or comparable downward movement of the spot (*right*), aligned on stimulus onset. *C*: visual response to moving random dots. Computer-generated moving random dots were presented in a 20 \times 20° square field centered on the FP for 2 s. Histograms and rasters are for dots moving upward (*middle*) or downward (*right*) at 11°/s; both are aligned on stimulus onset. The dots on the raster display indicate cell discharge, 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; the cell number is in the *bottom left* corner.

raster (*middle*, Fig. 1A) show the increase in discharge rate during this upward pursuit. The raster and histogram (*right*, Fig. 1A) show that the cell did not respond during downward pursuit. The response during upward pursuit could not be attributed to passive visual stimulation by background contours, since the room was completely dark except for the dim LED that served as the pursuit target.

Pursuit cells were almost always activated by visual stimulation during fixation. Of 176 pursuit cells tested using both spots and random dots, 172 cells (98%) showed a visual response to at least one of these stimuli. The pursuit cell shown in Fig. 1 responded weakly to a small moving spot (Fig. 1B) and strongly to moving random dots (Fig. 1C). For either spots or random dots, upward motion produced a stronger response than did downward motion. The dashed line in the schematic drawing indicates the extent of the visual receptive field that clearly included the fovea. The pursuit-related response of this cell, therefore, might result from visual stimulation by the pursuit target within the receptive field. Alternatively, the pursuit response may be more directly related to performance of the pursuit movement, and this issue is considered in detail in the following paper (37). In the present paper, we are concerned first with the anatomical localization and then with the visual responses of the pursuit cells.

Identification of MT and MST

Our procedure was to identify MT and MST physiologically, then assign pursuit cells to one of these areas, and finally to analyze the visual responses of these cells. These studies were carried out in an extensively mapped STS in one hemisphere, in the STS of two less completely mapped hemispheres, and in a series of guide tubes directed toward regions of particular interest in the STS of three other hemispheres. The extensively mapped hemisphere is shown on the two-dimensional map of the STS in Fig. 2A. The solid lines indicate the edge of a gyrus, the dashed lines the fundus of a sulcus. The orientation of the STS is indicated by the key for anterior and posterior (A, P) and medial and lateral (M, L). The fundus of the STS opens up into a floor indicated by the added dashed line in the lateral

STS. The myeloarchitectonically identifiable areas are also outlined and labeled. The densely myelinated area on the posterior bank includes MT, and another densely myelinated zone (DMZ), reported previously (7, 35), is outlined on the anterior bank; the striped edges in both cases indicate areas of uncertainty about the location of the border.

Figure 2B shows the portion of this map limited to the STS and indicates recording sites in relation to the boundaries of the same densely myelinated areas shown in Fig. 2A. In Fig. 2B circles indicate the approximate recording sites where we obtained visual responses to spots or slits of light or to random-dot stimuli. Closed circles indicate the sites where we obtained directionally selective visual responses. As can be seen in Fig. 2B, most of the cells located in the posterior half of the recording sites (*left* side in the figure) were directionally selective. Within this region of directionally selective cells, we used a physiological criterion to identify the border of MT and MST: the relationship between the eccentricity of the center and the size of the receptive field. We first recorded in MT well away from the MT-MST border, measured the relationship between eccentricity and receptive-field size, and obtained a linear regression line for this relationship (as in Fig. 3A). This regression line has a slope of 0.65 and a high correlation coefficient ($r = 0.93$). The slope falls between that of Desimone and Ungerleider (0.72) (7) and of Tanaka et al. (0.47) (44), which strengthens our assumption that we are sampling from a population of MT cells. We next used this linear regression line to assign cells near the border of MT and MST to one area or the other. We assigned cells close to the regression line to MT and those with larger receptive fields to MST. The border of MT thus identified is outlined on Fig. 2B by the thicker solid line. The boundary of physiologically identified MT cells agreed well with the densely myelinated area on the posterior bank of the STS (thinner solid line).

The dashed line in Fig. 2B encloses the area of directionally selective cells outside of MT that lie on the fundus, floor, and anterior bank of the STS. In this area, the average receptive-field size was larger than for MT cells, and the scatter of receptive-field sizes was also larger, as shown in Fig. 3B. The linear regres-

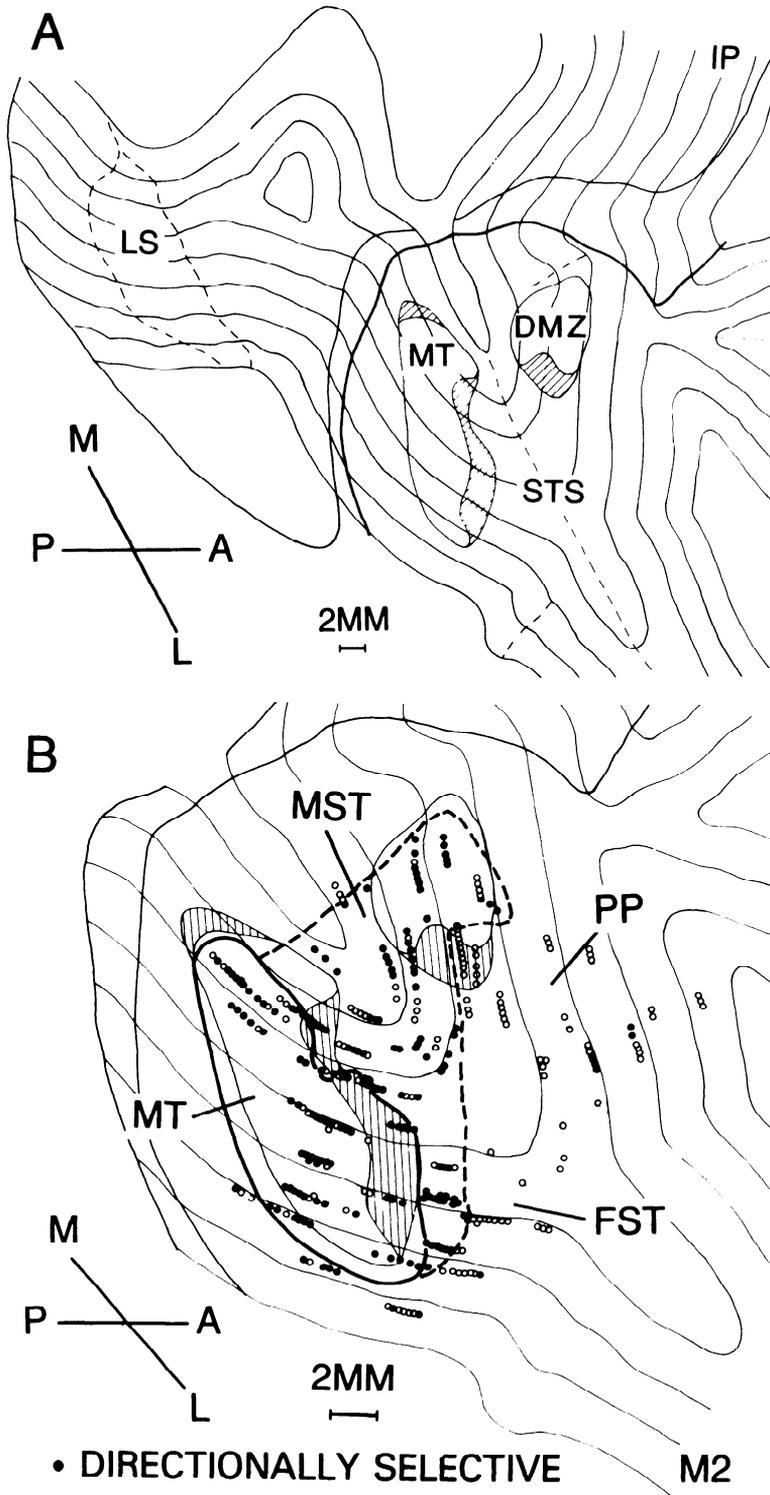


FIG. 2. Location of the middle temporal area (MT) and the medial superior temporal area (MST) within the superior temporal sulcus (STS). *A*: two-dimensional map of STS and surrounding cortex reconstructed from parasagittal sections by the method of Van Essen and Maunsell (47). Each thin line represents layer IV of 1 section; sections are 2 mm apart. The thicker line shows the boundaries of the STS at the cortical surface, and provides a reference in

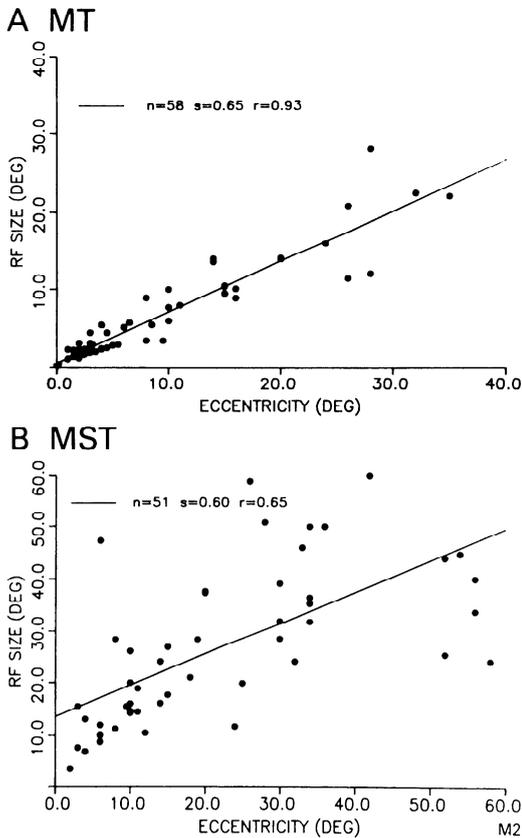


FIG. 3. Relationship between eccentricity of receptive-field (RF) center and receptive-field size of MT cells (*A*) and MST cells (*B*) from hemisphere *M2*. The linear regression lines were derived using the method of least squares. The receptive-field size is the square root of the receptive-field area. Eccentricity is the distance from the fixation point to the geometric center of the receptive field. See Fig. 2 legend for definitions of abbreviations.

sion line has a slope of 0.60 similar to that of MT but an intercept consistent with the larger receptive-field sizes in MST, as was

noted previously (7). The correlation coefficient ($r = 0.65$) was much lower than that for MT cells. We regarded this area as MST because of the similarity of this area to the descriptions of MST in the literature (7, 48), namely the high frequency of directionally selective cells, the anatomical location relative to MT, and the larger receptive-field size compared with MT. The lateral border of MST was fairly clear because of a sharp transition from directionally selective cells to nondirectionally selective cells. MST largely encompassed, although it was not coterminous with, the DMZ on the anterior bank (ovoid outlined by a thin solid line on the anterior bank). The dorsal border of this area was shown to nearly correspond to the border of the MT projection zone on the anterior bank (46).

In the area lateral and anterior to MT and MST along the floor of the STS, we found cells that showed no direction selectivity, preferred stationary flashes or spots of light, and had receptive fields that included the fovea. We designated this area [floor of the STS (FST) in Fig. 2*B*]. In contrast, cells located laterally on the anterior bank had receptive fields located in the periphery, and we designated this area as PP (posterior parietal). Both terms (FST and PP) are those of Desimone and Ungerleider (7), and our use of both terms is subject to limitations we will consider in the discussion. We also encountered many auditory cells and some polysensory cells in this anterior bank area. We do not have a large enough sample to determine whether these two nondirectionally selective areas on the posterior and anterior bank are two different areas or two parts of one larger area.

B and subsequent maps that shows only the STS region of this larger map. The dashed lines indicate the fundus of sulci [lunate sulcus (LS); intraparietal sulcus (IP); superior temporal sulcus; STS)]. Densely myelinated areas are enclosed by solid lines, with hatched areas indicating regions where the border is uncertain. The area on the posterior bank is labeled as middle temporal (MT) and on the anterior bank as densely myelinated zone (DMZ). The key in the bottom left corner indicates medial (M), lateral (L), anterior (A), and posterior (P) directions. *B*: location of directionally selective cells plotted on an expansion of the same map shown in *A* (hemisphere *M2*). Circles indicate the approximate recording sites. Recording sites were first determined on each section, projected onto layer IV, and then plotted on the unfolded map. When 2 recording sites were too close on the map, circles were displaced to reduce overlap. Closed circles indicate directionally selective cells; open circles indicate visually responsive cells that were not directionally selective. The thin lines with hatching at the edges outline the densely myelinated area as in *A*. The heavy line on the posterior bank is drawn at the border of physiologically identified MT as described in the text. The dashed line encloses the physiologically identified MST. The medial border of MST is only an estimate because the transition from directionally selective responses to nondirectionally selective responses is based on a single penetration. FST, floor area of STS; PP, posterior parietal area.

Location of pursuit cells

Figure 4 shows the location of pursuit cells in the same hemisphere as that shown in Fig. 2. In this hemisphere, 21 cells out of 210 cells tested responded during pursuit of a target in the dark. Pursuit cells were found primarily in three subregions of MT and MST.

In MT, pursuit cells were identified in the lateral-anterior region where the cells had small receptive fields close to the fovea. This corresponds to the known representation of the fovea in MT, and we will refer to this area as MTf. We found no pursuit cells in the me-

dial two-thirds of MT where the extrafoveal visual field was represented. Fig. 5C shows one of the penetrations made through MTf on which pursuit cells (P) were obtained at three recording sites. In this penetration, the recording sites on the posterior bank of the STS were from the zone with dense myelination (the borders of which are shown by small bars). The location and preferred direction of the receptive fields changed in an orderly way as has been reported previously for MT (2, 7, 8, 51). All receptive fields obtained in this penetration included part of the fovea ($<2^\circ$

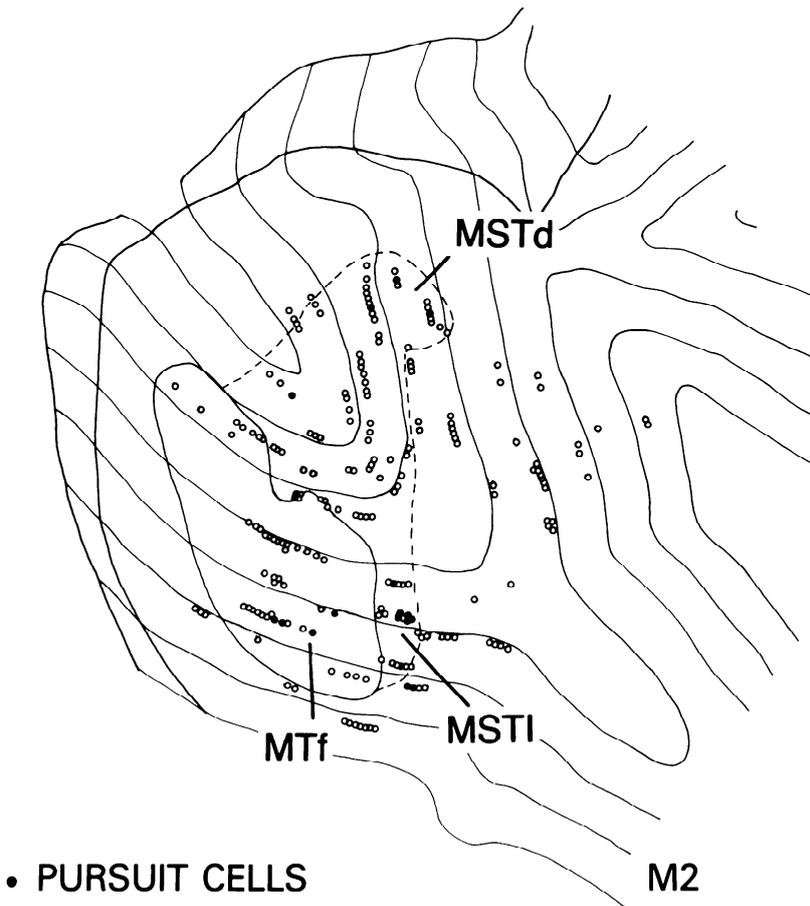


FIG. 4. Location of pursuit cells in MT and MST in 1 hemisphere (*M2*). ○, recording sites of cells that were tested for a response as the monkey pursued a moving target in the dark; ●, cells that responded during pursuit under these conditions. The solid line is the border of physiologically identified MT, the dashed line is physiologically identified MST as described in Fig. 2. Pursuit cells were found primarily in MT fovea (MTf), in the dorsal-medial region of MST (MSTd), and in the lateral edge of MST (MSTl). We were unable to identify with certainty the penetrations on which we found 2 other pursuit cells, so that only 19 of 21 cells found are plotted. Judging from the depth profile or the coordinates of the penetrations, we can infer that one was an MTf cell and the other was an MSTl cell. See Fig. 2 legend for definitions of abbreviations.

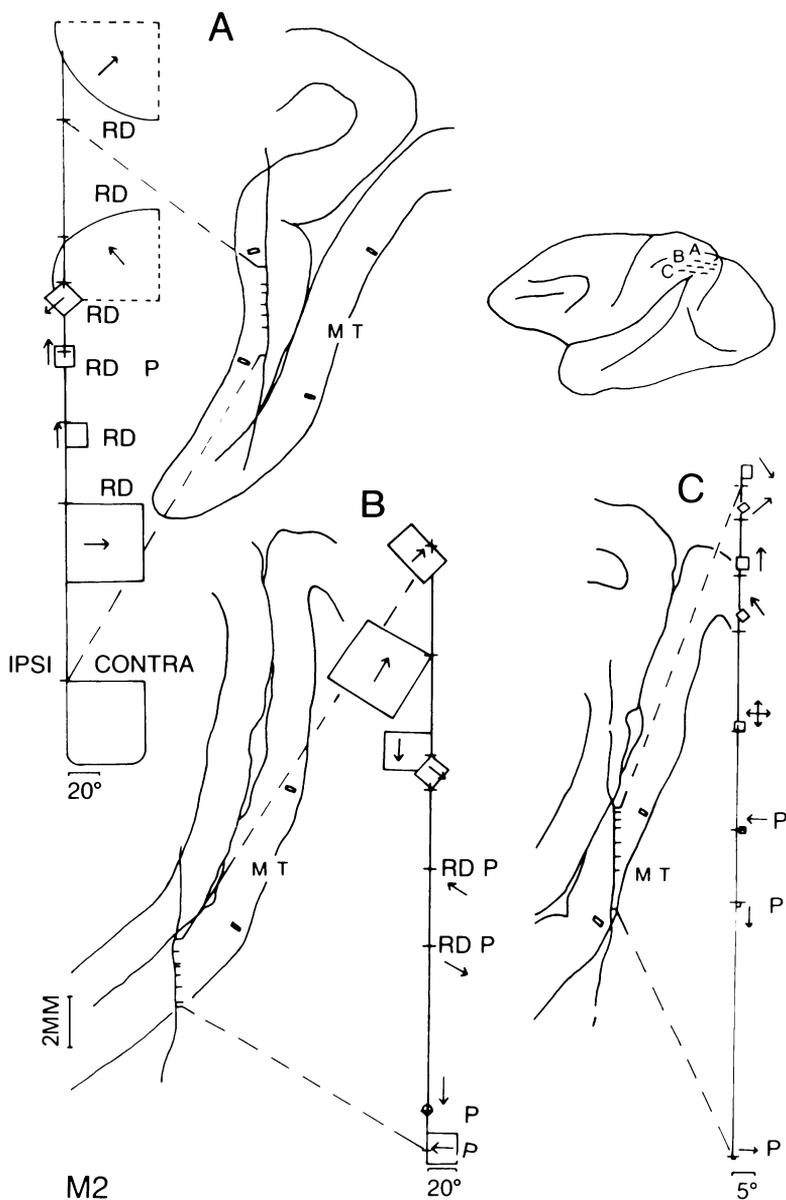


FIG. 5. Examples of individual penetrations that were used to make the map in Fig. 4. *A*: example of a penetration through MSTd; *B*: penetration through MSTl; *C*: penetration through MTf. The lateral view of the monkey brain in the *top right* shows the planes of the 3 parasagittal sections shown in *A*, *B*, and *C*. The drawing of each penetration consists of the outline of the anterior and posterior bank of the STS obtained from these parasagittal sections. Approximate recording sites (horizontal tick marks on the penetration) were obtained by comparing the depth of each recording with entrance or exit from gray matter as well as with electrolytic lesions made at several locations. The drawing at the side of each penetration shows the location of pursuit cells (*P*) and the visual receptive field of the cells (outline drawing). Arrows indicate the preferred direction of stimulus motion. On each receptive-field drawing, the intercept of the long vertical bar by a small horizontal bar indicates the fixation point, the *right* side of the vertical bar represents the contralateral (*CONTRA*) visual field; the *left* side, the ipsilateral (*IPSI*) visual field. Receptive-field boundaries are indicated by solid lines or by dashed lines for uncertain peripheral edges. The length of the horizontal bars at the lower end of vertical bar indicates 20° in *A* and *B* and 5° in *C*. Cells marked *RD* preferred random-dot stimuli over spots or slits. The other cells preferred spots or slits, or showed similar preference to both. *RD*, random-dot stimuli; *MT*, middle temporal area.

from the center of the visual field), and all cells preferred small spots or slits rather than random dots as visual stimuli.

Pursuit cells in MST were located laterally and anteriorly in the posterior bank and floor close to the MT-MST border, an area we will refer to as lateral MST (MSTl in Fig. 4). Figure 5B shows a penetration made through MSTl on which pursuit cells were obtained at four recording sites. In this penetration, the recordings on the posterior bank of the STS were from sites anterior and lateral to the MT zone of dense myelination. Every visual response obtained in this penetration showed direction selectivity but with no clear order of preferred directions. The size of the receptive fields was on average much larger than those of MT cells at corresponding eccentricities, and several receptive fields were located mainly in the ipsilateral visual field.

Other pursuit cells were found in the dorsal-medial area of MST, an area we will refer to as dorsal MST (MSTd in Fig. 4). Of these four MSTd pursuit cells, three were located in the densely myelinated area of the anterior bank (not shown in Fig. 4). Figure 5A shows one of the penetrations made through MSTd in which a pursuit cell was obtained. The vi-

sual receptive fields were recorded from the zone with dense myelination on the anterior bank of the STS, and at each recording site, except for the deepest one, cells were directionally selective and preferred random dots to spots or slits. Receptive fields were larger than those in MT and even larger than the MSTl cells shown in Fig. 5B. As in MSTl, we observed no clear order in the shift of preferred direction.

We did not find pursuit cells in the intermediate part of MST that occupies a wide area along the fundus of the STS. Two pursuit cells were found just outside of the lateral border of MST in the area classified as FST.

We attempted to confirm this distribution of pursuit cells by doing similar mapping in both hemispheres of a second monkey (*I1* and *I2*, Fig. 6). In these hemispheres, MT and MST cells were again identified using their direction selectivity to moving visual stimuli, their receptive-field size, and the myeloarchitectonic border between MT and MST. In Fig. 6A, cells were sampled throughout MT and the lateral and dorsal-medial part of MST, but only a few cells were studied in the intermediate part of MST. Pursuit cells were found in areas comparable to the MSTl and

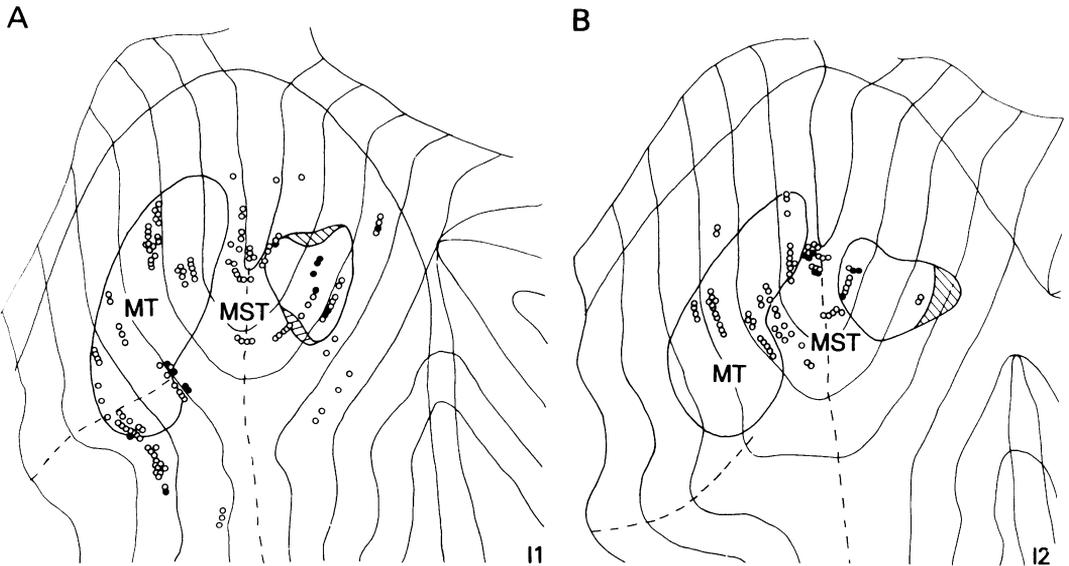


FIG. 6. Distribution of pursuit cells in MT and MST in 2 other hemispheres (*I1* and *I2*, A and B, respectively). Circles are single-cell recording sites, closed circles are pursuit cells. Solid line on posterior bank is MT identified by a combination of anatomical and physiological criteria. Solid line on anterior bank is the densely myelinated area. Dashed line in the middle is the fundus of the STS; leftward dashed line indicates where the fundus expands into the floor of the STS, which was prominent in these hemispheres. See Fig. 2 legend for definitions of abbreviations.

MSTd regions shown in Fig. 4. Although only one pursuit cell is shown in MTf of Fig. 6A, six more were found in that area as judged by their receptive-field properties but were not identified histologically with certainty. In Fig. 6B, recording was concentrated in the intermediate to dorsal-medial part of MST and pursuit cells were again identified in MSTd.

Whereas results of these two hemispheres were consistent with those shown in Fig. 4, the total number of pursuit cells sampled in our mapping procedure still remained small. To confirm the distribution of these cells, we implanted guide tubes directed toward specific areas after a series of exploratory penetrations. The *top* sections of Fig. 7 show the location of guide tubes in two hemispheres (Fig. 7, *A* and *B*, *M1* and *C1* respectively). The location and approximate extent of the recording sites are indicated by the numbered circles (referred to as *A1*–*A5* and *B1*–*B7*). Two guide tubes were located in MTf (*A5* and *B6*), one in the extrafoveal region of MT (*B4*), two in MSTl (*A3* and *B1*), four in MSTd (*A2*, *A4*, *B2*, and *B3*), one in the intermediate part of MST (*B5*), and two in the PP area (*A1* and *B7*).

The *middle* sections of Fig. 7 show the proportion of directionally selective cells at each of the guide-tube recording sites. The radius of the circle indicates the number of cells sampled, and the dark fraction of each circle indicates the percentage of cells with directionally selective visual responses. Cells within MTf, MSTl, and MSTd were largely directionally selective. In contrast, fewer than half of the cells obtained from PP (*A1* and *B7*) were directionally selective. In one guide tube (*B1*), we found a number of cells that were not directionally selective and that preferred a flashed, stationary spot of light. This guide tube was located close to the lateral border of MST, and it is plausible that some of the cells were recorded lateral to the border of this area, namely from FST, and we designated these cells as FST cells. In another guide tube (*B2*), many cells had receptive fields in the periphery, but the receptive-field sizes were smaller than those of typical MST cells. These cells showed a clear directionally selective response to moving spots as well as to the large random-dot patterns that are usually preferred by MSTd cells. These properties are similar to the cells in area MTP de-

scribed by Desimone and Ungerleider (7). They considered MTP to be an extension of MT beyond the densely myelinated area in which the far periphery is represented. We regarded these cells as MTP cells and excluded them from the population of MSTd cells recorded from this guide tube; there were no pursuit cells among them.

The *bottom* sections of Fig. 7 show the proportion of pursuit cells in the sample recorded from each guide tube. Pursuit cells were recorded from guide tubes *A2*, *A4*, *B2*, and *B3* (MSTd), *A3* and *B1* (MSTl), and *A5* and *B6* (MTf). No pursuit cells were recorded from other guide tubes. These results confirm our conclusion that pursuit cells were concentrated in the areas of MTf, MSTd, and MSTl. In addition, the high percentage of pursuit cells obtained from guide tubes directed toward MTf, MSTl, and MSTd shows that pursuit cells are encountered more frequently at specific sites within these areas. This observation was consistent with our impression from mapping studies (Fig. 5, *B* and *C*) that pursuit cells occur in locally enriched clusters.

The striped segment of the circles in the *bottom* section of Fig. 7 indicates a small proportion of cells whose spontaneous discharge was suppressed during pursuit. Such cells were seen in MST and also in MT (although not for the cases shown in Fig. 7). These neurons usually showed such a decrease in discharge rate for all directions of pursuit movements, in contrast to the directional response of cells showing an increase in discharge rate. We have not included these neurons on the maps for the other hemispheres (*M2*, *I1*, *I2*), since they are usually few in number.

Visual receptive fields of pursuit cells

What was very clear about the visual properties of the pursuit cells was that nearly all (167 of 176) showed a directionally selective visual response. The relationship between preferred direction of pursuit movement and preferred direction of stimulus motion was also highly predictable but dependent on the type of stimulus used as we describe in the third paper (22).

We tried to find a relationship between receptive-field characteristics of cells in the STS and the location of the pursuit cells. Figure 8 shows two different measures of visual recep-

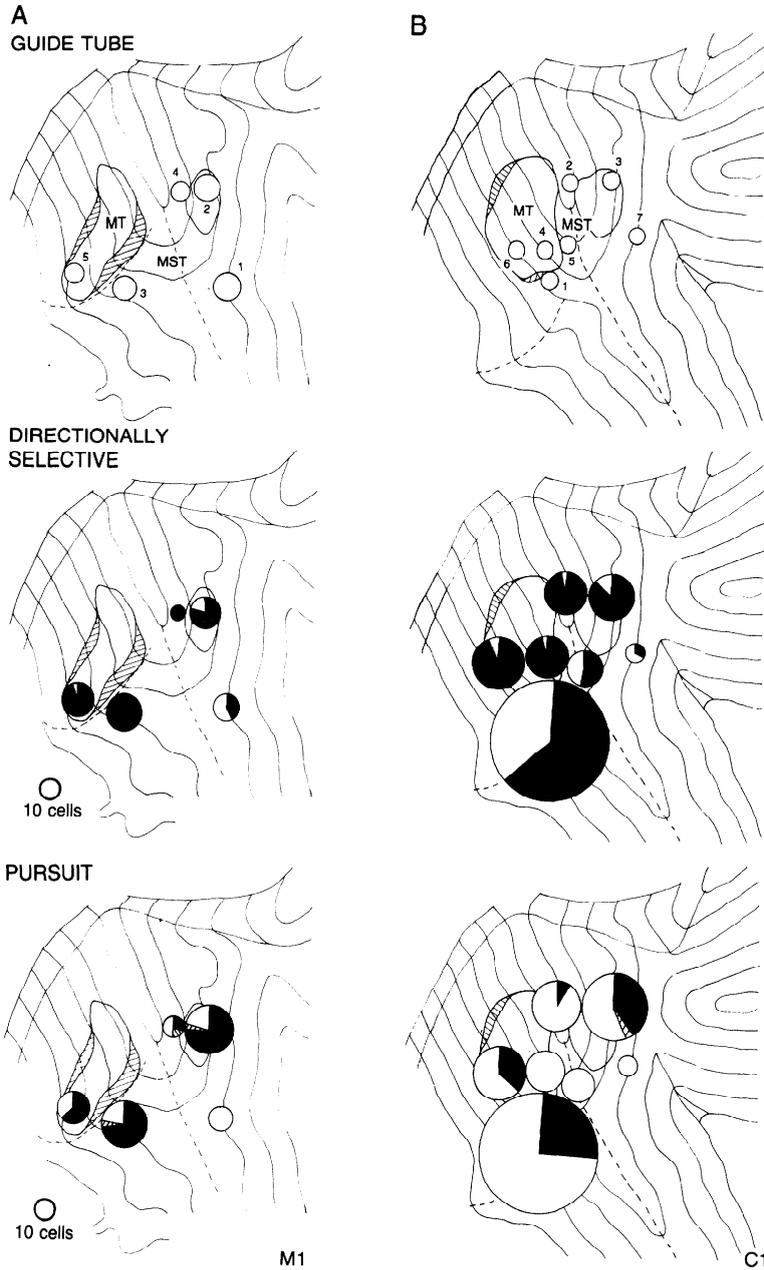


FIG. 7. Frequency of directionally selective and pursuit-related cells recorded through guide tubes implanted in several locations in the STS in hemisphere *M1* (A) and *C1* (B). *Top*: histologically verified location of guide tubes; approximate extent of the recording area is indicated by circles. The solid line on posterior bank is the anatomically identified middle temporal area (MT), that on anterior bank is the densely myelinated area. *Middle*: proportion of directionally selective cells in each guide tube. The radius of each circle is proportional to the number of cells recorded from each guide tube (key is for 10 cells). The dark area represents directionally selective cells; the light area, nondirectionally selective cells. *Bottom*: proportion of pursuit cells recorded in each guide tube. The dark area represents pursuit cells that discharged during pursuit in the dark, the hatched area shows pursuit cells whose discharge was suppressed during pursuit, and light area shows cells that showed no change in discharge during pursuit.

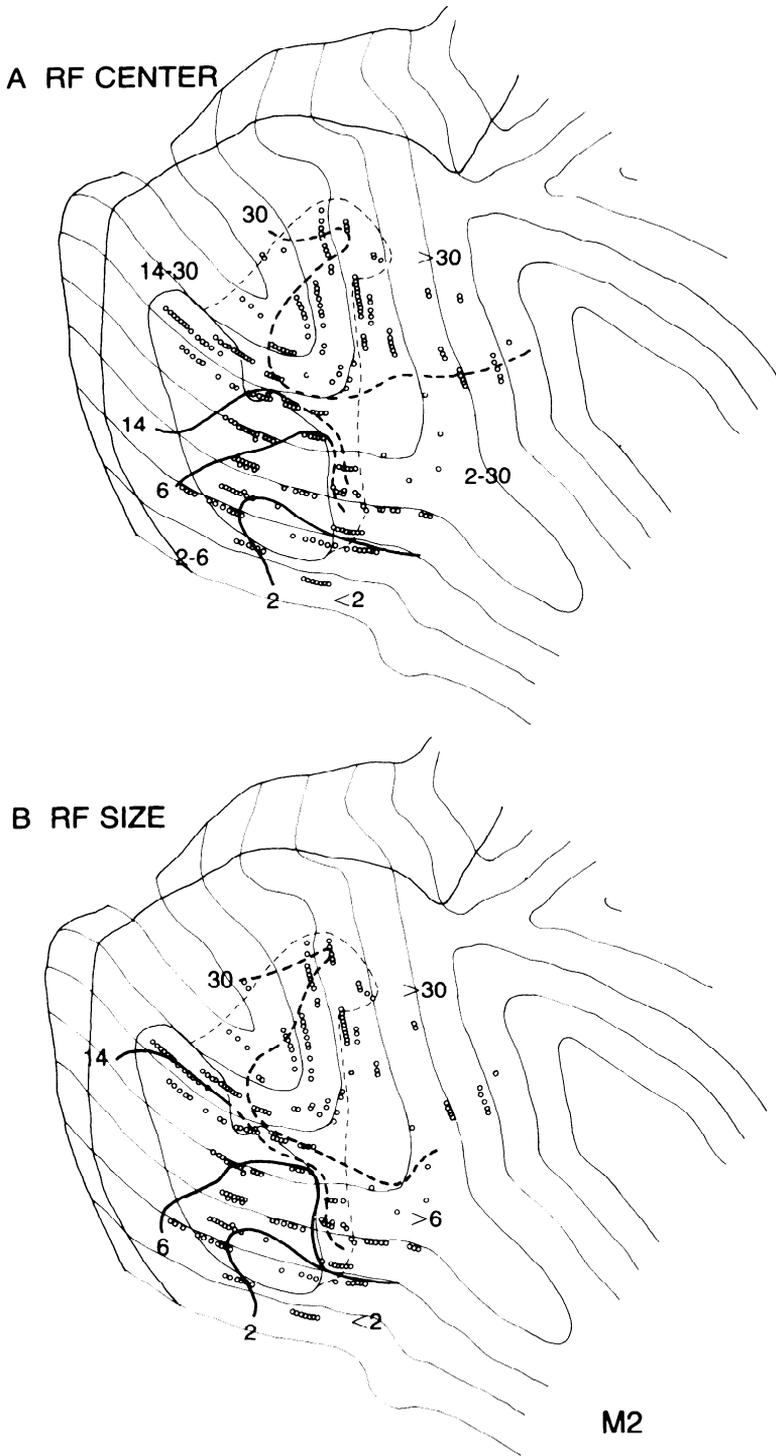


FIG. 8. Representation of eccentricity of receptive-field center (*A*) and receptive-field size (*B*) in MT and MST of hemisphere *M2*. Heavy lines are isocurves for a given eccentricity or size; solid lines are clear borders; dashed lines are uncertain borders. Circles indicate only recording sites where eccentricity (*A*) or size (*B*) information was obtained. RF, receptive field.

tive fields for the same hemisphere shown in Fig. 2. Figure 8A shows the eccentricity of receptive-field centers, and Fig. 8B shows receptive-field sizes. To measure the eccentricity of the receptive field, we determined the distance in degrees of visual angle between the geometric center of the field and the fixation point, used here as a measure of foveal location. We described receptive-field size by using the square root of the receptive-field area. The darker contour lines (with numbers at the ends) in Fig. 8 indicate the limit of a given eccentricity or size of the receptive field and are superimposed on outlines of MT (thin solid line) and MST (thin dashed line).

In MT, as expected, we found that the visual field was represented from the central visual field to the peripheral visual field along a lateral-to-medial axis (7, 14, 48). Along this axis, eccentricity of receptive-field center and receptive-field size increased systematically. By comparing the location of pursuit cells in MT shown in Fig. 4 to these visual field maps, it became evident that pursuit cells were located only in the area of MT where the center of the visual field was represented and where the size of the receptive fields was small.

The relationships were not so obvious in MST where we found only a crude representation of the visual field. The eccentricity of the receptive-field center in MST showed a tendency for cells located in MSTd (see Fig. 4) to have receptive fields that include the periphery ($>14^\circ$)¹ whereas cells located in MSTl had central and peripheral receptive-field centers that were intermixed ($2\text{--}30^\circ$). Thus, MSTd cells tended to have eccentrically centered receptive fields whereas MSTl cells were spread from center to periphery. There are a number of exceptions to this distinction, however, as indicated by the dashed isoeccentricity lines.

A difference between MSTd and MSTl was also evident for the representation of receptive-field size (Fig. 8B). Cells located in MSTd had a tendency to have large receptive fields, greater than 14° on a side, but cells in MSTl

had receptive fields ranging from 2 to $>30^\circ$ on a side. Thus cells in MSTd tend to have eccentrically centered receptive fields of large size, whereas cells in MSTl show an intermingling of eccentricities and sizes.

In both MT and MST the clearest relationship between pursuit cell location and receptive-field measures emerged when we determined the proximity of the central edge of the receptive field to the fovea (Fig. 9). In MT, the eccentricity of the receptive-field edge increased in the lateral-to-medial direction as was the case with the eccentricity of the receptive-field center. In MST there was not such a uniform progression but rather several clusters of cells with similar eccentricity as is delineated by the darker isoeccentricity lines in Fig. 9. All cells studied whose receptive fields included the fovea are indicated by closed circles and regions of different eccentricities are separated by contour lines. Cells with receptive fields including the fovea were located on the anterior bank in MSTd and on the posterior bank and floor in MSTl. In contrast, in the intermediate part of MST along the fundus of the STS as well as the medial part of MT, cells represented the periphery, and few pursuit cells were found. Thus pursuit cells in both MT and MST are located in subregions where the representation of the visual field approaches the fovea.

These observations on the relation of pursuit cells to visual receptive-field properties were confirmed when we sampled cells in different areas of MT and MST using the implanted guide tubes described in Fig. 7. The dark bars in Fig. 10 indicate the distribution of receptive-field size, eccentricity of receptive-field center, and eccentricity of receptive-field edge for pursuit cells, and the open bars indicate the same for all cells. The cells were from the same guide tubes directed at MSTd, MSTl, and MTf shown in Fig. 7. For receptive-field size and eccentricity of the center (*left* and *middle* in Fig. 10), MTf receptive fields were small and close to the fovea, MSTd receptive fields were large (all $>14^\circ$ in size) and eccentric, and MSTl fields were more mixed for both characteristics. The central edge of the receptive fields were obviously always within the fovea in MTf and, with a few exceptions, were also within the fovea in MSTl and MSTd.

¹ There were few MSTd cells that had receptive fields restricted to within 14° of the fovea. The 2 cells in the *middle* of Fig. 5A are examples of such an exception; these are the smallest MSTd cells obtained.

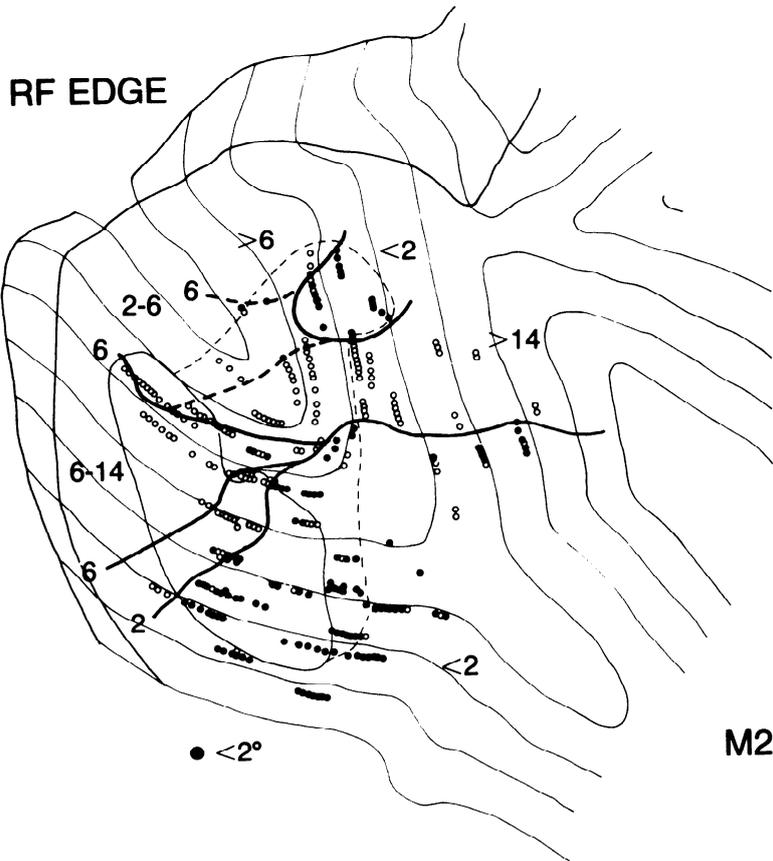


FIG. 9. Representation of eccentricity of the central edge of receptive fields in MT and MST of hemisphere *M2* both for pursuit and nonpursuit cells. Circles indicate the recording sites where the receptive-field (RF) edge was determined. Closed circles indicate cells whose receptive-field edges were within 2° of the fixation point. Solid iso-eccentricity lines indicate borders that surround cells with homogeneous eccentricities; dashed lines indicate less certain borders enclosing cells that do not all have similar eccentricity ranges.

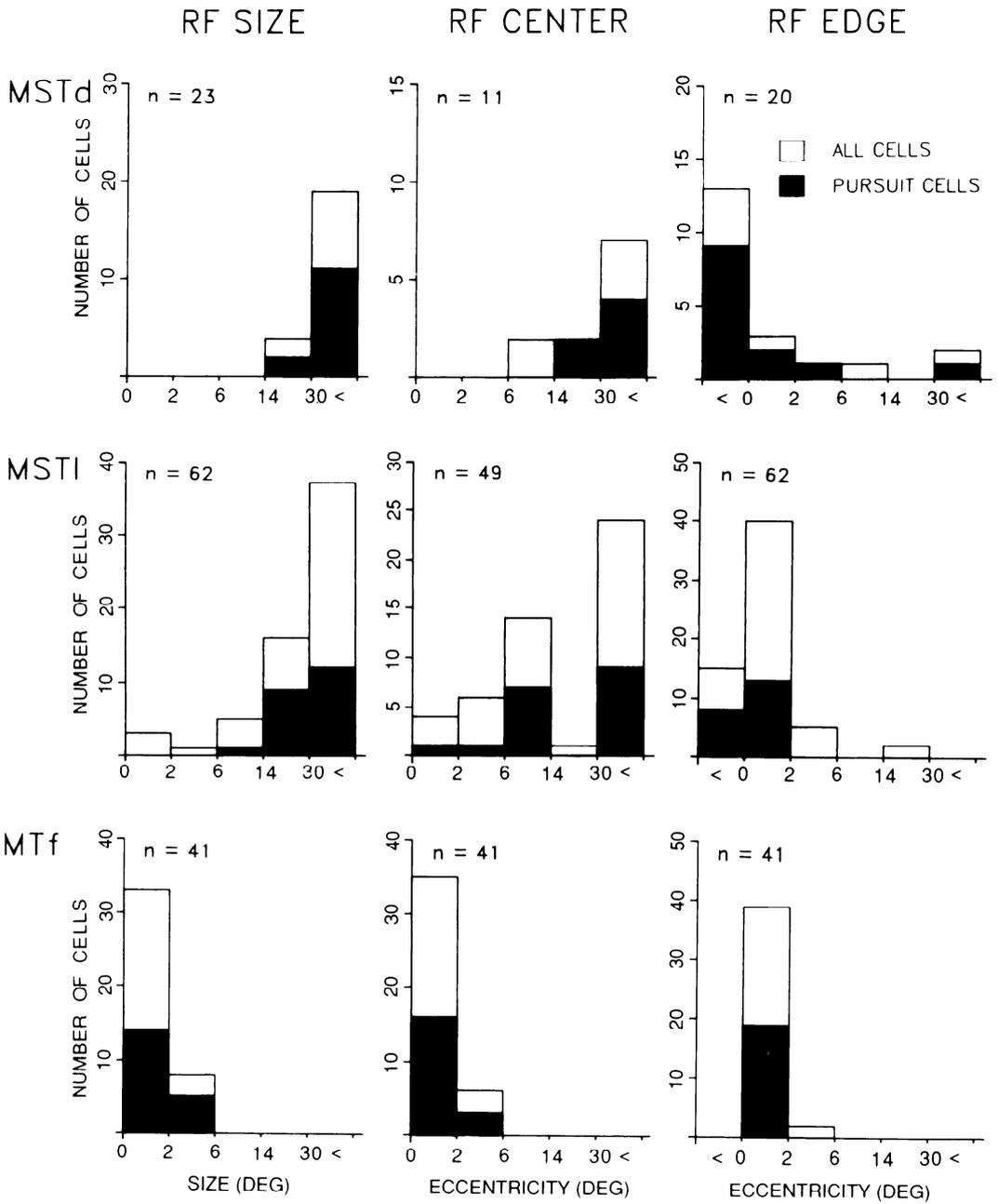
In net, whereas MTf represents a uniform population of cells with small receptive fields including the fovea, MST has regional differences. Both MSTd and MSTl cells have receptive fields that usually include the fovea. But MSTd cells tend to have large sizes and eccentrically centered receptive fields whereas MSTl contains an intermingling of cells with large and small fields and central and eccentric receptive fields.²

² From the mapping study, we know some MSTl cells have fairly small receptive fields (RF) close to the fovea. Therefore, the results indicated in Fig. 10 seem to be skewed toward larger eccentricity and size than expected. This is probably due to a restricted recording area and reflects the sharp increase of the RF size and eccentricity of the RF center in MSTl that is shown in Fig. 8.

For cells that did not have a pursuit-related discharge, Fig. 10 shows that in MTf the distribution of these nonpursuit cells is nearly identical to the pursuit cells. In MST the nonpursuit cells have a similar but usually somewhat wider spread of field characteristics. As far as we can determine, the pursuit cells appear to be a subpopulation of the directionally selective visual cells.

Preferred visual stimulus of pursuit cells

We have tested the visual response of cells in MT and MST using two types of stimuli, one a spot or slit and the other a field of random dots. Figure 11 shows the preferences of pursuit cells (Fig. 11A) and all cells (Fig. 11B) for these visual stimuli. A spot was produced



M1 C1

FIG. 10. Distribution of receptive-field (RF) size (left), eccentricity of receptive-field center (middle), eccentricity of receptive-field central edge (right) for cells recorded from the guide tubes shown in Fig. 7. The recording sites are divided into MSTd (top), MSTl (middle), and M1f (bottom). The abscissa is bins in degrees; the bin of (<0) in RF edge is for cells whose receptive fields included the fovea and which crossed the vertical meridian. The dark bars indicate pursuit cells, the light bars indicate all cells. See Fig. 4 legend for definitions of abbreviations.

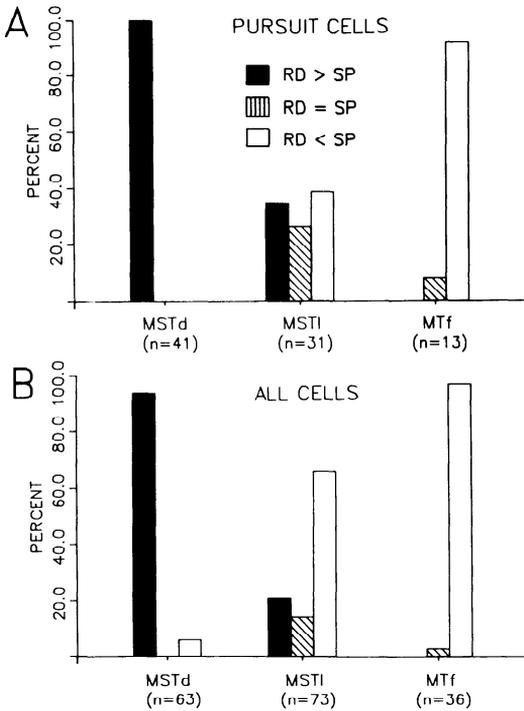


FIG. 11. Comparison of responses of MSTd, MSTl, and MTF cells to well-localized [spots and slits (SP)] and random-dot (RD) stimuli. *A*: results for pursuit cells; *B*: results for all cells studied. The light bars indicate cells preferring spots or slits of light; dark bars, those preferring random dots; hatched bars, those having nearly equal preference for both stimuli. Note that nearly all MSTd cells preferred random dots, nearly all MTF cells preferred spots. The results include data from the 4 hemispheres (*Ml*, *Cl*, *I1*, *I2*) in which single-cell recording was done. See Fig. 4 legend for definitions of abbreviations.

by a hand-held projector whereas dots were produced either by a hand-held projector with a dot pattern or by a wide field ($80 \times 66^\circ$) computer-generated random-dot pattern. Cells in MSTd nearly always preferred random-dot stimuli (RD, dark bars). Cells in MTF preferred spots or slits (SP, light bars) which is not surprising in light of the demonstration of suppressive surrounds of many MT cells (3, 44). Cells in MSTl had both of these types of stimulus preferences, and some MSTl cells responded equally to both kinds of stimuli (striped bars). For all MSTl cells, $\sim 65\%$ preferred small spots, 15% showed similar response to either spots or random dots, and 20% preferred random-dot stimuli. In the intermediate area of MST (not shown in Fig. 11) representing only the peripheral

visual field, $\sim 50\%$ of the cells preferred spots, 30% showed similar responses to either spots or random dots, and 20% preferred random-dot stimuli. The distribution of stimulus preference is therefore similar to that of the total sample of cells in MSTl.

Our random-dot stimulus differs from the spot and slit stimuli by being both larger and richer in texture. When we increased the size of a random-dot field while keeping the dot density constant, the response of the cells clearly increased. When we kept the size constant and increased the density, we observed no change in response. These results show a sensitivity to size but not to the texture of the stimulus. However, we also observed that these cells were not activated by a large area of light comparable to that of the random-dot pattern that indicates that contrast distributed over a wide area is necessary to activate these cells. More detail on the response of these cells to large-field stimulation will be given in a following paper (23).

We conclude that there are two kinds of pursuit cells with regard to the preferred visual stimulus; one group of cells is clearly activated by well-localized visual stimuli such as spots or slits, the other group requires a larger pattern such as random dots to be effectively stimulated. Nearly all cells in MTF prefer spots of light, nearly all cells in MSTd prefer random dots, and cells in MSTl may prefer one stimulus, the other, or respond equally well to both.

Preferred direction of the pursuit response

Chemical lesions within the STS that invade MTF or MST produce a directional pursuit deficit; pursuit toward the side of the lesion is impaired (9, 10). We therefore wanted to know whether there was any pronounced bias in the preferred direction of the visual or pursuit response for this population of neurons.

Figure 12 shows the preferred direction of the pursuit and visual response in relation to the side of the brain on which the cell was found, ipsilateral or contralateral. For the pursuit response (Fig. 12, *left*), cells in MST (MSTd, MSTl) showed a slight bias for pursuit in the contralateral direction. For the visual response (Fig. 12, *right*) cells in MST also showed a bias for motion to the contralateral

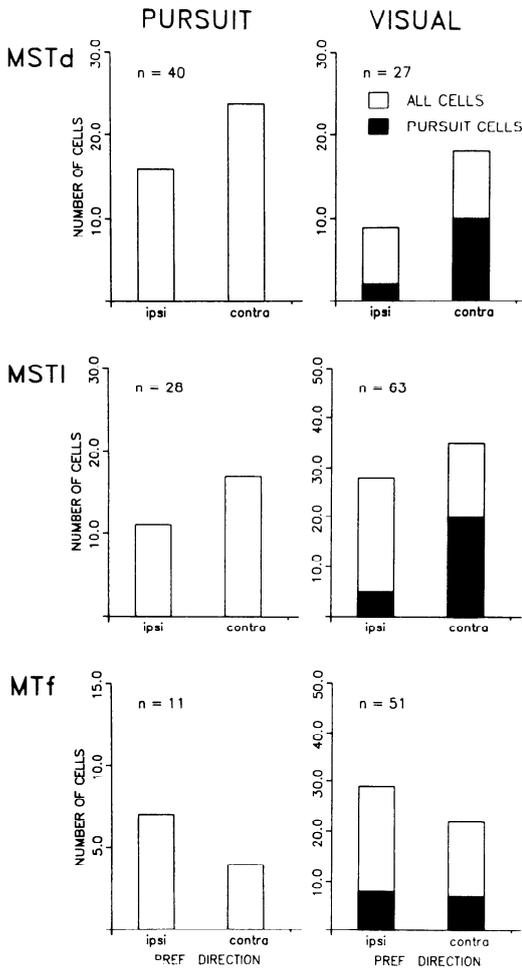


FIG. 12. Preferred directions of pursuit responses (*left*) and visual responses (*right*) of cells in MSTd, MSTl, and MTf. The horizontal components of all directions are grouped into those toward the side of the brain where the cell was located or away from that side. The results include directions of pursuit or visual motion 45° above or below the horizontal, but not up or down. For the visual response, the light bars are for all cells studied, the dark bars are for pursuit cells. The visual response is for cells where the response to spots or slits of light or a small field of random dots ($9 \times 11^\circ$ or less) was known. Results include cells obtained in the 2 hemispheres where single-cell recording was used for mapping and the 2 hemispheres where guide tubes were implanted. For MST a bias for pursuit movement or stimulus motion toward the contralateral (*contra*) side is evident. For MTf, a slight bias toward the ipsilateral (*ipsi*) side is evident. See Fig. 4 legend for definitions of abbreviations.

visual field. This bias was clearer for pursuit cells (dark bars in Fig. 12) than for all cells (light bars in Fig. 12). For both the pursuit

and visual response of cells in MTf, any bias was toward the ipsilateral side.

DISCUSSION

We have identified the motion areas within the STS, MT, and MST, on the basis of physiological and anatomical criteria. By determining the relation of cells to a behavioral output, pursuit eye movements, as well as to a visual input, we have been able to identify further functional subregions within MT and MST. We have found that cells discharging while the monkey pursues a target moving in the dark (pursuit cells) were located in foveal MT (MTf), an adjacent lateral-anterior region of MST (MSTl), and a dorsal-medial area of MST (MSTd). The regions where these pursuit cells were found also had specific visual properties. In the following sections, we will consider first the visual regions identified in this study in relation to those identified in previous studies and then the relation of pursuit cells to previous reports of similar cell types.

Visual areas anterior to MT

We think that our observations continue a series of refinements in the understanding of MST that have occurred in the last several years. Van Essen, Maunsell, and Bixby (48) were the first to note that the area adjacent and anterior to MT has a high proportion of cells that were directionally selective and had receptive fields larger than those of comparable eccentricity in MT. This area was subsequently included in what Maunsell and Van Essen (27) identified as the projection zone of MT within the STS, and which they designated as the MST. MST included the area on the floor and anterior bank of the STS as illustrated in their map shown in Fig. 13A. Their work was followed by two physiological studies that concentrated on MST.

The first study by Tanaka et al. (44) and by Saito et al. (40) found that the area anterior and adjacent to MT has a high proportion of directionally selective cells throughout its medial-to-lateral extent, and they regarded this area as MST (Fig. 13B). These authors also reported that in the medial two-thirds of their MST area, cells frequently responded to changes of size and rotation of visual stimuli. They called this subregion within MST the

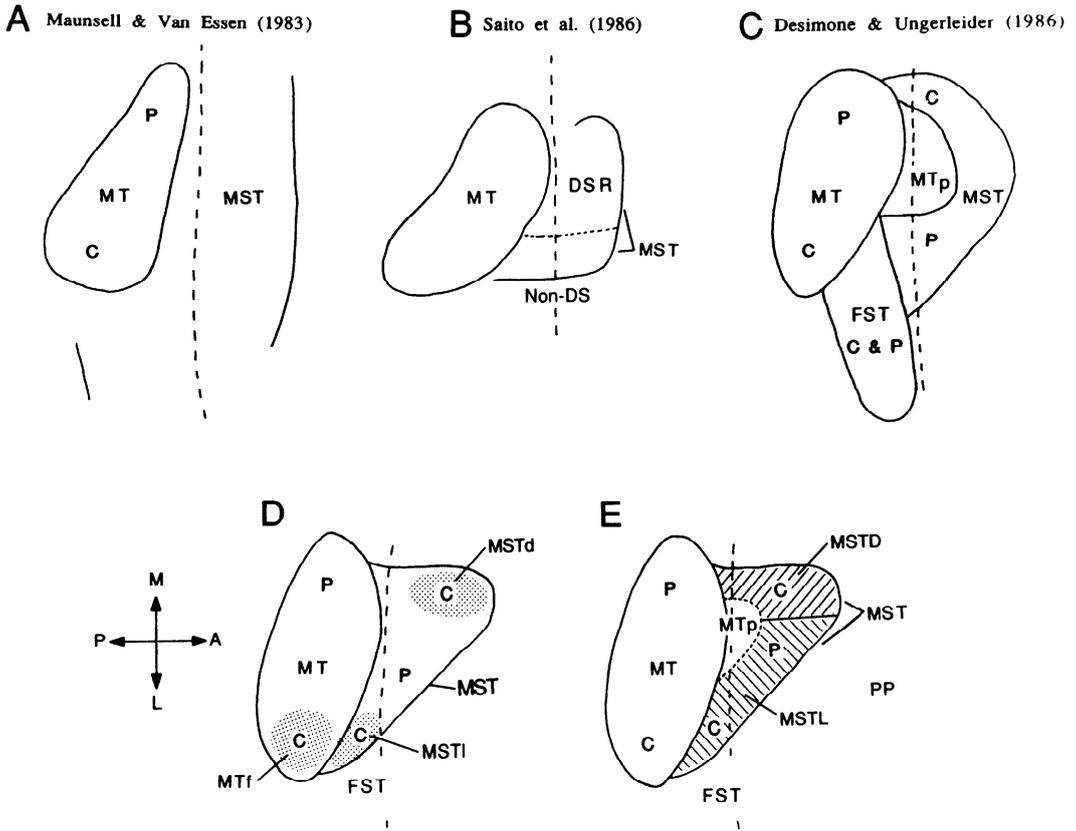


FIG. 13. Comparison of MST maps in this and previous studies. The map in *A* is from Ref. 27, *B* is from Ref. 40, and *C* is from Ref. 7. *D* shows a summary of the present experiments and *E* shows our hypothesized division of MST. Slightly different mapping procedures were used in each of the references. The solid lines outline the distinct areas within the STS, the fundus of which is shown by the dashed vertical line. *C*, areas representing the central visual field; *P*, areas representing the peripheral field. See DISCUSSION for details. See Fig. 2 legend for definitions of abbreviations.

direction-size-rotation area (DSR) (Fig. 13*B*). At the lateral edge of MST, they found a clear shift in visual properties; cells were still visually responsive, but few cells were directionally selective (non-DS area in Fig. 13*B*).

In a second study, Desimone and Ungerleider (7, 46) also found that within the projection zone of MT in the STS (the original definition of MST) there are several areas that have different properties. They found that more medial areas on the anterior bank of the STS had a higher proportion of directionally selective cells than the lateral area on the floor of the STS. They designated the former area with directionally selective cells as MST, and the latter as FST as shown in Fig. 13*C*. They found that the area they desig-

nated as MST had a crude retinotopic organization; the medial region represented the central visual field and the lateral region the peripheral field. On the other hand, FST had no retinotopic organization. They described the FST area as being rich in radial fibers that allowed them to make a distinction between FST and MST on myeloarchitectonic grounds. MST also included a densely myelinated area on the anterior bank of STS, the dorsal edge of which was coterminous with the MT projection zone. This densely myelinated area in MST overlapped the representation of the central visual field in one case but in other cases it did not.

In the present study, we confirmed the results of these previous experiments showing

that the original MST region consists of subregions of cells with different properties. We found that the area anterior to MT has a high proportion of directionally selective cells, and we have used Desimone and Ungerleider's (7) designation of this area as MST (Fig. 13*D*). At the lateral edge of this MST region, we find a clear shift in the visual properties of the cells; most cells in this more lateral area on the floor of the STS were not directionally selective. Because of the similarity in location and properties of the cells in this lateral area and Desimone and Ungerleider's FST area, we also adopted the name FST for this region. Pursuit cells were concentrated in two subregions of our MST (MSTd and MSTl) as well as in the MTf. All these areas are indicated in Fig. 13*D* by the shading.

Our map extends MST more lateral and posterior than does that of Desimone and Ungerleider. We include in MST a small triangular area that is on the floor of the STS and anterior and adjacent to the foveal representation of MT (designated MSTl in Fig. 13*D*). This area would probably be included in FST on the map of Desimone and Ungerleider, but we consistently found a high proportion (80%) of directionally selective cells in the area. This is consistent with the results of Tanaka et al. (44) and of Saito et al. (40) in which MST is adjacent to MT throughout its medial-to-lateral extent without being invaded by a nondirectionally selective area. In addition, of the three maps shown by Desimone and Ungerleider, two have no samples in this small triangular area, and one has three of seven points showing a directionally selective response. It seems this area might have been included in FST mainly because of the myeloarchitectonic pattern. However, as has now been shown for other areas within the STS, such as the MTp area of MT (7, 45), a pattern of myelination sometimes does not exactly match the border of a functionally identified visual area. In spite of this distinction in our map compared with that of Desimone and Ungerleider, we used the same term, MST, to represent the entire area with a high proportion of directionally selective cells in the anterior area adjacent to MT. We did this because the general location and property of the cells are still consistent with the areas that were designated as MST by previous authors (7, 40, 44), and we

thereby avoided the introduction of a new term.

Our MST area, however, contains two regions representing the central visual field, one of which is located medially on the anterior bank (MSTd), and the other laterally on the floor of the STS (MSTl). These two areas are separated by an intervening zone representing only the peripheral visual field. This dual representation of the central visual field raises the possibility that this MST region should be further divided into two subregions. The visual properties of the cells are also consistent with such a division. Cells in MSTd almost always respond best or only to a large moving pattern rather than to small spots of light. On the other hand, ~80% of the cells in both MSTl and the central area of MST representing the peripheral visual field responded as well or better to spots or slits of light.

We suggest, therefore, that our MST area might best be regarded as consisting of two subregions (as in Fig. 13*E*)—one occupying the lateral two-thirds of our MST, including both MSTl and the area in the central part of MST; the other occupying the remaining one-third of our MST, which corresponds to MSTd. The more lateral area (labeled MSTL, Fig. 13*E*) has a high proportion of cells preferring well-localized stimuli such as spots or slits. This subregion also has a crude retinotopic organization with the lateral area adjacent to MTf representing the fovea and more medial areas representing the periphery. The medial subregion, MSTd (labeled MSTD in Fig. 13*E*), has a high proportion of cells responding preferentially to large textured stimuli such as random dots. Cells here have large receptive fields that usually include the fovea but no detectable retinotopic map. Cells in MSTd have generally similar properties suggesting a relatively homogeneous area. This area overlaps the DMZ on the anterior bank of the STS.

In comparing the maps summarized in Fig. 13, it also seems likely that our MSTd area overlaps the DSR region of Saito et al. (40) on the anterior bank of the STS. In addition to the characteristic direction selectivity of many of these cells, Saito et al. reported a large proportion of cells on the anterior bank that responded to changing size or rotation. We encountered such cells occasionally, but since we did not systematically test for these

properties, it is not possible to compare our results to theirs.

We also have been able to recognize two other areas within the STS identified by Desimone and Ungerleider (7). On the anterior bank, we identified an area comparable to that designated as posterior parietal or PP (Fig. 13E), but we have not studied it extensively, since we found few pursuit cells there. We have probably also sampled some cells adjacent to MT in an area designated by Desimone and Ungerleider as MT periphery or MTp. We found cells here (particularly in guide tube B2 in Fig. 7) that were directionally selective, with large peripheral receptive fields that fell near the regression line for size versus eccentricity for area MT. Unfortunately, our sampling of this area was limited to only a few cells and was therefore too limited to identify this area on our maps of the STS, other than the dashed line in Fig. 13E.

Comparison to previous studies of pursuit cells

The first cells in the parietal cortex that were shown to discharge during pursuit eye movements were reported by the laboratories of Hyvarinen and Mountcastle (17, 24, 30). They studied neurons located in anterior area 7a on the dorsal convexity of the parietal cortex. Since pursuit was tested against a lighted background, many of these cells might have been stimulated by the motion of the visual background on the retina during the pursuit movement. Subsequently, many cells in this region of area 7a were shown to be responsive to such visual stimulation by the background, and they failed to respond during pursuit in the dark (39).

Sakata and his collaborators (41) subsequently identified cells they referred to as "true pursuit cells", that is, those that discharge during pursuit of a target moving in total darkness. These pursuit cells were concentrated in the depths of the STS in an area they referred to as posterior area 7a and pre-striate cortex. Such cells were rarely observed in the anterior region of area 7a previously studied by Hyvarinen and Mountcastle and their collaborators. Many pursuit cells were on the anterior bank of the STS in a region that almost certainly corresponds to our MSTd, and others were located on the floor and posterior bank, probably in our MTf or

MSTl. No further localization is possible from their report, and they did not study the visual properties of the cells except for the preferred direction of motion. Both our criteria for identifying pursuit cells and the location of our recordings, indicate that the population of cells we have studied overlaps that of Sakata et al.

Erickson (11) also identified cells on the floor of the STS that discharged during pursuit eye movements, and these cells would seem to correspond to our MSTl pursuit cells. He placed his cells in what he called FST in spite of his observation that over 70% of his sample of cells showed direction selectivity. We think the cells and the location are probably similar in our experiments and those of Erickson; only the name for the location varies.

We have now found that pursuit cells seem to be concentrated into the subregions that we have designated as MTf, MSTl, and MSTd (as in Fig. 13D). There were two consistent characteristics of areas where pursuit cells were located. First, the pursuit cells almost always had a directionally selective visual response. Second, pursuit cells had a strong tendency to have visual receptive fields that include the fovea. This relation of pursuit and visual properties is very reasonable if we consider the nature of pursuit eye movements. Pursuit eye movements deal with moving visual objects, and it is reasonable that pursuit cells be located in areas such as MT and MST where directionally selective cells predominate. In addition, pursuit eye movements are designed to keep visual objects on the fovea, and this behavior is in fact observed only in species with well-developed foveas. It is again very reasonable that pursuit cells receive visual inputs from the foveal region.

Pursuit behavior, however, has several components, including the visual motion generated by the slip of the target on the retina and the motor behavior related to maintaining the pursuit. Therefore, the discharge of the pursuit cells observed in different areas such as MTf, MSTl, and MSTd might be related to different aspects of pursuit. To understand the contribution of these cells to pursuit behavior, the nature of the pursuit-related inputs must be determined, and this is the subject of the following paper.

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