Functional Properties of Neurons in Middle Temporal Visual Area of the Macaque Monkey. I. Selectivity for Stimulus Direction, Speed, and Orientation

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SUMMARY AND CONCLUSIONS

1. Recordings were made from single units in the middle temporal visual area (MT) of anesthetized, paralyzed macaque monkeys. A computer-driven stimulator was used to make quantitative tests of selectivity for stimulus direction, speed, and orientation. The data were taken from 168 units that were histologically identified as being in MT.

2. The results confirm previous reports of a high degree of direction selectivity in MT. The response above background to stimuli moving in a unit's preferred direction was, on average, 10.9 times that to stimuli moving in the opposite direction. There was a marked tendency for nearby units to have similar preferred directions.

3. Most units were also sharply tuned for the speed of stimulus motion. For some cells the response fell to less than half-maximal at speeds only a factor of two from the optimum; on average, responses were greater than half-maximal only over a 7.7-fold range of speed. The distribution of preferred speeds for different units was unimodal, with a peak near $32°/s$; the total range of preferred speeds extended from 2 to $256°/s$. Nearby units generally responded best to similar speeds of motion.

4. Most units in MT showed selectivity for stimulus orientation when tested with stationary, flashed bars. However, stationary stimuli generally elicited only brief responses; when averaged over the duration of the stimulus, the responses were much less than those

to moving stimuli. The preferred orientation was usually, but not always, perpendicular to the preferred direction of movement.

5. A comparison of the results of the present study with a previous quantitative investigation in the owl monkey shows a striking similarity in response properties in MT of the two species.

6. The presence of both direction and speed selectivity in MT of the macaque suggests that this area is more specialized for the analysis of visual motion than has been previously recognized.

INTRODUCTION

To understand cortical function it is of obvious importance to know how the cortex is subdivided into physiologically or anatomically distinct areas. In the macaque monkey there is evidence for at least nine visual cortical areas, and there are likely to be more (see Ref. 57). Differences among the functional properties of several of these areas have been reported (see Ref. 63), but our understanding of functional processing remains fragmentary. Detailed knowledge of the types of neuronal responses occurring in different visual areas is likely to be important for understanding the functions that each serves in the processing of visual information.

The present study concerns the functional organization of the middle temporal area (MT), a small but well-defined visual area in the macaque. It lies in the posterior bank of the superior temporal sulcus, receives a direct

projection from striate cortex (V1) (10, 60), and is characterized by a pattern of heavy myelination that makes it readily distinguishable from neighboring cortical areas (55, 56). Previous physiological studies have demonstrated a strikingly high proportion of neurons that are selective for the direction of stimulus motion, whereas stimulus form seems to be relatively unimportant to the great majority of MT neurons (16, 61). Although this suggests that MT may somehow be involved in the analysis of motion, it does not resolve the nature of the processing actually occurring within MT nor does it identify which specific aspects of motion analysis might be served.

Motion analysis is a complex process and may be divided into distinct components such as motion detection, discrimination of visual motion caused by eye or body movements from movements in the visual field, and the calculation of trajectories of objects moving in three-dimensional space. It may be that MT is concerned only with restricted aspects of visual motion. It is known that many neurons in macaque V1 are direction selective (14, 46), and the only conspicuous difference between this population and neurons in MT is the larger receptive fields of the latter. However, it may simply be that not enough is known about the responses of direction-selective cells in either V1 or MT to see differences between them. Clues to such differences might come from an analysis of all aspects of stimulus motion—in particular, motion at different speeds and at different depths in space. This information can then be usefully compared with the properties of cells in other areas and also with psychophysical data pertaining to different aspects of motion sensitivity. It is also of interest to compare responses of neurons in macaque MT with its homologue in other primate species to see the degree to which function in conserved between species.

We have examined quantitatively the responses of single units in MT of anesthetized and paralyzed macaque monkeys. The experiments included tests for selectivities to stimulus direction, speed, orientation, fixed disparity, and changing disparity (motion in depth). The analysis of binocular interactions (selectivity for fixed and changing disparities) turned out to be a sufficiently interesting and

complex issue that we felt it appropriate to deal with them in a separate paper, which immediately follows the present one (36).

MATERIALS AND METHODS

Animal preparation

Chronic recordings were made in five male *Macaca fascicularis* weighing between 2.9 and 3.7 kg, using a procedure similar to that of Desimone and Gross (13). A stainless steel cylinder with an 18-mm inner diameter was mounted over a hole in the skull using dental acrylic. Small stainless steel screws inserted into the skull helped secure the chamber's attachment. The chamber was mounted over the striate cortex on the right hemisphere so as to allow a posterior, approximately horizontal approach to MT. This implant was performed under aseptic conditions using sodium thiopental anesthesia. When the animal was not being used for a recording session, the chamber was filled with sterile mineral oil and sealed with a threaded lid.

After recovery from this initial surgery, recording sessions were conducted twice weekly for up to 11 sessions. For each recording session, the animal was initially sedated with ketamine (10 mg/kg, im) and placed in a holder that restrained the animal's head. After intubation with a tracheal cannula, the animal was administered a mixture of 70% N_2O and 30% O_2. An initial dose of paralytic solution (Flaxedil 10 mg/kg, ip) was given and followed by continuous infusion (7.5 mg $\cdot$ $kg^{-1} \cdot h^{-1}$, ip) for the duration of the experiment. During paralysis the animal was hyperventilated with a mixture of 70% N_2O, 27.3% O_2, and 2.7% CO_2. The electrocardiogram and expired CO_2 were monitored throughout the experiment; body temperature was maintained near 37°C with a thermostatically controlled heating pad.

After the chamber was opened, most of the tissue growing over the exposed dura was removed with fine-toothed forceps. With the aid of an electrolytically sharpened tungsten dissecting needle, one or more small (300–500 μm) holes were made at appropriate places in the dura to serve as entry points for the electrode penetrations. The deepest layer of the dura was left intact to protect against infection. This procedure greatly reduced the risk of damaging electrodes during dural penetration and provided consistently good recording.

Recordings were made with electrodes held in a stepping-motor–driven microdrive. The microdrive was equipped with an X-Y stage, which in turn was mounted on the chamber over the skull. The microdrive was held by adjustable couplings, and once it was on the chamber all couplings were tightened firmly so that the microdrive kept the animal's head from moving. The X-Y stage al-

lowed accurate measurement of electrode position. Atropine (2%) and Neo-Synephrine (2.5%) were administered to dilate the pupils and achieve cycloplegia. The eyes were then covered with contact lenses and focused with correcting lenses onto a screen 114 cm from the animal. Artificial pupils 8 mm in diameter were placed in front of the eyes. The positions of foveas and retinal landmarks were plotted on the projection screen using a reversing ophthalmoscope. Foveal positions were frequently checked, and the drift was usually about 1° over the recording session. Recordings were made with varnish-coated tungsten electrodes (24) with impedances of 0.2–5 MΩ at 1 kHz. Recordings were amplified in a conventional manner and isolation of units established by standard criteria of impulse amplitude and waveform. A window discriminator was used to convert the signal into digital pulses. An oscilloscope display of the recording signal was triggered on smaller responses than the unit under study so that fluctuations in the degree of isolation could be readily detected. When a penetration was completed, two or more electrolytic lesions (10 μA for 10 s) were placed at strategic positions along the track to facilitate the later reconstruction.

Recording sessions lasted between 12 and 16 h. Usually only one penetration was made in a session. Recovery of the animal was begun by stopping the paralytic infusion. About 2 h later atropine (0.15 mg/kg, im) was administered, followed in 10 min by neostigmine (0.25 mg/kg, im). The animal normally was respiring spontaneously 10 min later and was put back in its cage soon afterward.

Stimulation

The stimulator used for these experiments could be operated either manually, using a joystick, or under computer control. It included a projector that imaged a slit whose length, width, and orientation were controlled by stepping motors. A cube beam splitter was used to produce duplicate beams, which were sent to separate pairs of X-Y galvanometers (General Scanning, model G330) to create one stimulus bar for each eye. The two beams were passed through cross-polarized filters, projected onto a planar, nondepolarizing screen at 114 cm, and viewed by the animal through a second pair of cross-polarized filters (11). We checked the polarization by viewing the images through cross-polarized glasses and by ensuring that units could not be driven through one eye using the wrong monocular stimulus. The images were normally 1.5 log units above the background illumination of 10–20 cd/m². The stimulator was mounted directly below the animal, 20 cm beneath its eyes, to minimize distortion of the stimulus shape from excessive parallax. The stim-

ulator could cover 30° of elevation and azimuth. When a unit was isolated, rectangular minimal response fields were plotted for each eye. The positions of these fields were then fed into a computer (DEC PDP11/34A), which was used for stimulus generation and response storage and analysis. When the computer controlled stimulation, it adjusted the position of the stimulus for each eye to compensate for any misalignment of the direction of gaze for the two eyes under paralysis.

Sensitivity to color was tested only when the Polaroid filters had been removed and the foveas aligned by inserting a prism of appropriate strength and orientation in front of one eye. This was done to permit stimulation of corresponding locations in the two eyes with a single slit, which was projected onto a screen of uniform reflectance. Colors were produced by inserting the interference filters (Rolyn Optical) in the light path. Neutral-density filters were used to adjust all colors to equal energy. Background illumination for the screen was at a low mesopic level, produced by a tungsten light source filtered to produce illumination of flat spectral content.

The overall accuracy of stimulus positioning with computer-generated sets of stimuli was about 0.1°. Several considerations were important in achieving this accuracy over the working range used. The computer had to correct for parallax errors resulting from the relative positions of the X-Y galvanometers, animal, and projection screen. The driving signals to the galvanometers were passed through low-pass filters to prevent oscillations at their resonant frequencies. It was also necessary to compensate for a small amount of mechanical hysteresis in the galvanometers. Finally, slow drifts in galvanometer position were compensated each time the computer was fed new receptive-field positions.

In the present study, unit responses were quantitated by varying one stimulus parameter while all other independent parameters (length, width, direction, speed, disparity, and color) were held constant. The nonvarying parameters were initially held at their best settings, as judged by manual stimulation. When testing for a given parameter was completed, the setting that gave the best response was used in test selectivity to other parameters. Moving stimuli started and stopped a short distance outside the receptive field, usually 10–20% of receptive-field width. The slit orientation was kept perpendicular to the direction of stimulus motion. In some cases the stimulus length was short enough to approximate a small spot. There was a 5-s interval between successive stimulus sweeps over the receptive field; normally five repetitions of each stimulus were averaged. Values for the stimulus parameter being tested

were presented in a random order. The computer controlled shutters in front of the eyes that were used to interleave binocular and monocular stimuli randomly when the latter were tested. Usually the best direction was determined first, followed by other parameters in varying order, according to what appeared to be most important to each unit. A complete analysis took 2–3 h, but many units were lost before they had been fully examined.

Data analysis

Action-potential data were displayed on-line in a raster dot form on an oscilloscope as they were collected by the computer, and summaries of results were printed after each test was completed. This initial feedback was important in determining the course of the subsequent testing. After recording sessions were finished, summed histograms and plots of responses were produced by the computer.

Responses were measured as the average rate of firing during the time the stimulus was turned on, but with two provisions that were necessary owing to the finite latency of visual responses. This latency can cause most of the response to a stimulus of short duration to occur after the presentation is over. We accommodated this in two ways. First, because there is a minimum delay to visual cortex, the time window during which impulses were counted was arranged to lag the presentation by 40 ms. This is slightly shorter than the minimum delay for the onset of evoked potentials in macaque V1 (22). Second, to compensate for the variability in delay among different units, a minimum window of 250 ms was used for determining the average response to even very brief stimuli. This value was found empirically to be long enough to include the major part of all responses and not so long as to dilute the rate of firing unduly by including long periods after the briefest responses had ended. These compensations were important for very fast moving stimuli in tests of speed selectivity but had little effect on other tests. Another source of inaccuracy came from the fact that stimuli were outside the receptive field for a small fraction of each presentation. Hence, our measurements underestimated the actual response during the time stimuli were crossing the receptive field. No correction was made for this, however, because the borders of receptive fields were often not sharply defined and, in any event, such adjustments would have had only a small effect on response magnitudes and even less effect on the shapes of the tuning curves being measured.

Histology

Following the final chronic recording session, the animal was used for about 10 days as a subject for anatomical and physiological experiments, which will be reported elsewhere. At the end of these, the animal was deeply anesthetized with sodium pentobarbital and perfused through the heart with 4% Formol saline. The brain was blocked and equilibrated with 30% sucrose, and frozen sections were cut parallel to the electrode penetrations at a thickness of 31 μm. One series of sections was stained with cresyl violet and used to reconstruct the electrode penetrations. Recording sites were assigned on the basis of lesions and microdrive coordinates. Another series of sections was stained for myelin by the method of Gallyas (19) and used to determine the boundaries of MT (56). A total of 62 penetrations were made into the superior temporal sulcus in 44 sessions; 37 penetrations were identified as passing within the myeloarchitectonic boundaries of MT.

RESULTS

Of the 176 single units in the superior temporal sulcus that were examined quantitatively, 168 were identified histologically as being in MT; only this latter population is included in the analysis below. All recording sites were in the right hemisphere, and receptive-field centers were all in the left visual hemifield, within 25° of the fovea. Most receptive fields were in the inferior quadrant, reflecting the biased representation of the visual field in MT (56). Although lesions were made on completion of each penetration, the likelihood of gradual drifts in the position in the cortex with respect to apparent depth readings prevented the unambiguous assignment of recording sites to specific layers of cortex. However, it was possible to designate many sites as supragranular (layers II or III) or infragranular (layers V or VI). There were no consistent differences between these groups with respect to any of the response properties that were examined.

Direction

One hundred sixty-three units in MT were examined for selectivity to the direction of stimulus motion. Most were strongly direction selective, as previously reported (16, 56, 61). Figure 1 shows the responses of one such unit in MT to a small slit of light moved in various directions across the receptive field. This unit preferred movement that was to the left and downward, and it gave no response to the opposite (null) direction. Movement perpendicular to the best direc-
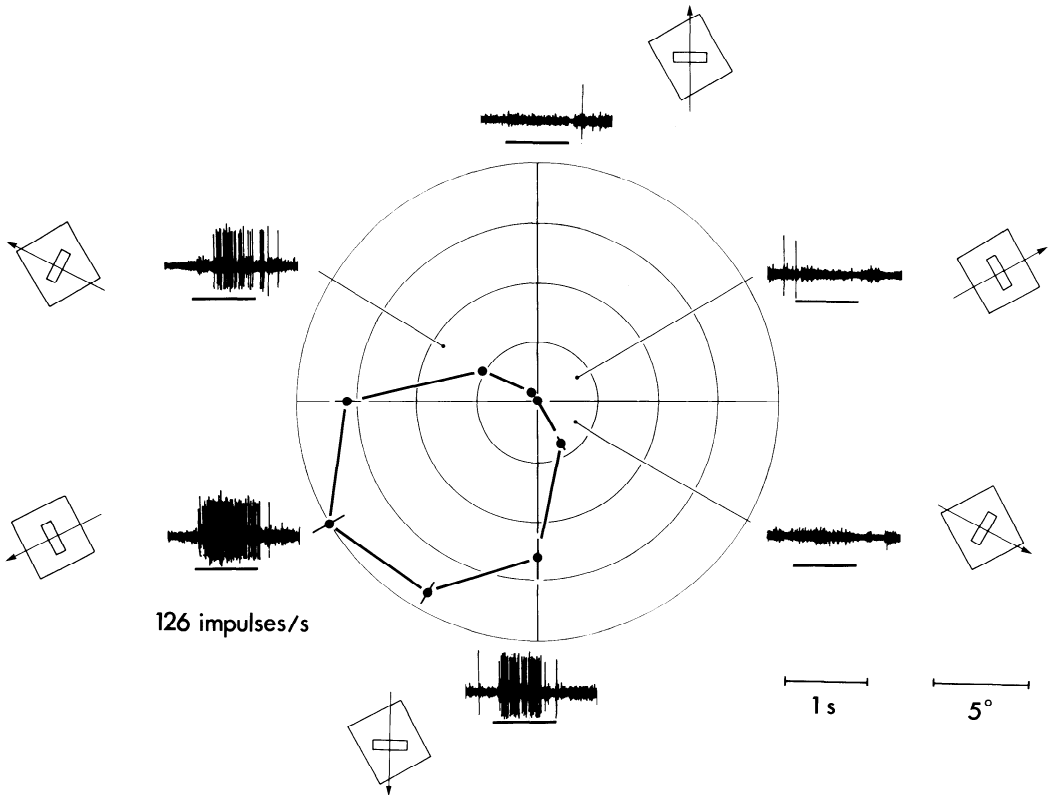
FIG. 1. Direction selectivity of a single unit in MT. Oscilloscope records of extracellularly recorded responses are shown for individual presentations of the six indicated directions of motion. Bars below each trace mark the time the stimulus was on. The size of the stimulus and its direction of motion relative to the receptive-field outline are indicated alongside each trace. The polar plot is the average rate of firing during stimulus presentation for five repetitions of 12 directions of motion. Bars indicate the standard error of the mean for each point.

tion caused only a weak response. The polar plot displays the average responses of this unit to 12 directions of movement. Bars indicate the standard errors of the means. Most units had tuning curves that were symmetric about the peak response; the slight asymmetry in this particular tuning curve is probably due to the unit having a preferred direction slightly counterclockwise from the curve's peak. Although direction-tuning curves were routinely taken at 30° increments, several units were tested at higher resolution; none of these tests revealed peak responses that were substantially larger or tuning that was markedly sharper than those from curves taken at the standard interval. Because direction selectivity was generally tested with elongated stimuli, the sharpness of the tuning curves might have been affected by whatever orientation selectivity the cells

had. This is unlikely to have been a major effect, however, since neurons in MT are relatively nonselective for form (16, 61), and there was little correlation between the sharpness of tuning for direction and for orientation (see below).

The tuning curves from three other representative units are shown in Fig. 2A. Bars again indicate standard error of the mean for each point, and average background activity is indicated by dashed lines. Two of these units, like many in MT, were inhibited to motion in their null directions. Even in this subpopulation, though, there is obviously a considerable degree of variability in the sharpness of direction tuning. The full width at half-maximal response is less than 30° for the uppermost unit but is more than 100° for the lowermost. For these three units the maximal rate of firing is related to the broad-

A

B

10.5

26.8

BEST
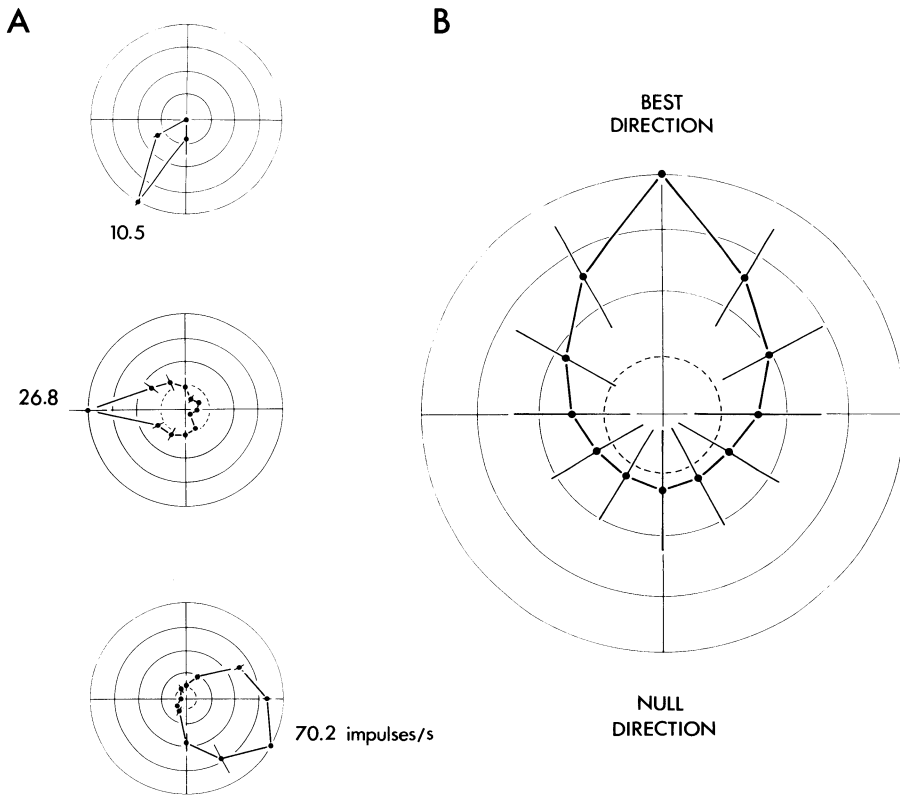DIRECTION

70.2 impulses/s

NULL
DIRECTION

FIG. 2. *A*: direction tuning curves for three representative single units in MT. Each plot is normalized to the greatest average rate of firing during five presentations of each stimulus. Bars indicate standard errors of means and dashed lines mark average background rate of firing. *B*: average direction tuning curve for 163 units in MT. The tuning curve of each unit was normalized to its peak response and rotated to bring the peak to the top. The corresponding values from all curves were then averaged. Bars indicate the standard deviation for each point and the dashed line is the average normalized background rate of firing.

ness of tuning, but this was not consistently the case for the overall sample. Among all the units tested, 88% had a response above background that was at least twice as large in the preferred direction as in the null direction (cf. Fig. 12*A*).

The overall quality of direction tuning in MT is indicated by the average tuning curve in Fig. 2*B*. This curve was produced by normalizing each of the 163 tuning curves to their best responses, rotating the curves to bring the best direction of movement to the top, and then averaging the normalized responses for each of 12 points. Thus, the first point clockwise from the top represents the average normalized response to a stimulus whose direction of movement is 30° clock-

wise from a unit's preferred direction. Bars indicate the standard deviations and the dashed line marks the average normalized background rate of firing. Tuning curves appear significantly sharper if the background rate of firing is subtracted; the given format is used because it conveys more information. The response above background to motion in the best direction is 10.9 times greater than the response to the null direction and it falls to 50% of the peak value when the direction of movement is 30° from the best direction. It is also apparent that the slope of the curve is greater near the peak. This indicates that neurons in MT usually have their greatest sensitivity to differences in stimulus direction near their best direction. The average level

of spontaneous activity was 7.1 impulses/s, but there was considerable variability among different units within MT.

Most units in MT responded to stimulation through either eye alone (36, 61). Each unit was tested manually with monocular stimuli to see if there was a difference in preferred direction between the two eyes. In addition, 40 units were examined quantitatively for monocular direction preferences. The monocular direction preferences were always close to one another and to the binocular direction preference. In the quantitative tests, the directions that gave the greatest rate of firing in the left and right eyes sometimes differed by 30° and occasionally more, but in these cases the tuning curves generally were broad and the differences are largely attributable to random fluctuations in response levels. We saw no units with opposite preferred directions when stimulated with either eye alone, although such units have been seen in small numbers in macaque V1 and MT (43, 44, 62).

The distribution of preferred directions for MT is plotted in Fig. 3A. Interestingly, there is a significant underrepresentation of units preferring movement in the range from rightward to downward (χ^2 test, $P < 0.05$). Since all of our recordings were from the right hemisphere, we do not know whether a bias, mirror symmetric or otherwise, exists in MT of the left hemisphere, subserving the right visual hemifield. Dubner and Zeki (16) also saw an uneven distribution of preferred directions in MT, but their bias consisted of an underrepresentation of all directions of movement with components toward the vertical meridian, whereas ours was confined to about half this range.

Because the receptive fields were taken from a limited part of the visual field, the bias in Fig. 3A might reflect a preference for motion in a particular direction relative to the fovea. In Fig. 3B the same data have been replotted, taking into account the position of each receptive field, to indicate the preferred direction relative to motion toward the fovea. Preferred movements that are directed toward the fovea are at the top of the diagram, preferred directions away from the fovea are at the bottom. While more units preferred movement away from the fovea than toward

it, the overall distribution is more balanced than Fig. 3A and is not significantly different from uniform (χ^2 test, $P > 0.25$). Thus, the uneven distribution of preferred directions does not arise from a tendency to favor directions of movement toward or away from the fovea. We have no simple explanation for why there should be an underrepresentation of a particular range of preferred directions in MT. A nonuniform distribution of preferred directions has also been reported for the posterior parietal cortex of the macaque (37), but the distribution is not the same as that in MT.

Given the broadness of the tuning curves of most MT neurons, the existence of an underrepresented range of preferred directions does not necessarily imply that the population of neurons is collectively less able to detect movement within that range. The average response of the population to different directions of motion is illustrated in Fig. 3C, which was produced by normalizing the tuning curves for each unit and averaging the responses to each direction without rotating the curves. The curve is much smoother than the plot of preferred directions in Fig. 3A; this smoothing is clearly attributable to the breadth of individual direction tuning curves. Nevertheless, the overall responsiveness to movements downward and to the right is significantly less than that to other directions, especially when measured relative to the background. The minimum response above background occurs in this quadrant and is only 60% of the maximum. Figure 3D shows the responsiveness replotted as a function of direction relative to movement toward the fovea. Again, the plot is smooth but not perfectly circular; the minimum response relative to background is less than 60% of the maximum.

Previous studies have shown a clustering of cells having similar direction preferences in MT (1, 56, 61). The nature of the present study was not optimal for examining this clustering, since few units were sampled in each penetration. Also, preferred directions were determined by computer only to the nearest 30°, and stochastic fluctuations in average rates of firing presumably made the accuracy worse for some units. Despite these shortcomings, direction clustering was robust
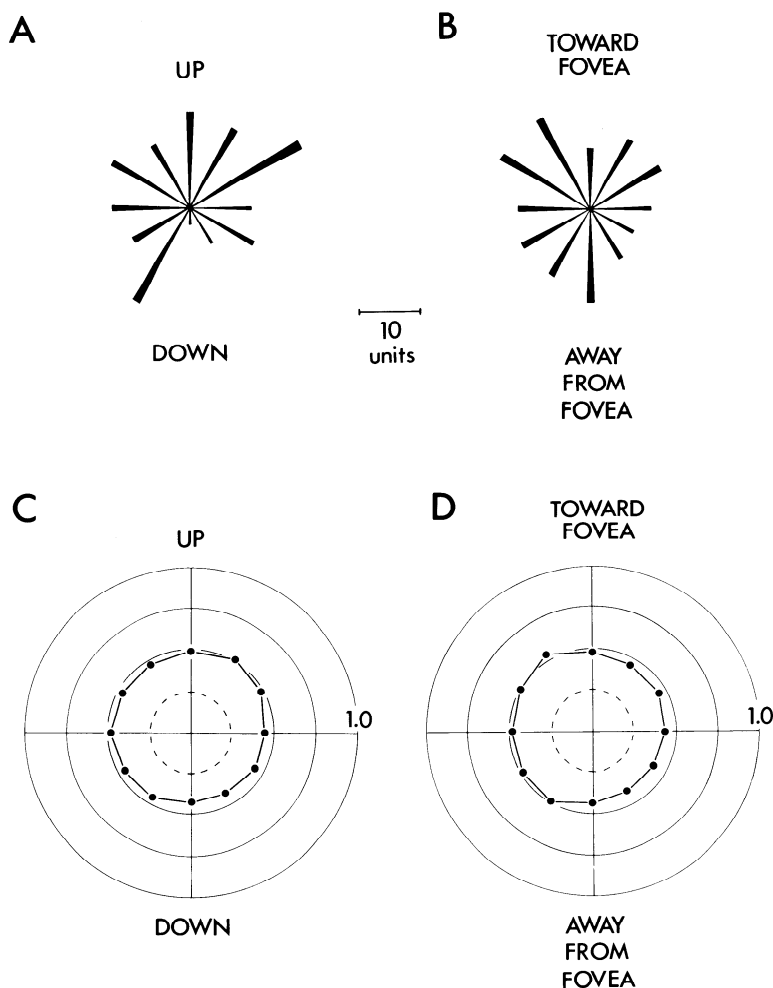
FIG. 3. *A*: distribution of preferred directions for 152 units in MT. Units with no clear preferred direction were excluded. There is a significant underrepresentation of directions in the range from rightward to downward. *B*: distribution of preferred directions relative to motion toward the fovea. Data of Fig. 3*A* were replotted, taking receptive-field position into account. Units whose preferred directions were toward the fovea are represented by the upper vertical bar, those that preferred motion directly away from the fovea are represented by the lower vertical bar. While more units prefer motion away from the fovea than toward it, the distribution is more uniform than that of *A*. This indicates that the underrepresented directions in the other distribution do not result from biased direction preferences relative to the fovea. *C*: average normalized response of units in MT to different directions of movement. The direction tuning curves of all tested units were normalized and then averaged. Standard errors of means are smaller than the size of dots. The dashed line is the average normalized background rate of firing. Responses in the range of directions from rightward to downward are significantly smaller than others. *D*: average normalized response of units in MT to different directions of movement relative to the fovea. The normalized tuning curves used for *C* were rotated before averaging to bring the direction toward the fovea to the top. Standard errors of the mean are smaller than the size of dots. The dashed line is the average normalized background rate of firing.

enough to be obvious. Figure 4 shows the change in preferred direction between pairs of units whose separation, measured parallel to the cortical surface, was less than 200 μm. Pairs that included a unit with very broad

direction tuning were excluded. The distribution is not uniform (χ^2 test, $P < 0.005$) and there is a strong peak around zero, corresponding to no detectable change in preferred direction from one unit to the next.
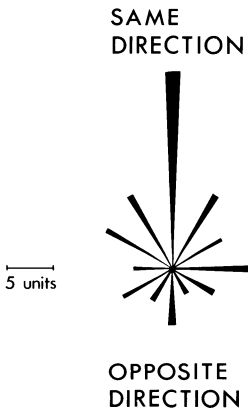
SAME
DIRECTION

5 units

OPPOSITE
DIRECTION

FIG. 4. Distribution of change in preferred direction between pairs of units in MT. Eighty-nine pairs of units separated by no more than 200 μm, measured parallel to the cortical surface, are included in the distribution. There is a strong tendency for nearby units to have the same preferred direction.

This clustering is consistent with evidence from previous studies (1, 8) for some form of columnar organization of preferred direction in MT.

Albright et al. (1) observed frequent 180° reversals in preferred direction in MT. We saw such reversals in some penetrations, but there is no clear peak at the corresponding position at the bottom of Fig. 4. It is possible that a small peak in this position could be obscured by scatter introduced by the maximum separation between adjacent units (200 μm) accepted for this plot. The value used is large relative to the reported rate of change of preferred direction in MT (180°/500 μm, Ref. 1), but was necessary in order to include a reasonable number of pairs. This can also account for many of the changes close in the 60–120° range. However, there were several unambiguous examples of particularly closely spaced units having sharp direction preferences that differed by about 90°. These cases may have included recording from dendrites of relatively distant somata or they may be examples of sequence irregularities among neighboring direction columns.

Speed

If MT plays an important role in the analysis of motion, one might anticipate finding neurons capable of signaling how fast an ob-

ject is moving as well as its direction of movement. We shall use the term speed in referring to rate of motion rather than the more commonly employed term of velocity because the latter is in a strict sense a vectorial measure, which by definition encompasses both the rate and the direction of stimulus motion.

One hundred nine units in MT were examined for selectivity to the speed of a stimulus moving in the preferred direction. The great majority (89/109) responded well to only a limited range of speeds. Figure 5 shows a plot of the average rate of firing of a typical unit in MT to stimuli moving at different speeds. The abscissa is logarithmic, and bars indicate the standard errors of the means. The unit preferred stimuli moving at about 64°/s and its response to speeds far from that value was markedly diminished.

Responses were measured as the average rate of firing during stimulus presentation (see METHODS). Although different measures of neuronal response typically yield similar results, it is important to recognize that this is not always the case, especially when stimulus duration varies from one trial to the next, as in tests for speed selectivity. In such tests, measures based on the total number of impulses during a stimulus presentation emphasize responses to slower speeds (which have longer duration) in a manner that seems inappropriate. For this reason the average rate of firing and the peak rate of firing are more commonly used. Average and peak rates of firing often yield similar response versus speed curves (38, 40). The summed response histograms in Fig. 5 show that the best speed as determined from the peak rate of firing is identical to the best speed determined from the average rate of firing. In our overall sample the best speeds determined by these two methods occasionally differed by a factor of two but rarely by more. The shapes of the response versus speed curves were generally similar as well, except that cells typically appear more responsive to slower speeds when measured by the peak rate of firing. It is difficult to know which measure more accurately reflects the functional significance of activity in MT or any other area. Our preference for the average rate of firing is based on the practical consideration that this measure requires fewer
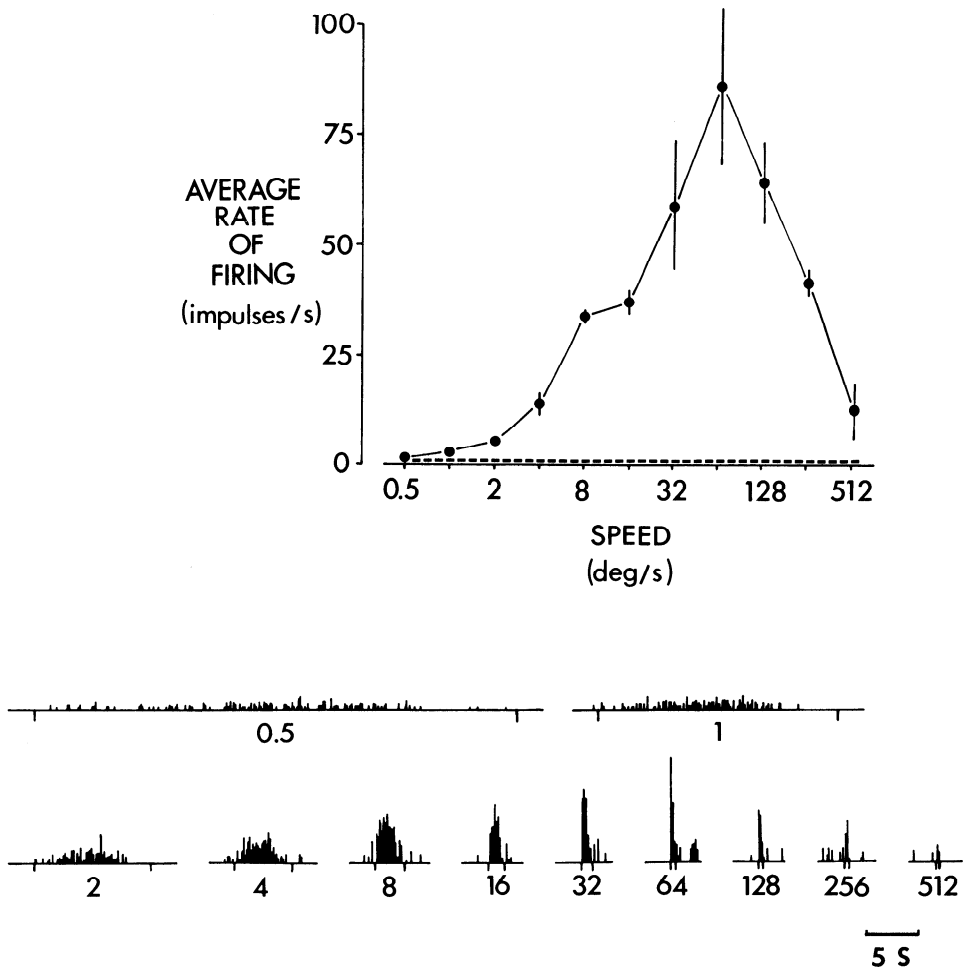
FIG. 5. Responses of a representative unit in MT to stimuli moving in its preferred direction at different speeds. In this and all subsequent plots the speed axis is logarithmic. Bars indicate the standard errors of the mean for five repetitions of each speed. A dashed line marks the background rate of firing. This unit, like most in MT, had a sharp peak in its response curve. Summed response histograms in the lower half of the figure show that the peak rate of firing closely follows the average rate of firing. Tic marks under each histogram denote times of stimulus onset and offset. The receptive field was 15° across and each stimulus traversed 20°.

stimulus repetitions to achieve a satisfactory standard error of the mean.

Responses from four units that showed narrow tuning for stimulus speed are illustrated in Fig. 6A. The abscissa is again logarithmic. All these units showed inhibition to speeds that were far from their preferred speed, and portions of the tuning curves that are below background rate firing are indicated by dashed lines. In the overall population, a few units had responses that remained high toward one end of the range or the other, but the great majority had a clear peak. Inhibition at speeds far from the op-

timum was seen only occasionally on the slow side of the peak but was more common on the fast side. There was no obvious correlation between the sharpness of tuning for speed and that for direction in our sample. Many units were examined with manual monocular stimulation for evidence of different preferred monocular speeds. As with preferred direction, the monocular preferred speeds were similar to one another and to the binocular value.

Orban et al. (41) reported that neurons in cat areas 17 and 18 could be grouped into four distinct classes based on the speeds to
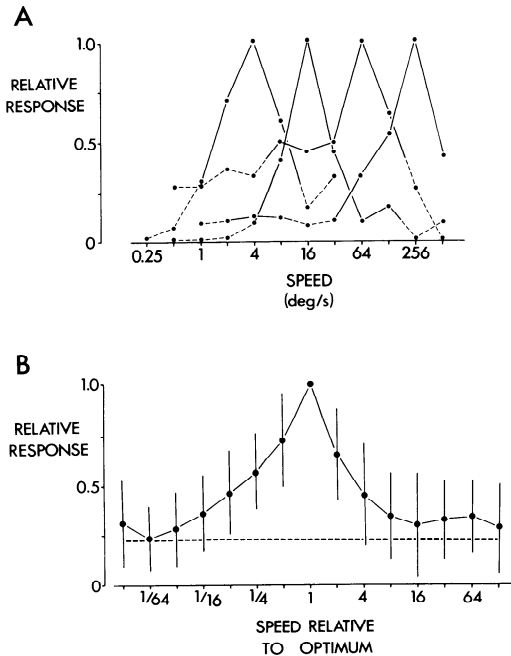
A

B

FIG. 6. *A*: responses of four units in MT to different speeds of motion in their respective preferred directions. Each curve has been normalized to its greatest average rate of firing response. Portions of curves that are below the background rate of firing for each unit are dashed. Each unit's tuning curve is narrow compared to the range that they covered collectively. Each unit's response fell to background level or showed inhibition at speeds far from the peak. *B*: average speed tuning curves of units in MT. The tuning curves of 109 units were normalized to their greatest average rate of firing and each shifted so their peak responses were superimposed. Points on either side were then averaged. Bars indicate the standard deviation of each point and a dashed line marks the average normalized background rate of firing.

which they responded and the broadness of speed tuning. While our sample had differences in preferred speed and in broadness and symmetry of tuning, the appearance is one of a continuum rather than distinct classes. Figure 6*B* is the average tuning for speed from all units examined. The peaks of the normalized curves were aligned, and points on either side were averaged. Bars show the standard deviation for each point, and the dashed line is the background rate of firing. The average tuning for speed in MT is impressively sharp, with full width at half-peak (relative to background) equivalent to a 7.7-fold change of speed. As with the average direction tuning curve, the slope is greatest near the peak, yielding greatest sen-

sitivity to differences in speed near the preferred speed. Of the 20 units that did not have well-defined optimal speeds, most were only weakly responsive and only a few responded vigorously over the full range of speeds tested.

The distribution of preferred speeds is shown in Fig. 7*A*. The total spans two orders of magnitude, from 2 to 256°/s, and there is a single peak near 32°/s. This conflicts with the report of Dubner and Zeki (16), based on qualitative analysis of responses, that 73% of units in macaque MT had best responses to speeds in the range 1–5°/s and that 10% had optimal responses to speeds in the range 100–200°/s. In our sample, 78% responded best in the intervening range. In a later study,
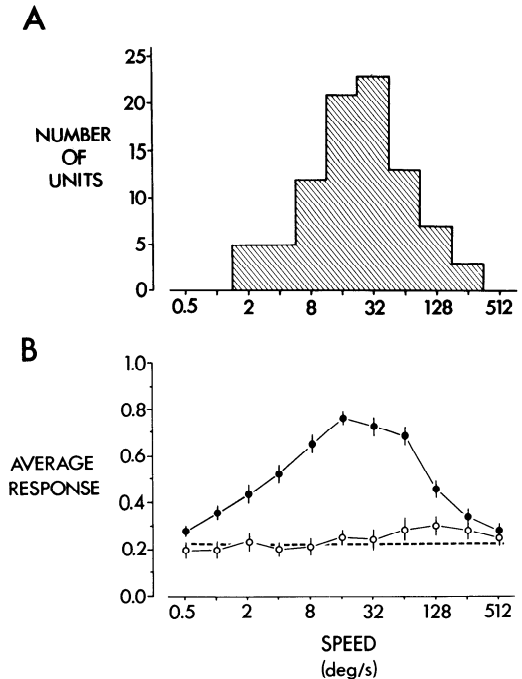
A

B

FIG. 7. *A*: distribution of preferred speeds for 89 units in MT. Twenty units with no clear preferred speed were excluded. The distribution has a single peak near 32°/s. *B*: average normalized response of units in MT to different speeds. The filled circles show the average normalized response to motion in the preferred direction for 45 representative units (including several lacking clear tuning for speed), which were tested with speeds from 0.5 to 512°/s. The open circles show the average normalized response of 20 units to motion in the null direction. Bars show the standard errors of means and the dashed line is the average normalized background rate of firing. Collectively, neurons in MT are most sensitive to speeds in the range from 8 to 64°/s.

Zeki (61) reported that most units in MT have best speeds in the range from 5 to 50°/s, which is in good agreement with the present results.

The overall sensitivity of MT to stimuli moving at different speeds is shown in Fig. 7B. For the 45 units tested over a range from 0.5 to 512°/s, normalized curves were averaged and plotted as filled circles, with bars indicating the standard errors of the means. The curve peaks near the peak of the preferred speed distribution, suggesting that the shape of tuning curves does not change drastically with preferred speed (see also Fig. 6A).

Since many units had weak responses or clear inhibition in the null direction, it was of interest to determine whether there was any tuning for speed in the null direction. In most cells the response in the null direction, be it inhibition or excitation, was greatest at the speed that evoked the largest response in the preferred direction. The only systematic relationship we noted was that many units gave a weak excitatory response to fast stimuli in the null direction, whether or not the response was excitatory or inhibitory at slower speeds. The open circles in Fig. 7B indicate the average normalized response to movement in the null direction as a function of speed. It remains at background for most of the range except at fast speeds, where a small response is evident. Responses were

sometimes better to the null direction than the preferred direction when speeds were far from the best value. However, this loss of direction selectivity occurred only when responses to both directions were small relative to the response to motion in the best direction at the best speed.

The relation between preferred speed and eccentricity is shown in Fig. 8. Each bar indicates the width of speed tuning at half peak height above background for a particular unit. There was substantial scatter at all eccentricities, indicating that information may be extracted over a wide range of stimulus speeds in all parts of the visual representation. The least-squares regression line through these points had a slight positive slope, indicative of a threefold increase in average preferred speed at 20° eccentricity relative to that at 0°. For comparison, the square root of receptive-field area in MT increases more than 10-fold over the same range (20). A similar relationship between preferred speed and eccentricity has been seen in area 17 of the cat (58).

There was a clear tendency for units recorded in a single penetration to have similar preferred speeds. The taller histogram in Fig. 9 is the fractional change in preferred speed between pairs of units in MT whose separation, measured parallel to the cortical surface, was less than 200 μm. The hatched his-
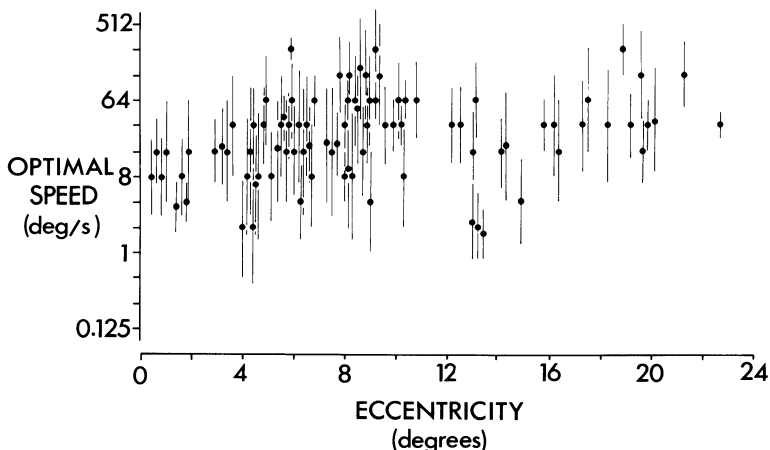

FIG. 8. Preferred speed as a function of eccentricity for 89 units in MT. The 20 units having no clear preferred speed were excluded. Bars indicate the full width of each tuning curve at half of the peak height above background. The range of speeds represented at each eccentricity is broad compared to the width of individual tuning curves. A linear regression of points yields a small correlation coefficient (0.27) and indicates that the average preferred speed increases only about threefold from 0 to 20° eccentricity.
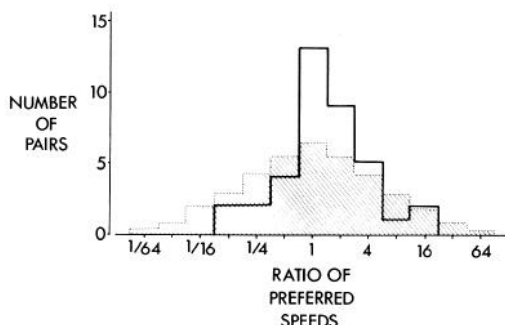
FIG. 9. Distribution of change in preferred speed between pairs of units in MT. The taller histogram is the change in preferred speed for 38 pairs of units separated by less than 200 μm, measured parallel to the cortical surface. There is a tendency for closely spaced units to have similar preferred speeds. The lower, hatched histogram is the distribution that would be expected if the probability of finding a given preferred speed were independent of that previously encountered and were given by the distribution of Fig. 7A. The standard deviations of the two distributions are significantly different ($P < 0.05$). Although the weak correlation between eccentricity and preferred speed would tend to make the distribution slightly narrower than the indicated theoretical distribution, this would not account for the sharpness of the actual distribution.

togram is the distribution that would be expected if the probability of finding a given preferred speed was independent of the previous unit's preference and was given by the distribution in Fig. 7A. The standard deviation of the observed distribution is significantly different than the expected value (F test, $P < 0.05$), indicating a clustering of preferred speeds.

Form and color selectivity

Orientation selectivity is commonly tested with bars that are swept across the receptive field along an axis perpendicular to the length of the stimulus. However, this type of test cannot distinguish unambiguously between true orientation selectivity on the one hand and, on the other hand, selectivity for a particular axis of movement that is independent of stimulus orientation (see Ref. 23). Because units in MT have clear direction selectivity that is largely unaffected by other parameters of the stimulus, we tested for orientation selectivity using flashed, stationary bars. For these tests the length of the bar was usually close to that of the receptive field and the bar's width was about 0.1 its length.

Seventy units were tested for orientation selectivity and 54 (77%) showed clear tuning, with a peak response substantially greater than that to the orthogonal orientation. Figure 10 shows polar plots of the responses of three representative units. Because only 180° of orientation are possible with a rectangular bar, each data point has been plotted twice to complete the circle. Arrows indicate the preferred direction of motion for each unit. Note that the preferred direction is orthogonal to the preferred orientation only for the unit on the left. Summed response histograms for the preferred orientations are displayed below each plot. Responses to flashed stimuli were almost always transient, while those to stimuli moving in the preferred direction were sustained for the duration of the movement (cf. Fig. 1). The peak rates of firing to stationary and moving stimuli were generally very similar though. Among the units that were classified, 30% (14/37) responded best to stimulus onset, 16% (6/37) responded much better to stimulus offset, 38% (14/37) responded well to both, and 16% (6/37) gave no obvious response to flashed stimuli. Receptive fields were not conspicuously segregated into zones giving different types of responses to flashed stimuli.

Figure 11A illustrates the average orientation tuning for units in MT. The 70 tuning curves were normalized, rotated to align the peaks, and averaged. Responses for each orientation are again plotted twice. On average, the best response above background is about 8 times the response when the bar is rotated 90°.

Responses were often best for orientation in which the bar's long axis was perpendicular to the direction preferred when tested with a moving bar. This can be inferred from the average response curve of Fig. 11B. In this figure, the orientation tuning curves for all units were normalized and then rotated to bring the orientation that was perpendicular to the unit's preferred direction to the top. Responses were then averaged. The curve is not circular; the responses for orientations perpendicular and parallel to the preferred direction differ significantly (Student's two-tailed t test, $P < 0.001$). When the background is subtracted, their ratio is about 2. If every unit preferred an orientation that was perpendicular to its preferred direction,
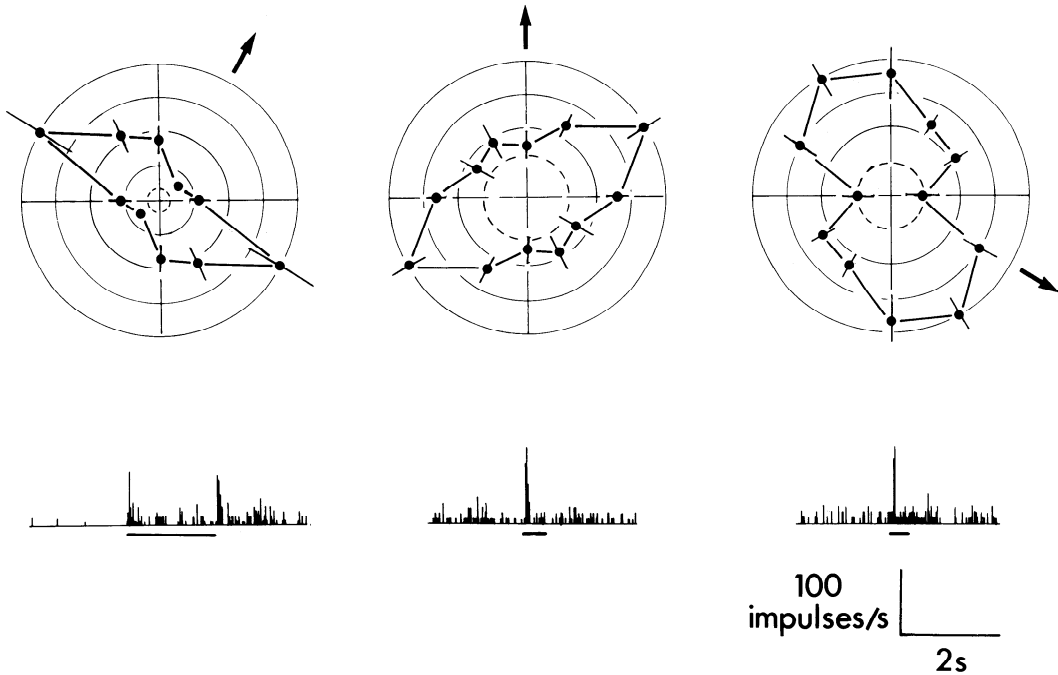
FIG. 10. Responses of three representative units in MT to bars flashed at different orientations. Because only 180° of orientation are possible using a bar, each point has been plotted twice to complete the curves. The response to a vertical bar is on the vertical axis, that to horizontal is on the horizontal axis. Dashed line indicates the average background rate of firing and standard errors of means are indicated for each point. Five presentations of each stimulus were used. The summed histogram below each plot is the response to the best orientation. Arrows indicate each unit's preferred direction of movement.

this curve would be identical to that in Fig. 11*A*. Indeed, some cells actually preferred a stimulus orientation approximately parallel to their preferred direction (see also Fig. 10). However, most of the differences between the two curves is probably due to the effect of
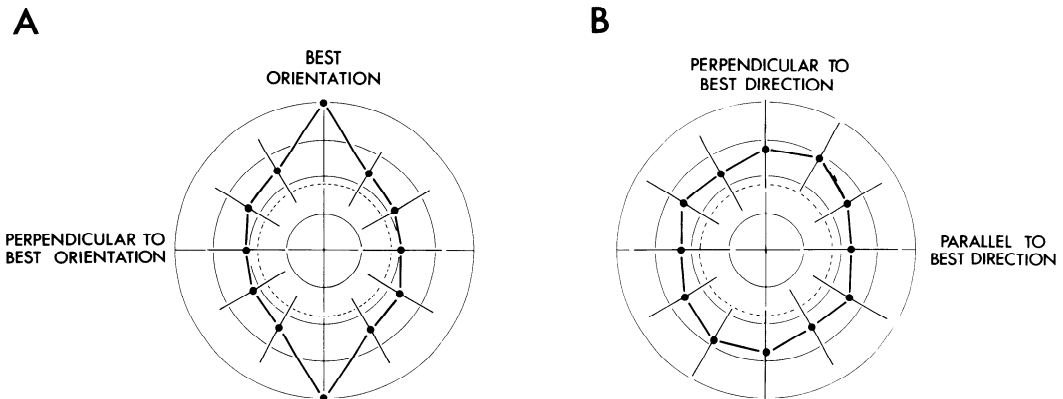

FIG. 11. *A*: average orientation tuning curves for 70 units in MT. The orientation tuning curve for each unit was normalized and rotated to bring the best response to the top. Values from all curves were then averaged. As in Fig. 10, each point is plotted twice to complete the curve. Bars show the standard deviations and the dashed line is the average normalized background rate of firing. The best average response above background is 8 times that when the bar is rotated 90°. *B*: average orientation tuning curve relative to the preferred direction. The tuning curves used for *A* were rotated before averaging to bring to the top the orientation that was perpendicular to each unit's preferred direction of movement. The average response above background to an orientation perpendicular to the preferred direction is twice that to an orientation that is parallel.

combining random fluctuations in the separate measurements of preferred direction and orientation. We found no obvious correlation between the sharpness of tuning for direction and orientation for individual neurons.

The demonstration of a high incidence of orientation selectivity should not be construed to mean that flashed bars are particularly good stimuli for MT neurons or that stimulus orientation bears as much weight as the direction of motion in determining a unit's response when stimuli are moving. Rather, it was generally the case that a short bar of any orientation evoked a near-maximal response as long as it moved in the preferred direction at the preferred speed. Orientation selectivity similar to that just described has been found in MT of the owl monkey (see below), but it apparently does not occur in the lateral suprasylvian area of the cat (53).

Eighteen units in MT were examined for selectivity to the length and width of a bar moving in the preferred direction. Stimulus intensity was not compensated as the stimulus size changed. Stimulus dimensions were varied from 1 to 8° in 1-deg increments, covering a range from about 0.25 to 1.5 of the receptive-field dimensions for the units examined. In most cases, the shortest stimulus approximated a small spot. Most units were only slightly influenced by changes in these parameters. For three units, responses decreased steadily with increasing bar length, indicating substantial end stopping. Such preferences for short stimuli have previously been described in macaque MT (61). For two units, responses increased significantly and for the remainder, responses were largely independent of stimulus length. No significant effects of changes in stimulus width were seen.

Ten units were examined for selectivity to color with moving bars of monochromatic light. All responded about equally well to each of six wavelengths tested over a range from 445 to 640 nm and to white light of equal luminance, with none showing a significant preference for a given wavelength.

The samples tested for selectivity to length, width, and color were small, and interesting properties may have been missed. However, they did indicate that these parameters were of less overall importance to units in MT

than are the others examined in this study. This agrees with earlier observations (16, 61).

Comparisons with owl monkey

Substantial evidence exists for a homology between MT in the macaque and the corresponding area in other primate species (see Refs. 5, 56). It is of interest, therefore, to know how similar the response properties of MT neurons are in different species. The quantitative data on the macaque in the present study and on the owl monkey (5) provide for an accurate comparison along these lines.

Figure 12 shows indices for four aspects of response properties (directionality, direction tuning, speed preference, and orientation tuning) for the macaque (solid histograms) and the owl monkey (hatched histograms). Directionality (Fig. 12A) reflects the relative responses to stimulus motion in the preferred and null directions; it is defined as 1 − ((response to best direction − background)/(response to null direction − background)). Thus a directionality of 0 implies no difference between best and null direction, 1 implies no response to the null direction, and values greater than 1 imply an inhibition to the null direction. The two distributions are very similar and both show a high degree of directionality. The small difference in mean values is significant ($P < 0.005$, Student's t test), suggesting that there is somewhat greater directionality in macaque MT.

Direction tuning for both animals is shown in Fig. 12B. The tuning index measures how quickly responses fall as the direction of motion changes from optimum; it is defined as 1 − area under a normalized direction tuning curve for 90° on either side of the peak, where the curve is normalized to a background of 0 and a peak response of 1. Again, the distributions are quite similar; the average values near 0.5 are equivalent to that obtained for a response that declines linearly to the background level at 90° from the optimal direction.

The preferred speed histograms of the two species are plotted in Fig. 12C. The data for the owl monkey were grouped into bins that are different than those used for the present study, but the overall distributions are similar. The median values are indistinguishable.

Orientation tuning distributions are shown in Fig. 12D. Again, the distributions for the two sets of results are similar. The most con-
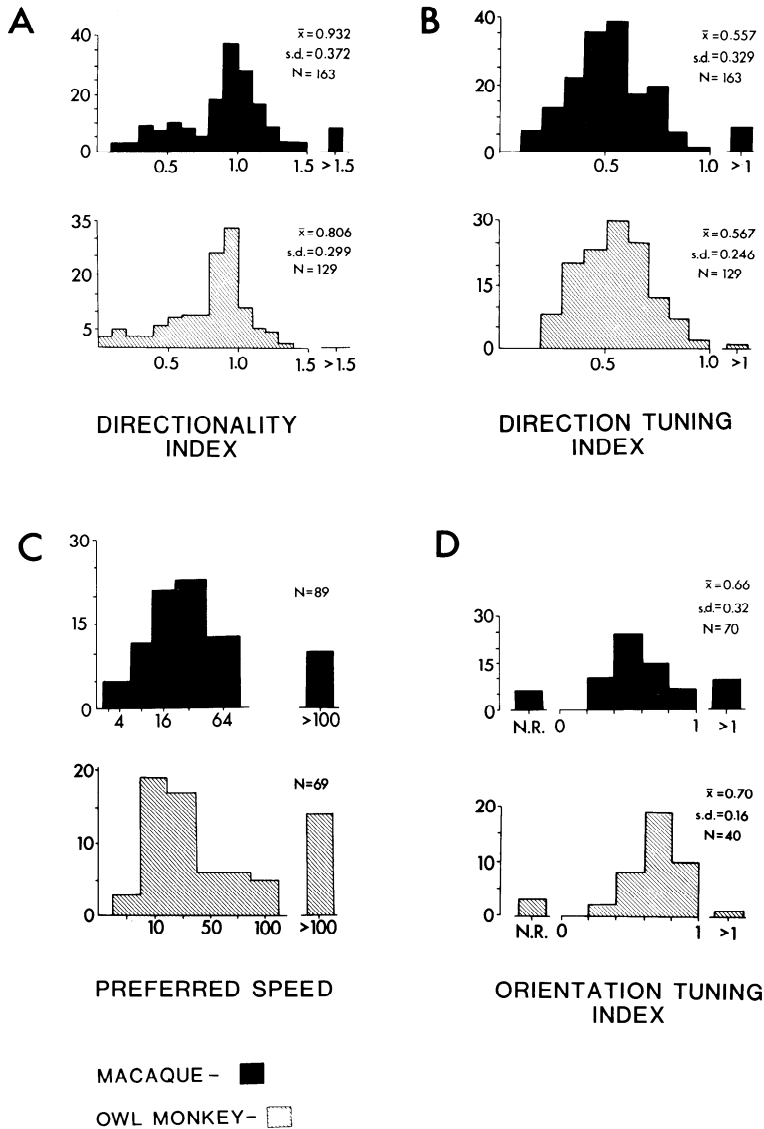
FIG. 12. A comparison of responses in MT of the macaque with those in MT of the owl monkey. Data on the owl monkey are taken, with permission, from Baker et al. (5) and are compared with those from the present study. *A*: directionality index. This index reflects the difference between responses to the preferred and null directions (see text). Distributions are very similar. The small difference in mean values is significant, suggesting that there is somewhat greater directionality in the macaque. *B*: direction tuning index. This index measures how quickly responses fall as the direction is changed from the optimal (see text). These distributions are also very similar, and the slight difference in means is not significant. *C*: preferred speed. Data for the owl monkey were grouped into bins that are different from those used in the present study. The bin widths in the histogram for the macaque have been adjusted to compensate for this difference. MT in both species has neurons with comparable speed preferences, and the median values for the distributions are indistinguishable. *D*: orientation tuning index. This index measures how quickly response falls as the orientation is changed from the best setting; it is calculated in the same way as was done for the direction tuning index. The means of the two distributions are not significantly different.

spicuous difference is that the distribution is somewhat broader for the macaque than for the owl monkey. Neither the means for direction tuning nor for the orientation tuning is significantly different ($P > 0.1$, Student's *t* test) between the species.

Overall, these two sets of data suggest that the selectivities of neurons in MT of the owl

monkey and macaque are remarkably similar. While minor differences undoubtedly exist, the species appear far more alike than had previously been suggested (see DISCUSSION).

DISCUSSION

This study has described the selectivity of units in MT of the macaque for stimulus orientation, speed, and direction of movement. The results confirm previous qualitative results on the existence of direction selectivity and clustering of preferred directions. More importantly, they have demonstrated sharp tuning for speed and clustering of preferred speed. Finally, it has been demonstrated that contrary to earlier reports, there exists clear orientation selectivity in the majority of MT neurons, although orientation is not crucial to attaining strong responses.

The widths of tuning curves for speed are narrow compared to the range of speeds over which units respond. In this sense, their tightness of tuning is comparable to the direction tuning within MT. This suggests even greater specialization for the analysis of visual motion than had previously been recognized. While relatively little is known about speed selectivity in other parts of the macaque visual system, the selectivity seen in MT does not appear to be universal. For example, visual neurons in the posterior parietal cortex are reported to be largely insensitive to stimulus speed (37).

Comparison with V1

MT is one of three extrastriate visual areas that receives a major, direct input from V1 (10, 60). A comparison of the response properties in MT and V1 may give insights into the nature of visual processing in higher cortical visual areas.

In primates, direction selectivity is first generated at the cortical level (25) and direction tuning like that in MT can be found in V1 (47). In a quantitative study of V1, Schiller et al. (46) found that about 48% of the units examined gave responses to motion in their preferred direction that were twice that in the null direction. In MT, 86% of the neurons meet this criterion (Fig. 12A). However, the projection to MT arises selectively from layers IVb and VI in V1 (34), and there is physiological evidence suggesting that layer

IVb is enriched in direction-selective neurons relative to other layers in V1 (14). Thus, the differing incidence of direction selectivity in the two areas may represent selective input rather than processing within MT.

Unfortunately, a detailed study of sensitivity to speed has not been made in macaque V1. Reports of neurons responding well to slow (14) and fast (59) speeds make it unlikely that MT is sensitive to speeds that are not represented in V1, but it is unclear whether any sharpening of tuning occurs.

Many neurons in MT are sensitive to the orientation of flashed bars. Orientation sensitivity exists in V1 (25) but is commonly assessed with moving bars. If one accepts that the two tests can be compared, then the average orientation tuning in MT is similar to that found in V1. However, a difference exists between the two areas in that flashed bars typically evoke only a weak response in MT, and in our experience the response to a moving stimulus is far more dependent on its direction of movement than on its orientation. In V1, a neuron's response may be dependent on having an elongated bar of the correct orientation.

Comparison with MT in owl monkey

Zeki (64) compared the responses of units in MT of the owl monkey and MT (the "motion area") of the macaque and claimed that the differences between the species were as striking as the similarities, to the extent that the areas ought not to be considered homologous. This suggestion can be disputed on two grounds. First, it obviously is not essential that homologous areas be identical in all respects. Second, a quantitative comparison of neuronal response properties in MT of the macaque and the owl monkey does not substantiate the previous suggestion of major differences. In particular, Zeki stated that MT in the owl monkey differs from MT in the macaque in having much higher proportions of neurons that are orientation selective, that require a near-optimal stimulus before responding, or that display strong binocular interactions. In contrast, a comparison of the results of the present study with those of Baker et al. (5) for owl monkey MT reveals a striking similarity in sensitivities to stimulus direction, orientation, and speed. Furthermore, we report in the following paper (36) that most neurons in macaque MT

have binocular interactions as pronounced as those reported for the owl monkey.

There are several factors that could account for the apparent functional differences reported by Zeki. Studies using qualitative assessment of responses are subject to greater variability through drift in subjective criteria and testing procedures from one experiment to the next. A relevant example is the fact that although Zeki (64) reported only 5% orientation selectivity among units in macaque MT, in an earlier study using nominally similar methods (63) he reported 45% orientation selectivity in units and small groups of units. Another source of difference might come from inadvertent inclusion in the overall sample of cells outside the myeloarchitectonic borders of MT. For the macaque Zeki used the pattern of interhemispheric connections to identify MT, but this has been shown to be a less accurate guide than the pattern of myelination (56). For the owl monkey he apparently relied on the topographic organization of receptive fields, and it is possible that some of these recordings were outside MT.

The similarity in a variety of response properties for MT in the macaque and owl monkey adds to the extensive evidence for a homology of this area in the two species (see Ref. 5). The functional similarities are actually rather striking in view of the fact that the owl monkey is a nocturnal, New World monkey and the macaque is diurnal and from the Old World. Little is known about the degree to which homologous brain structures differ in their physiological properties, but differences do occur. For example, direction selectivity exists in the superior colliculus of the squirrel monkey (28) but not the macaque (48). The organization of ocular dominance in V1 shows wide variation among primates (27). Also, the color selectivity seen in visual centers in some species can be expected to be absent in the homologous structures in species lacking color vision. There are differences in the visual topography in MT of the owl monkey and macaque (3, 56), and other differences may emerge from future studies. Nonetheless, the presence of highly conserved properties between species that are distinct in many ways may provide a useful clue to the function of MT.

Relationship to magnocellular and parvocellular projections

Although the separation of the lateral geniculate nucleus (LGN) of primates into distinct magnocellular and parvocellular laminae is one of its most striking anatomical features, it is only in recent years that an appreciation of the functional significance of this dichotomy has begun to emerge. It has been shown in various primate species that most LGN cells (15, 39, 52) and retinal ganglion cells (12) can be classified into X-like and Y-like categories, which are similar in many respects to the X-cell and Y-cell classes in the cat (see Ref. 30). The parvocellular layers contain almost exclusively X-like cells, while the magnocellular layers contain a high percentage of Y-like cells (15, 30, 39, 52). Recent evidence indicates that the magnocellular layers also contain many X-like cells which, however, are not identical to the parvocellular X-like cells (29). Thus, there evidently is a functional counterpart to the anatomical dichotomy of layers in the primate LGN.

Several lines of evidence indicate that a considerable degree of segregation of magnocellular and parvocellular "streams" persists at the cortical level. The magnocellular layers project mainly to layer IVCα (terminology of Brodmann (7) and Lund (33)) of V1 (26), which in turn projects mainly to layer IVB (33). In contrast, the parvocellular layers project mainly to layers IVA and IVCβ (26), which in turn project mainly to more superficial layers (33). Since layer IVB is the major source of projections from V1 to MT (34), it seems likely that MT receives a strong input from the cells of the magnocellular layers. The lack of pronounced color selectivity in magnocellular LGN cells (15, 49) and in MT cells (61; present study) is consistent with this notion. It is possible, though, that there is a substantial parvocellular input to MT as well. In relation to this possibility it is instructive to note that experiments involving selective blockade of LGN laminae have shown, on the one hand, that the corticotectal projection from V1 receives almost exclusively magnocellular input (50), whereas on the other hand, many other V1 cells receive a mixed magnocellular and parvocellular drive (35). Thus, it is clear that the issue

of magnocellular/parvocellular segregation must be addressed separately for each of the functional pathways leading from V1.

Possible functions of MT

The preponderance of direction and speed selectivity in MT suggests it plays an important role in the processing of visual information related to motion. However, information about visual motion may be used for any of a number of purposes, and MT may contribute to only some of these. Different sensitivities are required for different functions, and the available evidence suggests that the information that MT can signal is not well suited for analysis of all aspects of visual motion.

One finding of the present study is that neurons in MT are responsive to a limited range of speeds. Most cells in MT respond poorly to speeds that occur during saccades (>200°/s; Ref. 18). They also do not respond well to very slow speeds such as those caused by drifts in eye position during stationary fixation (~0.1°/s; Ref. 4). During smooth-pursuit eye movements, eye acceleration is related to the speed at which the target is drifting across the retina (32). MT could obviously provide useful information about the speed and direction of target drift. However, during most smooth-pursuit eye movements the speed of target drift is slow, and target movements near the fovea are by far the most important. While MT might contribute to pursuit movement, its range of sensitivities is not well matched to that of the smooth-pursuit system. In this connection, it is interesting that bilateral cortical lesions including most or all of MT apparently do not affect the ability to discriminate real target movement from retinal image movement resulting from changing eye or body positions (9).

Among the functions for which MT does seem well suited is the detection and analysis of movements of objects in the visual field. Neurons in MT have selectivities for direction and speed of motion that could enable it to provide precise information about the trajectories of moving objects. There is psychophysical evidence that the detection of directions of movements in humans involves direction-selective channels, and the similarity between these channels and direction-se-

lective neurons has been noted (see Ref. 51). It is interesting that the width of the average direction tuning curve for MT is consistent with the spread of effects seen in studies of adaptation of human direction sensitivity (6, 31, 45) and masking by directional noise (6), which can reach well over 60° from the direction of adaptation or masking. Also, the range of speeds to which neurons in MT are most responsive closely matches the range for which human observers have the greatest ability to detect differential speeds (42). It will, of course, be important to learn whether other visual areas also show these properties.

Another aspect of motion analysis for which MT seems well suited is that of providing visual guidance for body movements (see Ref. 2). An animal moving through its environment experiences a flow of stimuli across its retinas (21). The structure of the flow, its local direction and speed, can provide a great deal of information about the relative distances of objects. Visual motion may also be important in guiding the movements of individual limbs (54). The suggestion that MT may contribute to the guidance of body movement is supported by the fact that MT has a major projection to the pontine nuclei (17; unpublished observations), which in turn project to the cerebellum, an important center for controlling eye and body movements. Ultimately though, evidence from other approaches, such as lesion studies, will be necessary to provide more critical tests of these hypotheses.

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