FUNCTIONAL ORGANIZATION AND CONNECTIONS OF THE MIDDLE TEMPORAL VISUAL AREA IN THE MACAQUE MONKEY

Thesis by

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Abstract

A variety of anatomical and physiological criteria have shown that the extrastriate visual cortex of the macaque monkey is subdivided into many distinct areas. There is evidence to suggest that there is functional specialization among these areas. Previous studies have shown that the middle temporal visual area (MT) contains a high proportion of cells which are selective for the direction of movement of visual stimuli, and yet relatively non-selective for stimulus color or form. The experiments reported here examined the response properties in MT in greater detail, and demonstrated the inputs and outputs of the area by means of anatomical tracers.

A computer-driven stimulator was used to examine quantitatively the responses of 163 single units from five anesthetized and paralyzed Macaca fascicularis. The experiments included tests of selectivity for stimulus direction, speed, orientation and disparity. Cells were also tested with stimuli which simulated trajectories with components of motion toward or away from the animal. The results show that in addition to direction selectivity, many cells in MT are sharply tuned for stimulus speed and disparity. This suggests that neurons in MT are well adapted for the analysis of motion in three-dimensional space.

Horseradish peroxidase and ^{3}H-proline were injected into MT in three animals to demonstrate its anatomical inputs and outputs. Connections were seen with a large number of subcortical and cortical areas. In addition, connections with MT provide evidence contributing to the identification of two previously unrecognized cortical areas, which we have designated the medial superior temporal area (MST) and the ventral intraparietal area (VIP). The cortical layers in which projections originate and terminate are shown to provide objective anatomical criteria for assigning most cortical visual areas to a hierarchical order.

Table of Contents

General Introduction

The association of the posterior part of cerebral cortex with vision was first established through the study of cortical injuries in the late nineteenth century. Soon afterward, Flechsig and others showed that visual cortex contains a discrete primary sensory area, surrounded by what was described as "association cortex" (see Polyak 1957). In primates, the primary visual area is the recipient of the main cortical projection from the eyes, and is characterized by a prominent striped appearance in histological sections. For this reason it is often called "striate cortex."

Although the characteristic histological structure of striate cortex makes it easy to distinguish from surrounding, extrastriate cortex, further subdivision of visual cortex has not been as easy. Far more progress has been made in experimental animals than is possible in the human brain. A great deal of research has been done on the visual system of the macaque monkey (usually Macaca mulatta or M. fascicularis), the closest genus to man which is readily available for experimental procedures. It has visual capacities similar to those of man, including high acuity, color vision, and stereopsis.

The modern understanding of the subdivision of macaque extrastriate visual cortex began with the demonstration that striate cortex sends topographically organized projections to three distinct extrastriate targets (Cragg 1969, Zeki 1969). Since that time, anatomical connections, topographic organization, and functional properties have been used to establish that extrastriate cortex in this animal contains at least nine distinct visual areas (see Van Essen et al. 1982). The work reported here has been directed at understanding the function of one of these: the middle temporal visual area (MT).

MT is a small area in the posterior bank of the superior temporal sulcus. There are several reasons for selecting it for detailed study. One is the fact that MT has a distinctive heavy myelination, which can be used to determine its complete borders

(Ungerleider and Mishkin 1979, Van Essen et al. 1981). This obviates the need for experimentally introduced markers to confirm that a recording or injection was within its borders. Also, there have been several studies of MT which have provided important clues about its function (Dubner and Zeki 1971, Zeki 1974a,b, Van Essen et al. 1981). In particular, MT has been shown to contain a high percentage of cells which are selective for the direction of stimulus motion, while showing little selectivity for stimulus color or form. Finally, MT in the macaque is homologous to visual areas which have been studied in several other primate species. Comparison of data from different species can provide insight into the degree to which its properties are conserved.

The present study has had two distinct thrusts: a physiological investigation to determine the functional properties of cells in MT in greater detail than before, and an anatomical study of its input and outputs to determine its position in the visual system. Because of previous evidence that MT is involved in analyzing motion, the physiology experiments were largely directed at testing sensitivity to this and other aspects of moving stimuli, including stimulus speed and disparity. Tests for disparity selectivity included stimuli which simulated trajectories with components of motion toward or away from the animal. Chapter 1 describes the responses of neurons in MT to tests of selectivity for stimulus direction and speed, as well as orientation, form and color. Selectivity for disparity is discussed in Chapter 2. These physiology experiments show that in addition to direction selectivity, many neurons in MT are selective for stimulus speed and disparity. These results indicate that MT is well equipped for the analysis of many aspects of motion in three-dimensional space.

Chapter 3 deals with the anatomical experiments. Using injections of anterograde and retrograde tracers, it was possible to demonstrate an extensive set of connection with cortical and subcortical structures. An important result of these experiments is the assignment of MT to a well defined position in a hierarchy of

cortical visual areas. In addition, these connections have provided evidence contributing to the identification of two previously unrecognized extrastriate visual areas.

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Chapter I

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 Van Essen et al. 1982). Differences among the functional properties of several of these areas have been reported (see Zeki 1978), but except for striate cortex our understanding of functional processing remains fragmentary. Detailed knowledge of the types of neuronal responses present in the 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) (Cragg 1969, Zeki 1969), and is characterized by a pattern of heavy myelination that makes it readily distinguishable from neighboring cortical areas (Ungerleider and Mishkin 1979, Van Essen et al. 1981). Previous physiological studies have demonstrated a strikingly high proportion of neurons which are selective for the direction of stimulus motion, while stimulus form seems to be relatively unimportant to the great majority of MT neurons (Dubner and Zeki 1971, Zeki 1974a). Although this suggests MT may somehow be involved in motion analysis, it does not resolve the nature of the processing actually occurring within MT, or which specific aspects of motion analysis it serves.

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 with only a subset of these. It is known that many neurons in macaque V1 are direction selective (Dow 1974, Schiller et al. 1976a), 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. Clues to these 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 is 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 orientation, speed, direction, 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 (Maunsell and Van Essen 1982a).

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 (1979). 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 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 pentothal 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 which restrained the animal's head. The trachea was then intubated, and the animal 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 an infusion of the same solution (7.5 mg/kg/h, IP) for the duration of the experiment. During paralysis the animal was hyperventilated on a mixture of 75% N_2O, 22.5% O_2, and 2.5% CO_2. EKG 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. One or more small (300-500 μm) holes were made at appropriate places in the dura using an electrolytically-sharpened tungsten dissecting needle 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 connected by adjustable couplings, and once it was on the chamber all couplings were tightened firmly so that the microdrive held the animal's head from moving. The X-Y stage allowed accurate measurement of electrode position. Atropine (2%) and neosynephrine (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 of 8 mm diameter were placed in front of the eyes. The positions of the 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 (Hubel 1957) with impedences of 0.2-5 Mohm 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 was normally 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 beamsplitter 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 on a planar, non-depolarizing screen at 114 cm, and viewed by the animal through a second

pair of cross-polarized filters (Cynader and Regan 1978). We checked the polarization by viewing the images through cross-polarized glasses and by insuring 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/m^2. The stimulator was mounted directly below the animal, 20 cm beneath its eyes, to minimize distortion of the stimulus shape from excessive parallax. The stimulator 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.

In some experiments, the projections of the foveas were superimposed on the screen by inserting a prism of appropriate strength and orientation in front of one eye. Initial alignment was confirmed by plotting receptive fields for a binocularly driven response in striate cortex. When the eyes were aligned, the two monocular stimuli were superimposed on the projection screen. No difference in responses were seen when the eyes were aligned in this way.

Sensitivity to color was tested only when the foveas had been aligned. For these tests the polarizing filters were removed, and only one stimulus bar was projected onto a screen of uniform reflectance. Colors were produced by inserting 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 lamp light filtered to produce illumination of relatively 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 signal to the galvanometers was passed through a low pass filter 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 non-varying parameters were initially held at their best settings as judged by manual stimulation. When testing for a given parameter was completed, the setting which gave the best response was used in testing 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 which were used to randomly interleave binocular and monocular stimuli 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. Hence, the number of units is not the same for tests of different parameters.

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 to visual stimulation. However, we did not simply use the average rate of firing during stimulus presentation, as this gives distorted measures for stimuli of very short duration owing to the variable latency of visual responses. We accommodated this in two ways. First, because there is a minimum delay to visual cortex, the time window during which impulses were counted lagged the stimulus presentation by 40 ms. This is slightly shorter than the minimum delay for the onset of evoked potentials in macaque V1 (Gouras and Padmos 1974). Second, a minimum of 250 ms were counted for the average, to compensate for the variability in delay among different units. 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 even 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.

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 pentobarbitol 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. A 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. A series of sections was stained for myelin by the method of Gallyas (1979) and used to determine the boundaries of MT (Van Essen et al. 1981).

RESULTS

A total of 62 penetrations were made in 44 sessions. One hundred and seventy six units in the superior temporal sulcus were examined quantitatively, of which 168 were identified histologically as being in MT. All recording sites were in the right hemisphere, and receptive field centers were all in the left visual hemi-field, within 25° of the fovea. Most receptive fields were in the inferior quadrant, reflecting the biased representation of the visual field in MT (Van Essen et al. 1981). Although lesions were made upon 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 or infragranular, and there were no consistent differences between these groups with respect to any of the response properties that were examined.

Direction

One hundred and sixty-three units in MT were examined for selectivity to direction of stimulus motion. Most were strongly direction selective, as previously reported (Dubner and Zeki 1971, Zeki 1974a, Van Essen et al. 1981). Figure 1 shows recordings from one such unit in MT. This unit preferred movement which was to the left and downward, and gave no response to the opposite, null, direction. Movement perpendicular to the best direction caused only a weak response. The polar plot displays the average responses of this unit to twelve directions of movement. Bars

indicate the standard errors of the means. Most units had tuning curves symmetric about the peak response; the slight asymmetry in this particular tuning curve is probably due to the unit having a preferred direction somewhat clockwise 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 had peak responses which were substantially larger or tuning which was markedly sharper than those from curves taken at the standard interval.

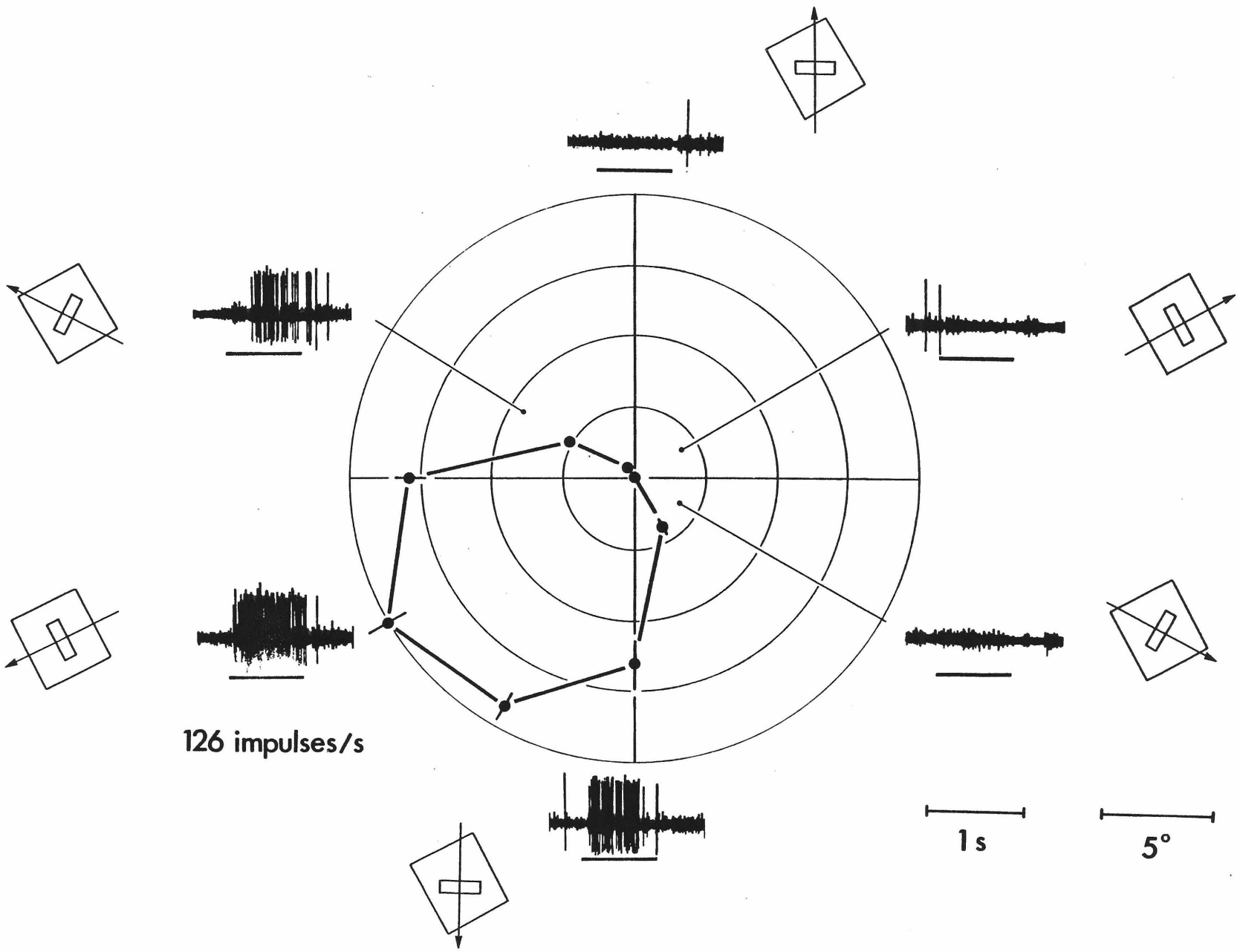
The tuning curves from three other representative units are shown in Fig. 2A. Bars again indicate standard error of the mean for each point, and average background activity is indicated by dashed lines. These units, like many in MT, were inhibited to motion in their null directions. Even in this subpopulation, 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 rate of firing is related to the broadness of tuning, but this was not consistently the case for the overall sample.

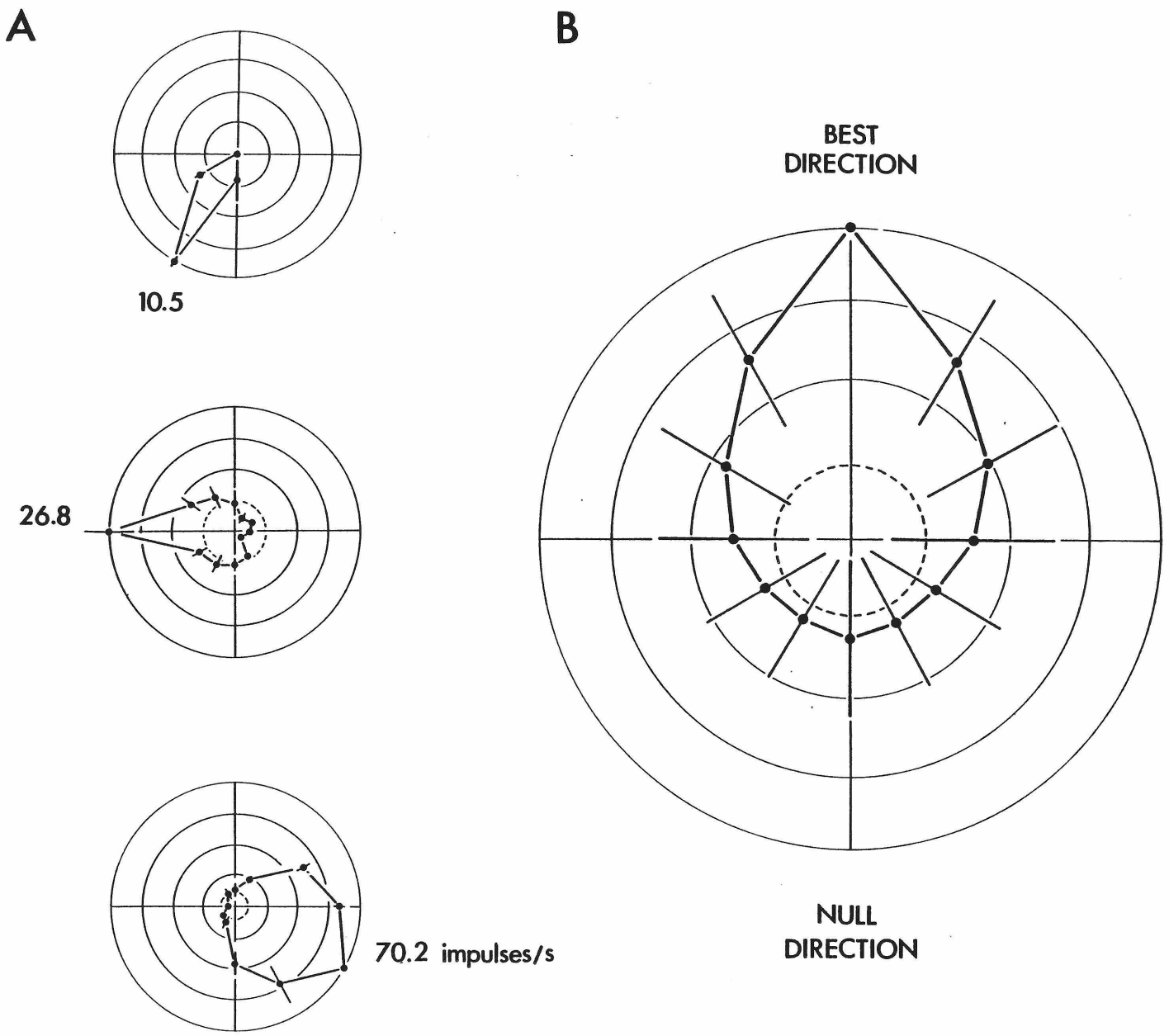
The overall quality of direction tuning in MT is indicated by the average tuning curve in Fig. 2B. This curve was produced by normalizing each of the 163 tuning curves to their best responses, rotating the curves to bring the best direction of movement to the top, and then averaging the normalized responses for each of twelve points. Thus, the first point clockwise from the top represents the average normalized response to a stimulus whose direction of movement is 30° clockwise 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 falls to 50% of the peak value when the direction of movement is 30°

Figure 1. Direction selectivity of a single unit in MT. Voltage traces are shown for individual presentations of the six indicated directions of motion. The bars below each trace mark the time that the stimulus was on. The polar plot is the average rate of firing during stimulus presentation for 5 repetitions of 12 directions of motion. Bars indicate the standard error of the mean for each point.

Figure 2A. 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 the means and dashed lines mark average background rate of firing.

2B. The 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.


126 impulses/s
1 s
5°


A
10.5
26.8
70.2 impulses/s
B
BEST
DIRECTION
NULL
DIRECTION

from the best direction. It is also apparent that the slope of the curve is greatest near the peak. This indicates that units have their greatest sensitivity to change in stimulus direction near their best direction.

Most units in MT respond to stimulation through either eye alone (Zeki 1974a, Maunsell and Van Essen 1982a). 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 which gave the greatest rate of firing in the left and right eyes sometimes differed by 30°, and occasionally more, but these cases generally had broad tuning curves, and are likely to be 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, V2, and MT (Poggio and Fischer 1977, Poggio and Talbot 1981, Zeki 1974b).

The distribution of preferred directions for MT is plotted in Fig. 3A. Interestingly, there is a conspicuous under-representation of units preferring movement in the range from rightward to downward. 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 (1971) also saw an uneven distribution of preferred directions in MT, but their bias consisted of an under-representation of direction of movement with components toward the vertical meridian, whereas ours was confined to about half this range.

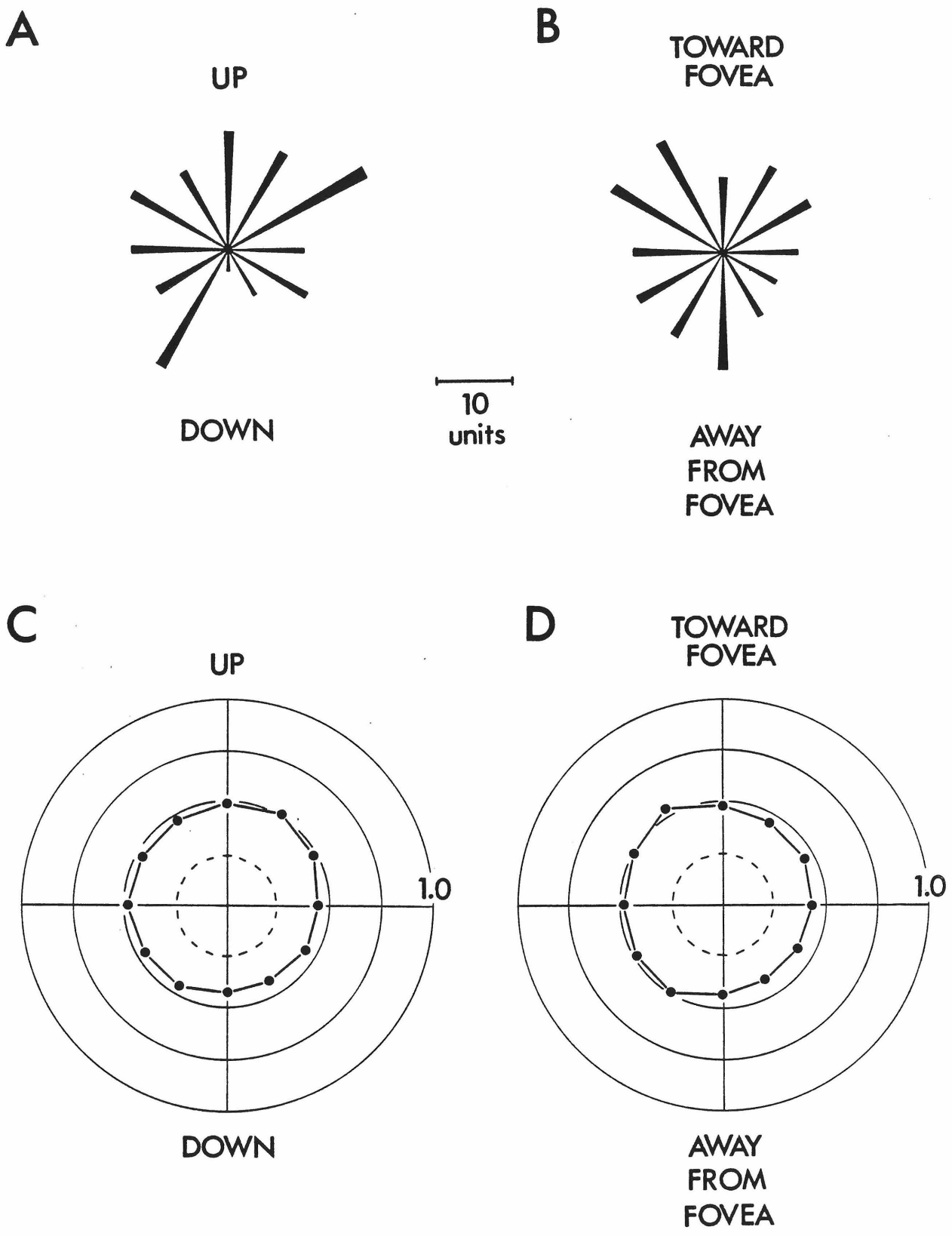
Because the receptive fields were taken from a limited part of the visual field, the bias in Fig. 3A might reflect a preference for motion in a particular direction relative to the fovea. In Fig. 3B the same data have been replotted, taking into

Figure 3A. Distribution of preferred directions for 152 units in MT. Units with no clear preferred direction were excluded. There is a significant under-representation of directions in the range from rightward to downward.

3B. Distribution of preferred directions relative to motion toward the fovea. The data of Fig. 3A were replotted taking receptive field position into account. Units whose preferred directions were toward the fovea are represented by the upper vertical bar, those which 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, this distribution is more uniform than that of Fig. 3A, indicating that the under-represented directions in that distribution do not result from a tendency to a particular direction of motion relative to the direction toward the fovea.

3C. 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 the means are smaller than the size of the 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.

3D. Average normalized response of units in MT to different directions of movement relative to the fovea. The normalized tuning curves used for Fig. 3C 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 the dots. The dashed line is the average normalized background rate of firing.


A
UP
DOWN
B
TOWARD FOVEA
AWAY FROM FOVEA
10 units
C
UP
DOWN
1.0
D
TOWARD FOVEA
AWAY FROM FOVEA
1.0

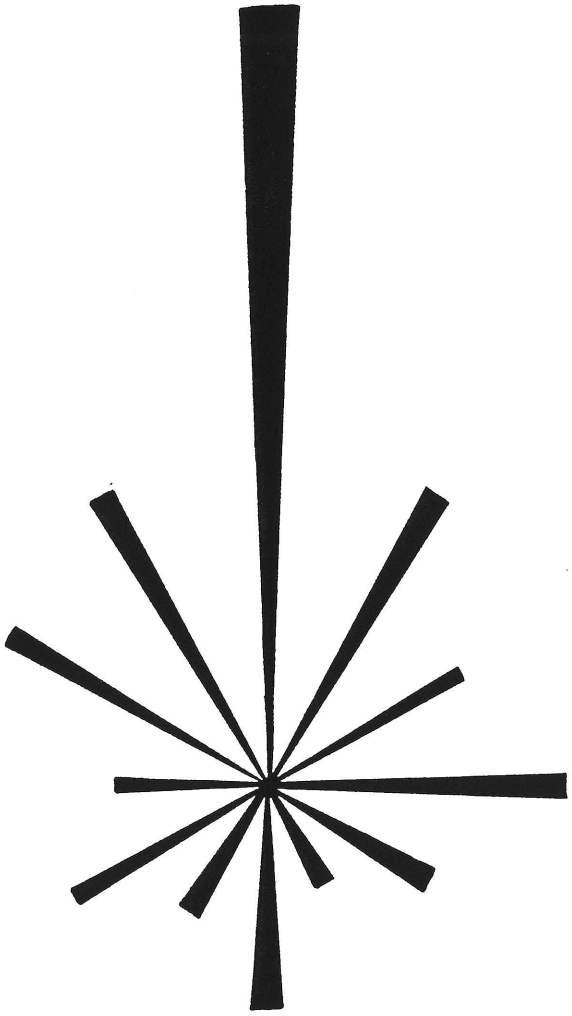
account the position of each receptive field to indicate the preferred direction relative to motion toward the fovea. Preferred movements which are directed toward the fovea are at the top of the diagram, preferred directions away from the fovea are at the bottom. While more units preferred movement away from the fovea than toward it, the overall distribution is more balanced than Fig. 3A. 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 under-representation of a particular range of preferred directions in MT. A non-uniform distribution of preferred directions has also been reported for the posterior parietal cortex of the macaque (Motter and Mountcastle 1981), but the distribution is not the same as that in MT.

Given the width of the tuning curves of most MT neurons, the existence of an under-represented range of preferred directions does not necessarily imply that the population of neurons are 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. Responsiveness to movements downward and rightward are noticeably smaller, especially when measured relative to background. The minimum response above background is fully 80% of the maximum, though, which reflects the breadth of direction tuning. Figure 3D is the responsiveness replotted with direction relative to movement toward the fovea. Again, the plot is not perfectly circular, and the peak response relative to background is nearly 1.3 times the minimum.

Previous studies have shown a clustering of preferred direction in MT (Zeki 1974a, Van Essen et al. 1981, Albright et al. 1981), suggestive of a columnar organization of preferred direction. The nature of the present study was not optimal for examining this property, since few units were sampled in each penetration. Also,

Figure 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.

SAME
DIRECTION



5 units

OPPOSITE
DIRECTION

preferred directions were determined by computer 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 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 which included a unit with very broad direction tuning were excluded. There is a strong peak around zero, corresponding to no detectable change in preferred direction from one unit to the next. This clustering is consistent with some form of columnar organization of preferred direction in MT (Burkhalter et al. 1981, Albright et al. 1981).

Albright et al. (1981) 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, Albright et al. 1981), but was necessary in order to include a reasonable number of pairs. This can also account for many of the changes close to 90°. However, there were several unambiguous examples of particularly closely spaced units having pronounced preferred directions which differed by about 90°. This result would not be expected if the sequential shifts in preferred direction were perfectly regular.

Speed

If MT plays an important general role in the analysis of motion, one might anticipate finding neurons capable of signaling how fast an object is moving, as well as the 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.

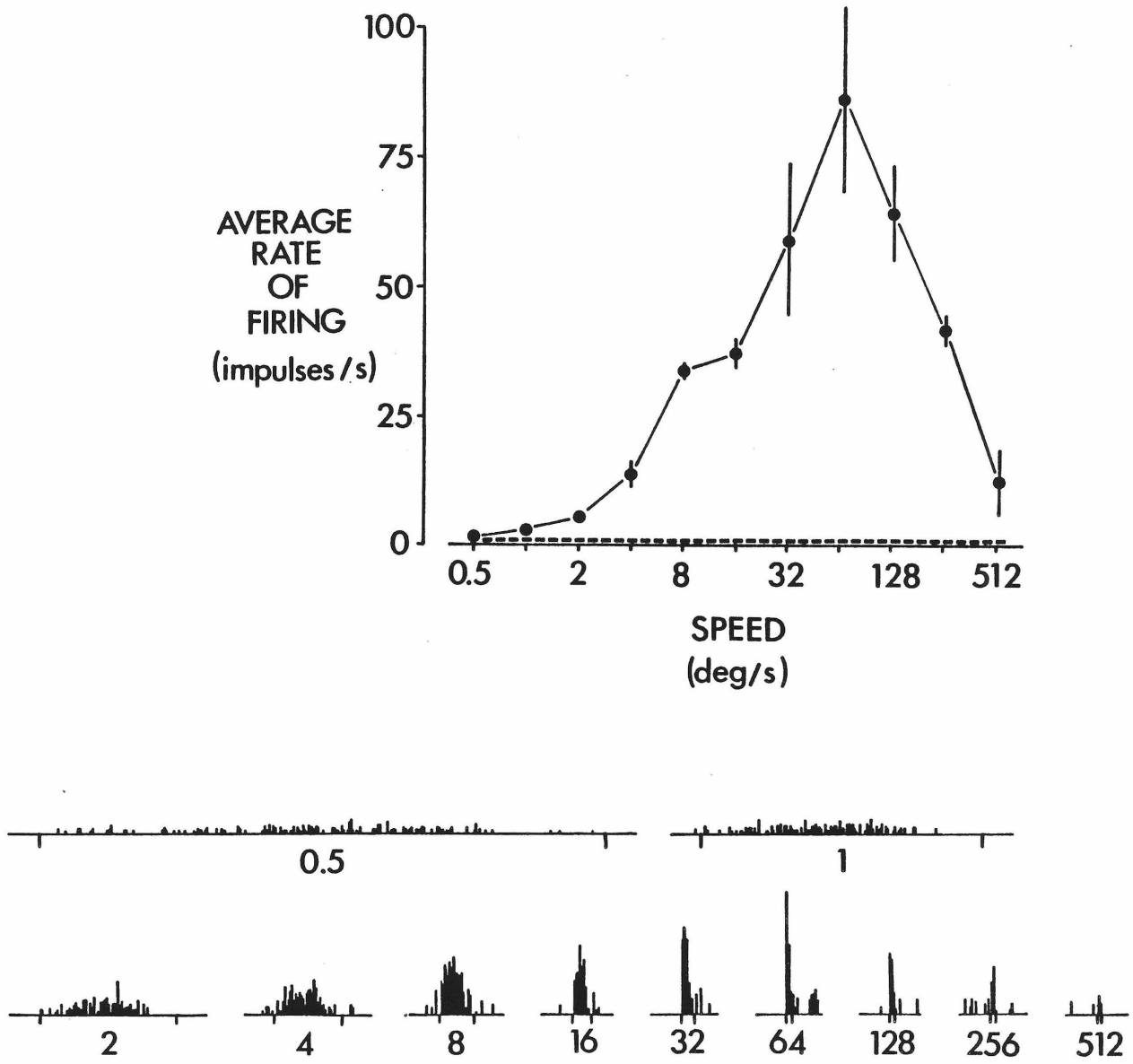
One hundred and nine units in MT were examined for selectivity to the speed of a stimulus moving in the preferred direction. Most units were clearly tuned to a preferred speed. Figure 5 shows a plot of the average rate of firing of a typical unit in MT to stimuli moving at different speeds. The abscissa 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.

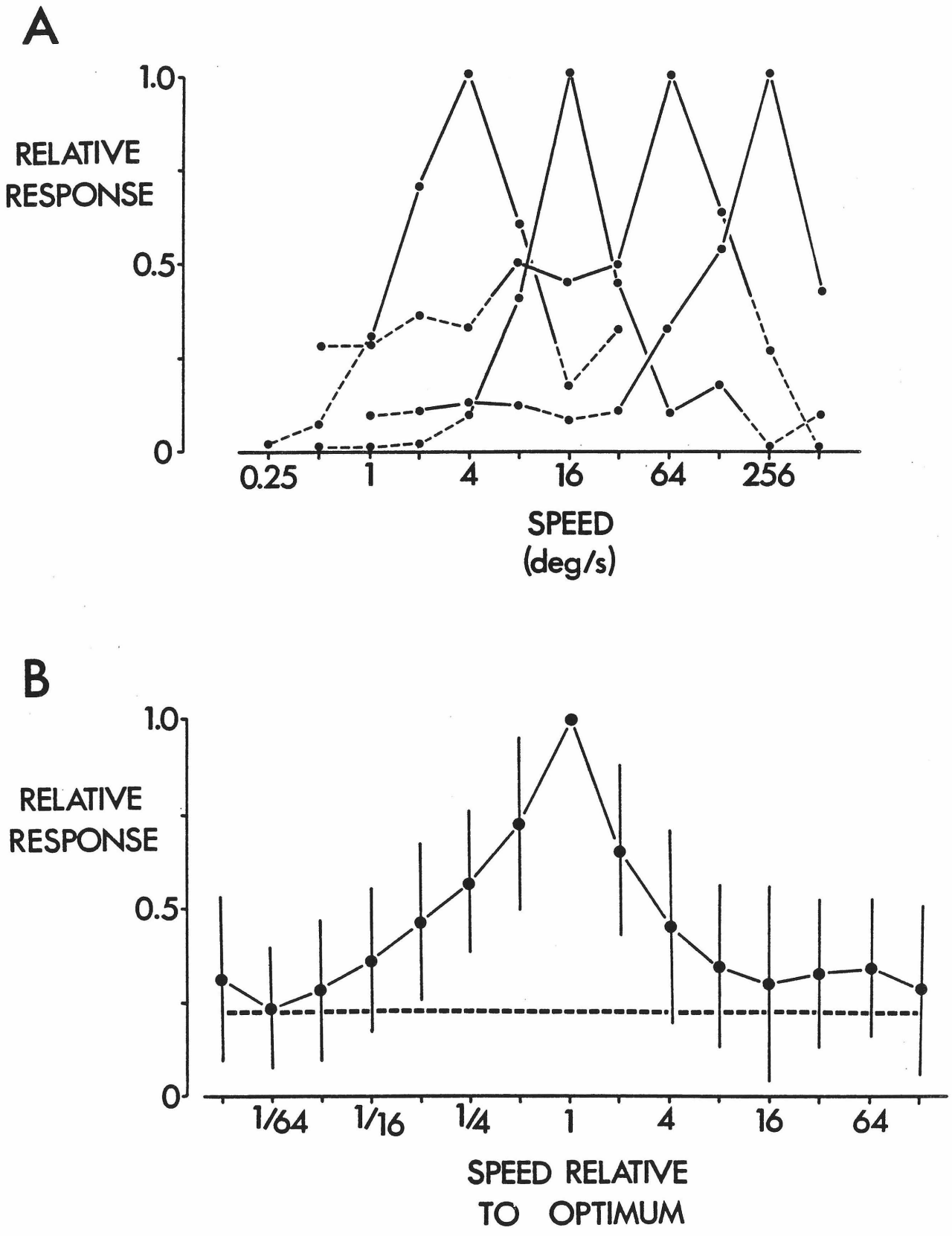
Responses were measured as the average rate of firing during stimulus presentation (see Methods). Although different measures of neuronal response typically yield similar results, it is important to recognize that this is not always the case, especially when stimulus duration varies from one trial to 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 which seems intuitively 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-vs.-speed curves (Movshon 1975, Orban and Callens 1977). 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-vs.-speed curves were generally similar as well, except that slower speeds typically appear more responsive 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 strictly on the practical consideration that this measure requires fewer stimulus presentations to achieve a satisfactory standard error of the mean.

Figure 5. Responses of a representative unit in MT to stimuli moving in its preferred direction at different speeds. The abscissa is logarithmic and 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.

Figure 6A. Responses of four units in MT to different speeds of motion in their respective preferred directions. The abscissa is logarithmic. Each curve has been normalized to its peak response. Portions of each curve which are below the background rate of firing for each unit are dashed. Each unit's tuning curve is narrow compared to the range which they collectively cover. Each unit's response fell to background level or showed inhibition at speeds away from the peak.

6B. The average speed tuning curves of units in MT. The tuning curves of 109 units were normalized to their peak response 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. The abscissa is logarithmic. The average speed tuning curve for MT is sharp; the full-width at half-peak height above background is equivalent to a 7.7 fold change in speed.


100
75
50
25
0
AVERAGE RATE OF FIRING (impulses / s)
0.5
2
8
32
128
512
SPEED (deg/s)
0.5
1
2
4
8
16
32
64
128
256
512


A
1.0
RELATIVE
RESPONSE
0.5
0
0.25
1
4
16
64
256
SPEED
(deg/s)
B
1.0
RELATIVE
RESPONSE
0.5
0
1/64
1/16
1/4
1
4
16
64
SPEED RELATIVE
TO OPTIMUM

Representative responses from four units are illustrated in Fig. 6A. The abscissa is again logarithmic. All of these units showed inhibition to speeds which were far from their preferred speed, and portions of the tuning curves which are below background rate of firing are indicated by dashed lines. In the overall population, a few units had responses which remained high toward one end of the range or the other, but the great majority had a clear peak. 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. (1981) found that neurons in cat area 17 and 18 could be grouped into four distinct classes based on the speeds to which they responded and the broadness of speed tuning. While our sample has differences in the preferred speed and broadness and symmetry of tuning, the appearance is one of a continuum rather than distinct classes. Figure 6B 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 sensitivity near the preferred speed.

The distribution of preferred speeds is shown in Fig. 7A. It covers a range of two orders of magnitude, from 2-256°/s, and has a single peak near 32°/s. This conflicts with the report of Dubner and Zeki (1971), 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 10% had responses to speeds in the range 100-200°/s. In our sample 78% responded best in the intervening range. In a later study, Zeki (1974a) reported that most units in MT have best speeds in the range from 5-50°/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 0.5-512°/s, normalized curves were averaged and displayed as closed 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).

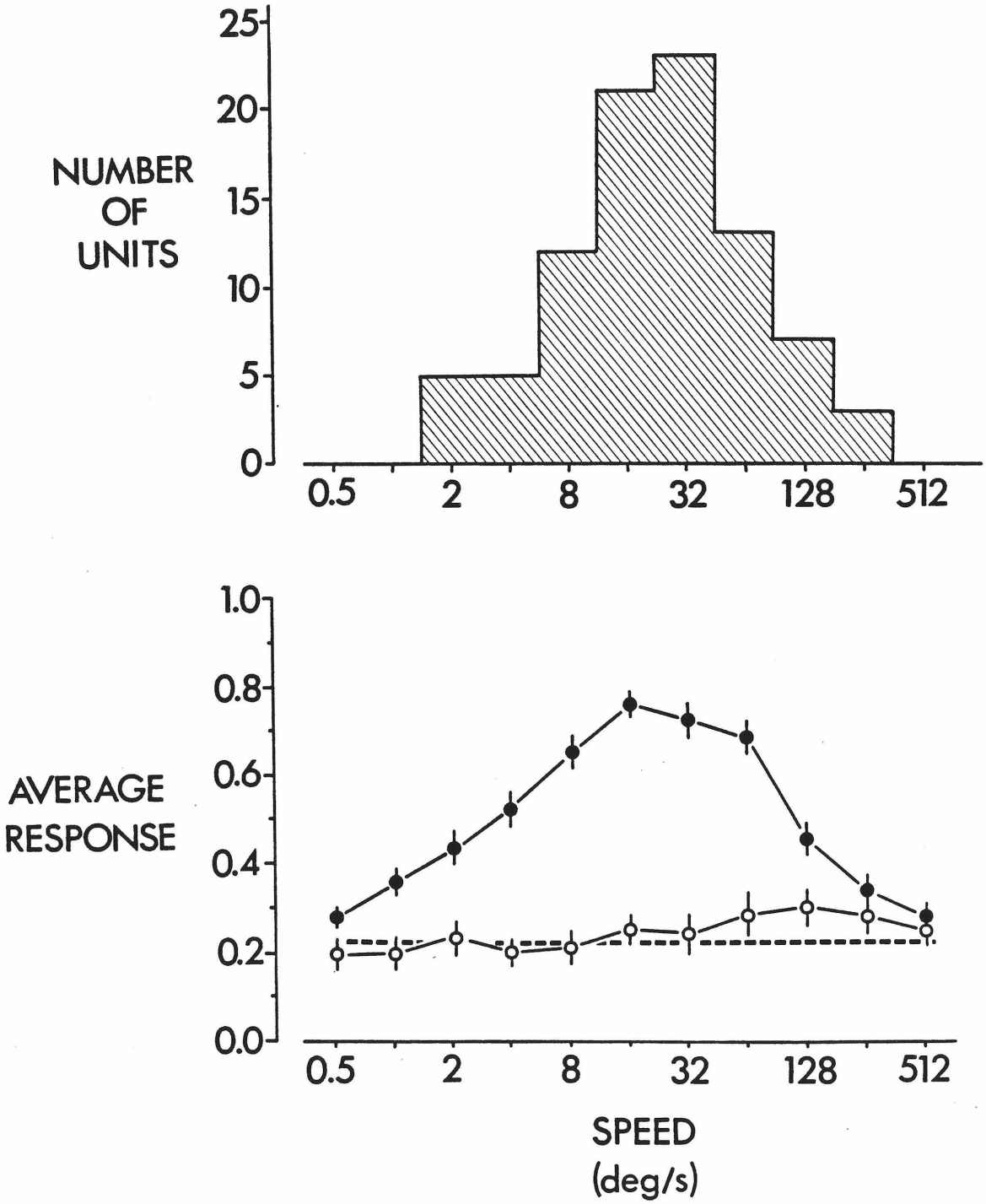
Since many units have weak responses or clear inhibition in the null direction, it was of interest to determine whether there was any tuning for speed in the null direction. In most cells, the response in the null direction, be it inhibition or excitation, was greatest at the speed which evoked the largest 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, it should be emphasized that 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.

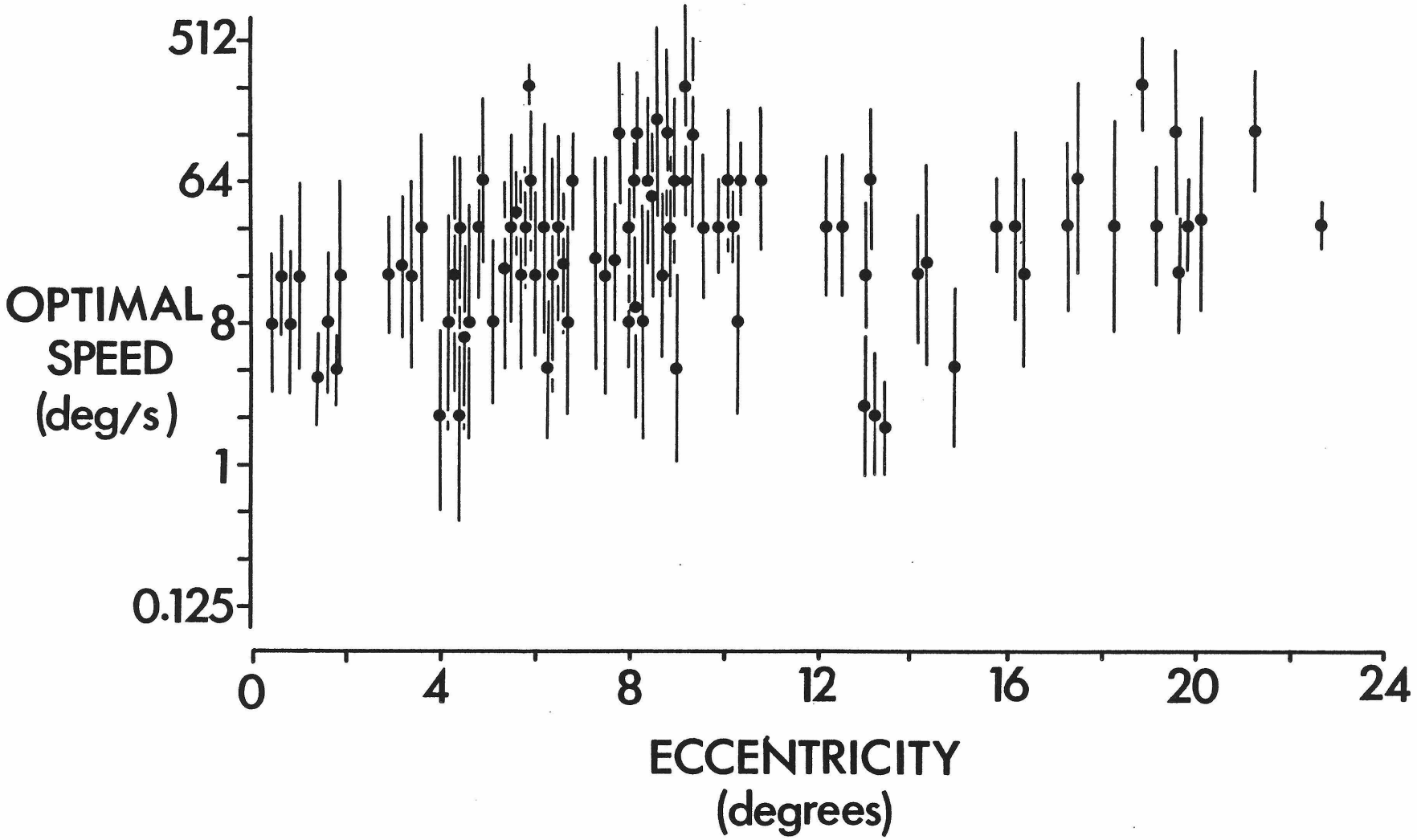
The relation between preferred speed and eccentricity is shown in Fig. 8. Each bar indicates the width of speed tuning at half peak height above background for a particular unit. There was substantial scatter at all eccentricities, indicating that information may be extracted over a wide range of stimulus speeds in all parts of the visual representation. There was a slight correlation to a linear fit ($r^2 = 0.27$) which suggested a three-fold increase in average preferred speed from 0-20° eccentricity. For comparison, the square root of receptive field area increases over ten-fold across

Figure 7A. The distribution of preferred speeds for 89 units in MT. Units with no clear preferred speed were excluded. The distribution has a single peak at about 32°/s.

7B. The average normalized response of units in MT to different speeds. The closed circles show the average normalized response to motion in the preferred direction for 45 units 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 the means, and the dashed line is the average normalized background rate of firing. Neurons in MT are collectively most sensitive to speeds in the range from 8 to 64°/s.

Figure 8. Preferred speed as a function of eccentricity for 89 units in MT. Units with no clear preferred speed were excluded. Bars indicate the width of each tuning curve at half-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 the points yields only a small correlation coefficient (0.27) and suggests that preferred speed increases only three-fold from 0-24° eccentricity.


NUMBER OF UNITS
25
20
15
10
5
0
0.5
2
8
32
128
512
AVERAGE RESPONSE
1.0
0.8
0.6
0.4
0.2
0.0
0.5
2
8
32
128
512
SPEED (deg/s)


512
64
8
1
0.125
OPTIMAL SPEED (deg/s)
0
4
8
12
16
20
24
ECCENTRICITY (degrees)

the same range (Gattass and Gross 1981). A similar relationship between preferred speed and eccentricity has been seen in area 17 of the cat (Wilson and Sherman 1976).

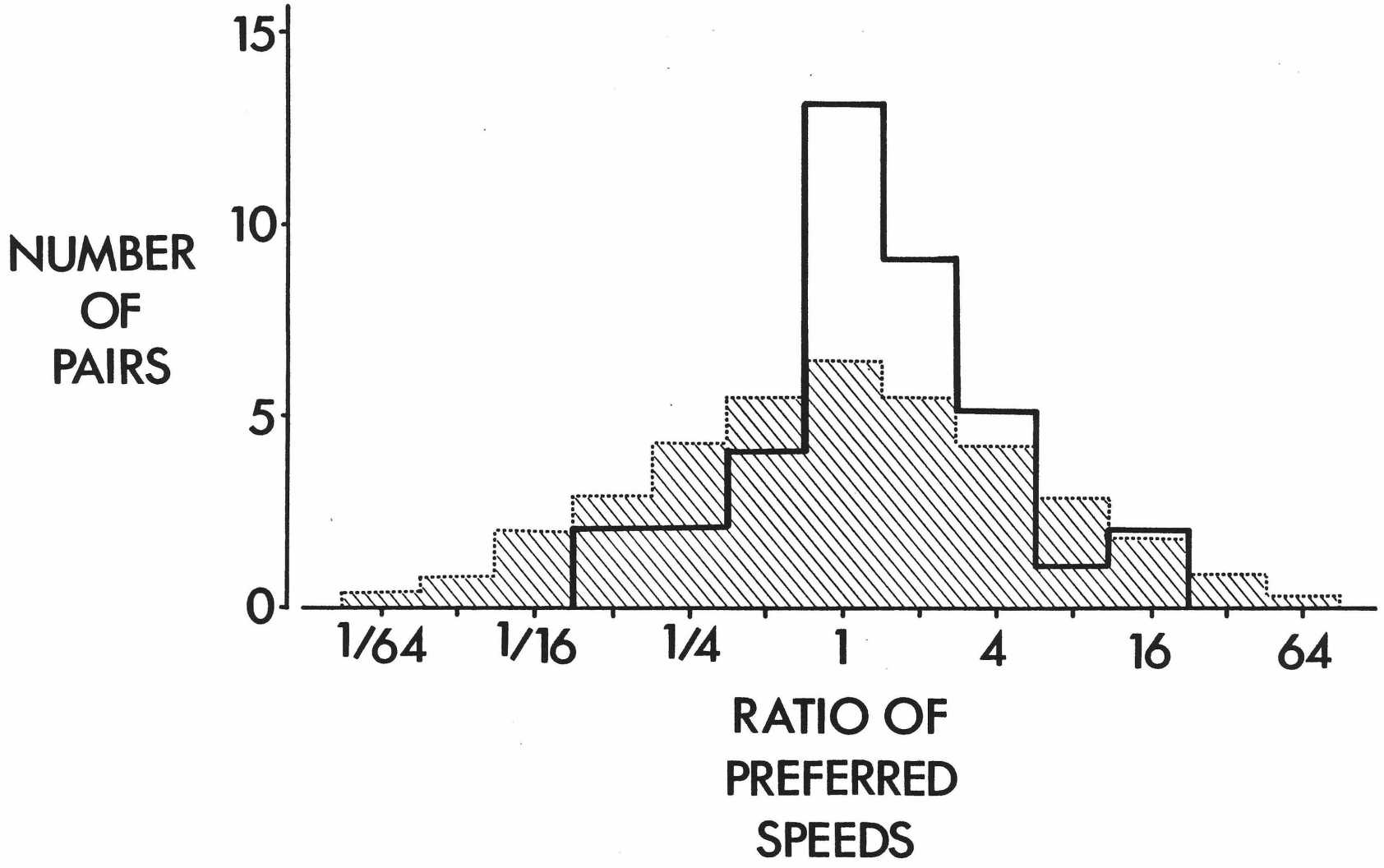
There was a clear tendency for units recorded in a single penetration to have similar preferred speeds. The taller histogram in Fig. 9 is the fractional change in preferred speed between pairs of units in MT whose separation, measured parallel to the cortical surface, was less than 200 μm. The hatched histogram is the distribution that would be expected if the probability of finding a given preferred speed is independent of the previous unit's preference and is given by the distribution in Fig. 7A. The standard deviations of the distributions are significantly different ($p<0.0005$), indicating that pairs had preferred speeds which were more similar than expected.

Form and color selectivity

Orientation selectivity is commonly tested with bars which are moved back and forth across the receptive field along an axis perpendicular to the length of the stimulus. The results of this test can be complicated by units which have a preference for a particular axis of movement which is independent of stimulus orientation (see Henry et al. 1974). Because units in MT have clear direction selectivity which is largely unaffected by other parameters of the stimulus, we tested for orientation selectivity using flashed, stationary bars.

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. 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

Figure 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 which would be expected if the probability of finding a given preferred speed was independent of that previously encountered, and was given by the distribution of Fig. 7A. The standard deviations of the two distributions are significantly different ($p<0.0005$), indicating that nearby units had preferred speeds which were more similar than expected.


15
10
5
0
NUMBER OF PAIRS
1/64
1/16
1/4
1
4
16
64
RATIO OF PREFERRED SPEEDS

rates of firing to stationary and moving stimuli were generally very similar, though. Among the units which were classified, 30% (14/37) responded only 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.

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. The best average response above background is about 8 times the response when the bar is rotated 90°.

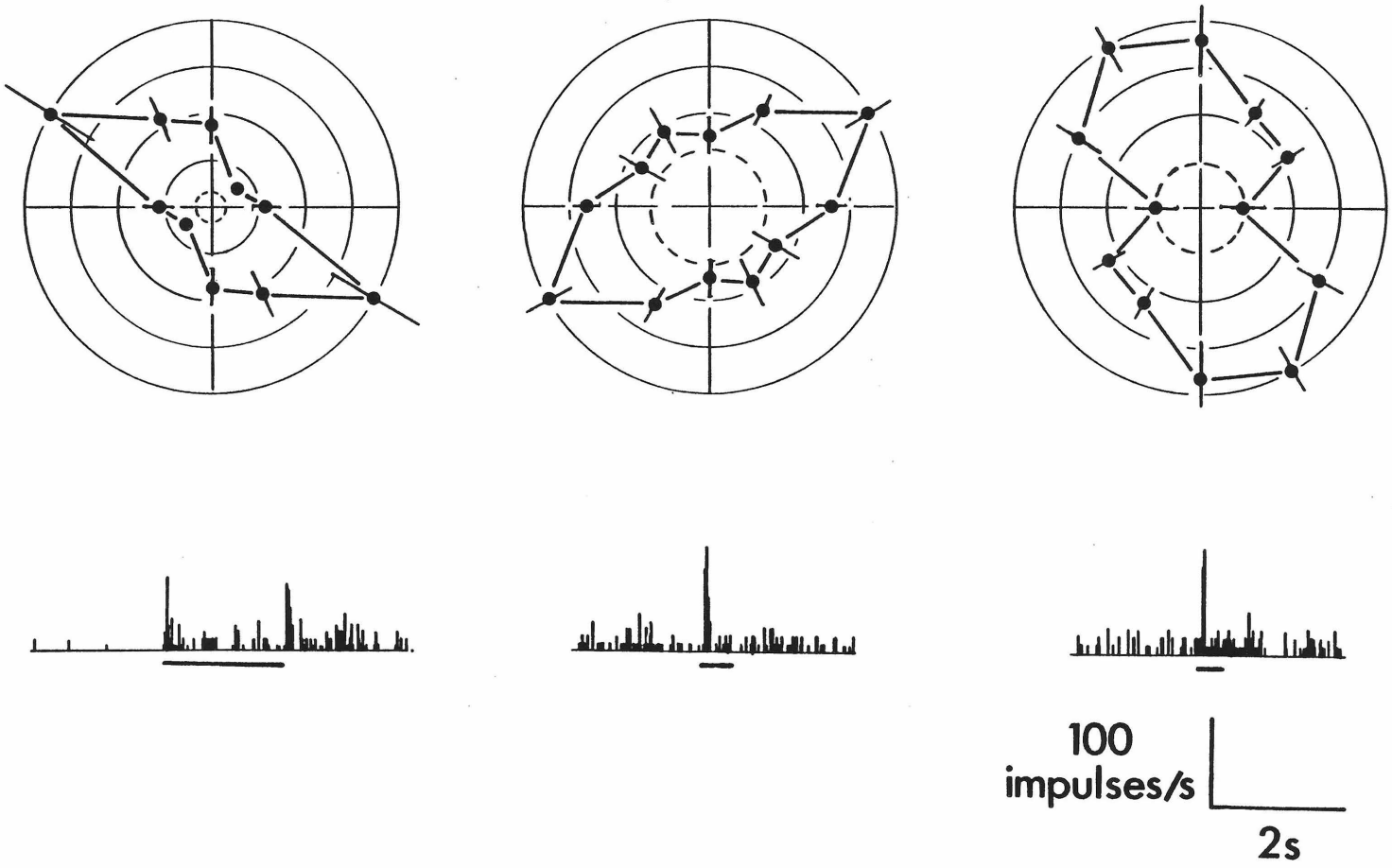
Responses were typically best for orientations in which the bar's long axis was perpendicular to the preferred direction of motion. This can be inferred from the average response curve of Fig. 11B. In this figure, the orientation tuning curves for all units were normalized and then rotated to bring the orientation which was perpendicular to the unit's preferred direction to the top. Responses were then averaged. The curve is elliptical, with the ratio of response above background for orientations perpendicular and parallel to the preferred direction at about 2. If every unit preferred an orientation which was perpendicular to its preferred direction, this curve would be identical to that in Fig. 11A. While some cells preferred orientation parallel to the preferred direction, most of the difference between the two curves is probably due to the effect of combining random fluctuations in both measurements of preferred direction and orientation.

The demonstration of a high incidence of orientation selectivity should not be construed to mean that flashed bars are very satisfactory 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. Specifically, any short bar of any orientation usually evokes a near-maximal response, as long as it is 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 (Spear and Baumann 1975).

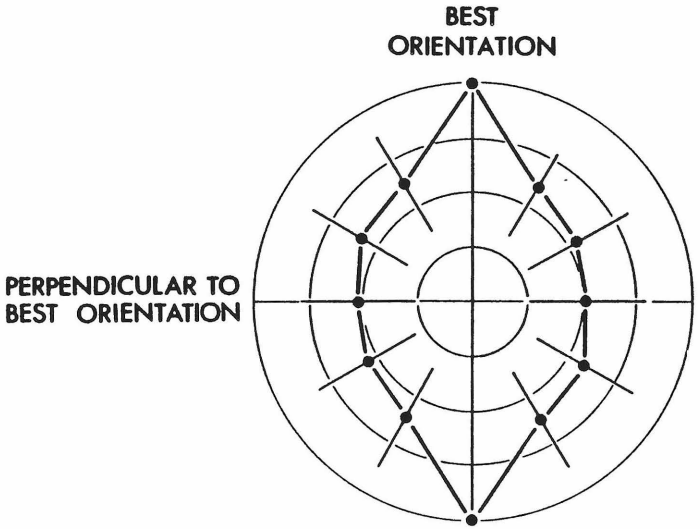
Figure 10. Responses of three representative units in MT to bars flashed at different orientations. Because only 180° of orientation are possible using a bar, each point has been plotted twice to complete the curves. The response to a vertical bar is on the vertical axis, that to horizontal is on the horizontal axis. Dashed line indicates the average background rate of firing, and standard errors of the 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. Like most units in MT, these gave transient responses to flashed stimuli, and some gave an off-response.

Figure 11A. The 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. The 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°.

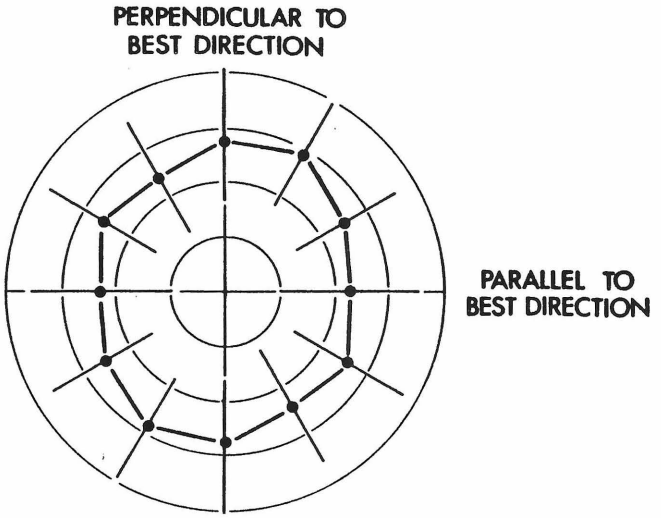
11B. The average orientation tuning curve relative to the preferred direction. The tuning curves used for Fig. 11A were rotated before averaging to bring to the top the orientation which was perpendicular to each unit's preferred direction of movement. The average response above background to an orientation perpendicular to the preferred direction is 2 times that to an orientation which is parallel.


100
impulses/s
2s

A


BEST
ORIENTATION
PERPENDICULAR TO
BEST ORIENTATION

B


PERPENDICULAR TO
BEST DIRECTION
PARALLEL TO
BEST DIRECTION

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 1-8° in 1° 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 two units, responses decreased steadily with increasing bar length, indicating substantial end-stopping. Such preferences for short stimuli have previously been described in macaque MT (Zeki 1974a). For one unit, responses increased significantly, and for the remainder, responses were apparently independent of stimulus length. No significant effects of width were seen.

Twelve units were examined for selectivity to color with moving bars of monochromatic light. All responded well to each of 13 wavelengths tested over a range from 445 to 640 nm, 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 (Dubner and Zeki 1971, Zeki 1974a).

Comparisons with the owl monkey

Substantial evidence exists for a homology between MT in the macaque and the corresponding area in other primate species (see Baker et al. 1981). However, Zeki (1980) claimed that single unit responses in macaque MT differ markedly from those in owl monkey MT in two important respects. He reported that MT in the owl monkey had much higher proportion of orientation selective units (70% vs. 5%) and a much higher proportion of cells with strong binocular interactions. Zeki used qualitative

judgements of unit responses in his study; the quantitative data on the macaque in the present study and on the owl monkey from Baker et al. (1981) provide for a more accurate comparison of MT in these species.

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 and is defined as:

$$1 - \frac{\text{response to best direction - background}}{\text{response to null direction - background}}$$

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 and 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 which declines monotonically to background level over 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 which are different than those used for the present study, but the overall distributions are similar. The median values are indistinguishable.

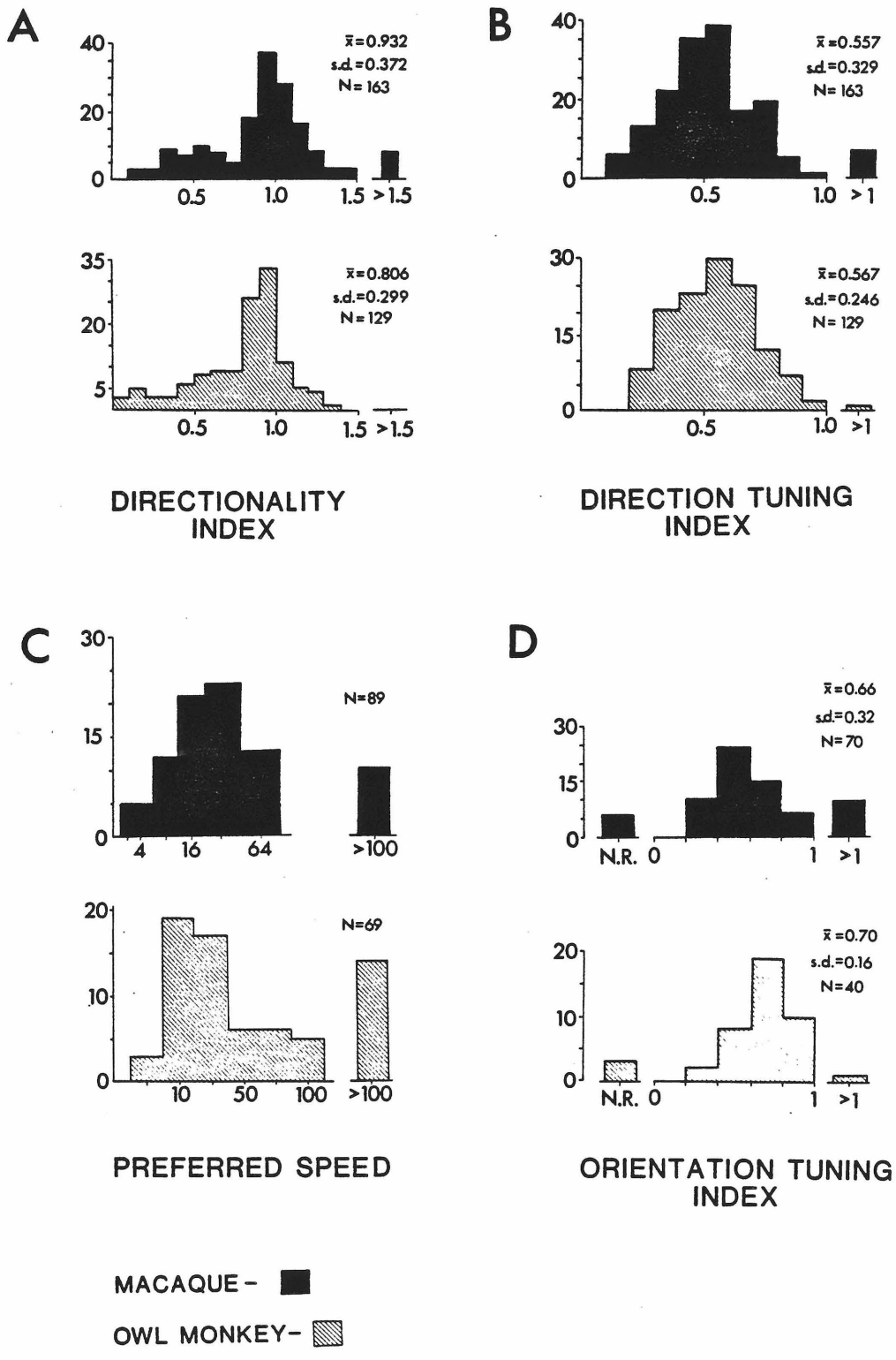
Figure 12. A comparison of responses in MT of the macaque with those in MT of the owl monkey. Data on the owl monkey from Baker et al. (1981) are compared with those from the present study.

12A. Directionality index. This index reflects the difference between the responses to the preferred and null directions (see text). The distributions are very similar. The small difference in mean values is significant, suggesting that there is somewhat greater directionality in the macaque.

12B. 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 the means is not significant, for the number of units sampled.

12C. Preferred speed. The data for the owl monkey were grouped into bins which are different than those used in the present study. The bins 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.

12D. Orientation tuning index. This index measures how quickly response falls as the orientation is changed from the best setting. The means of the two distributions are not significantly different for the number of units sampled. Data for the owl monkey are taken, with permission, from Baker et al. (1981).


A
40
20
0
x̄=0.932
s.d.=0.372
N=163
0.5
1.0
1.5
>1.5
35
20
5
x̄=0.806
s.d.=0.299
N=129
0.5
1.0
1.5
>1.5
DIRECTIONALITY INDEX
B
40
20
0
x̄=0.557
s.d.=0.329
N=163
0.5
1.0
>1
30
15
0
x̄=0.567
s.d.=0.246
N=129
0.5
1.0
>1
DIRECTION TUNING INDEX
C
30
15
0
N=89
4
16
64
>100
20
10
0
N=69
10
50
100
>100
PREFERRED SPEED
D
30
15
0
x̄=0.66
s.d.=0.32
N=70
N.R.
0
1
>1
20
10
0
x̄=0.70
s.d.=0.16
N=40
N.R.
0
1
>1
ORIENTATION TUNING INDEX
MACAQUE-
OWL MONKEY-

Orientation tuning distributions are shown in Fig. 12D. The distributions within both sets of results are similar. The most conspicuous difference is that the macaque orientation tuning distribution is broader than that of the owl monkey. With the number of samples taken, 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, the data of Baker et al. and the present study suggest that the selectivities of neurons in MT of the owl monkey and macaque are remarkably similar. While minor differences undoubtably exist, the species appear far more alike than was reported by Zeki (1980) (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. Lastly, 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 (Motter and Mountcastle 1981).

Comparison with V1

MT is one of three extrastriate visual areas which receive a major, direct input from V1. 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 (Hubel and Wiesel 1968), and direction tuning like that in MT can be found in V1 (Schiller et al. 1976b). In a quantitative study of V1, Schiller et al. (1976a) found that about 48% of the units examined gave responses to motion in their preferred direction which was twice that in the null direction. By this criterion, 86% of MT cells are direction selective or direction biased (Fig. 12A). However, the projection to MT arises selectively from layers IVb and VI in V1 (Lund et al. 1976), and there is fragmentary evidence suggesting that layer IVb is enriched in direction selective neurons relative to other layers in V1 (Dow 1974). 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 (Dow 1974) and fast (Wurtz 1969) speeds make it unlikely that MT is sensitive to speeds which 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 (Hubel and Wiesel 1968) but is normally 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 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 the owl monkey

Zeki (1980) 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. In particular, he stated that MT in the owl monkey differs from MT in the macaque in having far higher proportions of neurons which are orientation selective or which require a near optimal stimulus before responding, and in displaying a wide range of binocular interactions which he did not see in macaque MT. In contrast, a comparison of the results of the present study with those of Baker et al. (1981) for owl monkey MT reveals a striking similarity in sensitivities to stimulus direction, orientation, and speed. Furthermore, we report in the following paper (Maunsell and Van Essen 1982a) that most neurons in macaque MT have binocular interactions as pronounced as those Zeki reported for the owl monkey.

We suspect that the degree of difference reported by Zeki may be misleading for several reasons. 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 (1980) reported only 5% orientation selectivity among units in macaque MT, in an earlier study using nominally similar methods (1978), he reported 45% orientation selectivity in units and small groups of units. Another source of difference might come from Zeki's failure to verify that his recordings in either species were within the myeloarchitectonic borders of MT (Allman and Kaas 1971, Ungerleider and Mishkin 1979, Van Essen et al. 1981). For the macaque he used the degeneration of corpus callosum fibers as a guide, which has been shown to be less accurate (Van Essen et al. 1981). For the owl monkey he apparently relied on visual topography, 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 Baker et al. 1981). The similarities in response properties is 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 (Kadoya et al. 1971) but not the macaque (Schiller and Koerner 1971). The organization of ocular dominance in V1 shows wide variation among primates (Hubel et al. 1975). 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. While there are differences in the visual topography in MT of the owl monkey and macaque (Allman and Kaas 1971, Van Essen et al. 1981) and other differences may emerge, the presence of highly conserved properties between species which are distinct in many ways may provide a useful clue to the function of MT.

Y-cell input to MT

The responses of retinal ganglion cells in the monkey can be classified into categories similar to the X and Y cell types of the cat (see Lennie 1980). In the macaque, these classes remain largely separated through several levels of the visual system, as is demonstrated by the dominance of Y-type input in the projection from V1 to the superior colliculus (Schiller et al. 1979). There is some evidence to suggest that the projection from V1 to MT may also be dominated by Y-type input.

Y-type input to V1 terminates primarily in layer IVc α (Hubel and Wiesel 1972, Dreher et al. 1976), which has interlaminar projections to layers IVb and V (Lund and Boothe 1975). Layer V gives rise to the corticotectal projection, which, as mentioned above, is known to be dominated by Y input. Layer IVb is the principal source of projections to MT (Lund et al. 1976, Maunsell and Van Essen 1982b). The lack of color selectivity in MT (Zeki 1974a, present study) is also consistent with Y-type input (de Monasterio 1978, Schiller and Malpeli 1978).

X-type and Y-type responses are known to mix to some degree in V1 (Malpeli et al. 1981). It would clearly be of interest to know if segregation is preserved in some parts of extrastriate cortex. The resolution of this question will have to await further experiments.

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. Motion is used to detect objects in the visual field, and to determine their three-dimensional trajectories. It is also important for guiding smooth-pursuit eye movements, and could be used to correct the small drifts in eye position which occur during stationary fixation. Visual motion provides feedback for guiding body movements. Motion analysis also encompasses the differentiation of visual movements due to eye or head motion from those caused by objects moving in the visual field. Different sensitivities are required for these functions, and the available evidence suggests that the information which MT can signal is not well suited for all of them.

One finding of the present study is that neurons in MT are responsive to a discrete range of speeds. It is clear that they are not responsive to speeds which occur during saccades (>200°/s, Fuchs 1967). They also do not respond well to slow speeds, such as those caused by drifts in eye position during stationary fixation ($\sim$0.1°/s, Alpern 1962). During smooth-pursuit eye movements, eye acceleration is related to the speed at which the target is drifting across the retina (Lisberger et al. 1981). MT could obviously provide useful information about the speed and direction of target drift. However, the relationship between eye acceleration and target speed is linear only up to about 20°/s. Almost half the units in MT respond best to speeds greater than this (Fig. 7A). While MT might contribute to these eye movements, its range of

sensitivities is not well matched to that of the smooth pursuit system. Bilateral cortical lesions including MT apparently do not affect the ability to discriminate real target movement from retinal image movement resulting from changing eye or body positions (Collin and Cowey 1980).

Among the functions to which MT seems well suited to contribute is the detection and analysis of movements of objects in the visual field. The neurons in MT have selectivities for direction and speed of motion which 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 selective neurons has been noted (see review by Sekuler et al. 1978). 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 (Levinson and Sekuler 1976, Riggs and Day 1980) and masking by directional noise (Ball and Sekuler 1979).

Another aspect of motion analysis for which MT seems well suited is that of providing visual guidance for body movements (Allman 1982). An animal moving through its environment will experience a flow of stimuli across its retinas (Gibson 1950). The structure of the flow, its local direction and speeds, can provide a great deal of information about the relative distances of objects. 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 (Fries 1981, Maunsell and Van Essen 1982b), which in turn project to the cerebellum, a major center for controlling body movements.

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Chapter 2

INTRODUCTION

Stereoscopic vision makes use of the different views seen by the two eyes to judge the distance to points in visual space. This information is useful for assessing the shape of three dimensional objects, their distance from the eyes, and, in the case of moving objects, their trajectories through space. Since humans and animals have good capacities for all three of these functions, there is likely to be a substantial neural apparatus concerned with the various aspects of stereoscopic vision. In the cerebral cortex of the macaque monkey, V1 (striate cortex) and V2 have been shown to contain neurons which are selective for binocular disparity (Hubel and Wiesel 1970, Poggio and Fischer 1977, Poggio and Talbot 1981). However, little is known about the contribution of other visual areas to the processing of stereoscopic information.

In the present study, we have looked at the role of a particular visual area in the macaque, the middle temporal area (MT), in analyzing motion in three dimensional space. The preceding report (Maunsell and Van Essen 1982) provided quantitative evidence for a high degree of selectivity for both the direction and speed of stimulus motion for the majority of MT neurons. It is obviously of interest to know whether any of these neurons are in addition sensitive to the binocular disparity of moving stimuli, which would allow them to signal information about motion in three dimensions. We were especially curious because MT has been reported to contain a low percentage of cells which prefer opposite directions of motion when stimulated with either eye alone (Zeki 1974b). Such cells could respond best to objects moving directly toward or away from the animal (Regan and Beverly 1973a). We anticipated that with carefully controlled binocular stimulation we could study such opposed movement cells in detail. In addition, we hoped to find a substantial incidence of cells which were tuned for motion in depth even if their monocular direction preferences were similar.

To our surprise, no neurons in our sample from MT were truly selective for motion in depth, in the sense of responding maximally to stimuli which simulated movement with components toward or away from the animal (i.e. not fronto-parallel). Nevertheless, information about three-dimensional trajectories is extensively represented in MT, as a large proportion were selective for motion at particular fixed disparities. In the course of testing these disparity tuned neurons for motion in depth selectivity, we found that many appeared to change their preference from fronto-parallel movement to some motion in depth when tested in different conditions. However, a thorough examination showed this property to be a simple and predictable consequence of tuning for fixed disparities. The results of these experiments bear importantly on previous interpretations of selectivity for motion in depth, and on the understanding of the degree to which complex stimulus characteristics are extracted in the early stages of processing in the visual system.

MATERIALS AND METHODS

The basic methods for these experiments have been described in the preceding paper (Maunsell and Van Essen 1982). Techniques particularly relevant to the present experiments will be presented here.

Five Macaca fasicularis were used for semi-chronic recording. During recording sessions the animal was anesthetized and paralyzed. The visual stimulator used for these experiments could be operated either manually or under computer control; it imaged a bar whose length, width and orientation were all independently variable. Monocular stimuli which could be moved independently were produced using a beamsplitter and two pairs of X-Y mirrors. The two beams were passed through polaroid filters whose planes of polarization were at right angles, projected on a non-depolarizing screen, and viewed by the animal through a second pair of cross-polarized filters (Cynader and Regan 1978).

The positions of the foveas were checked frequently using a reversing ophthalmoscope. The initial positions were confirmed at the start of each penetration by plotting receptive fields for responses in V1 through each eye alone. Based on these plots and other measurements, the accuracy of the ophthalmoscope was judged to be roughly $\pm 1/2°$. Therefore the absolute disparity of our stimuli could be determined to about $\pm 1°$. The drift in eye position was small, usually about 1° over the course of a recording session.

When a unit was isolated, receptive fields were plotted for each eye alone, and their positions fed into a computer which was then used to generate stimuli and to record and analyze responses. The computer adjusted stimulus positions to compensate for misalignment of the animal's paralyzed eyes. The overall accuracy of stimulus positioning during computer control was about 0.1°. Stimuli were presented in a random order; monocular stimuli were interleaved with binocular when the former were being tested. Normally five repetitions of each stimulus were averaged in calculating the average rate of firing during stimulus presentation.

Units were tested for two types of disparity selectivity. The first was examined using sets of stimuli with different horizontal disparities. The disparity was constant during any given presentation. These stimuli simulated objects moving in fronto-parallel planes at different distances from the animal. For this type of test, the monocular stimuli always moved in the unit's preferred direction at the preferred speed, both of which were normally established with prior quantitative tests. Horizontal bars of infinite length can have no horizontal disparity, but when the optimal stimulus was close to horizontal, we made sure to use bars which were short compared to receptive field dimensions. In many cases, stimuli were short enough to approximate spots. Disparities were introduced by shifting each monocular stimulus one half of the total disparity. Care was taken to insure that each monocular stimulus began and ended its traverse a short distance outside the receptive fields,

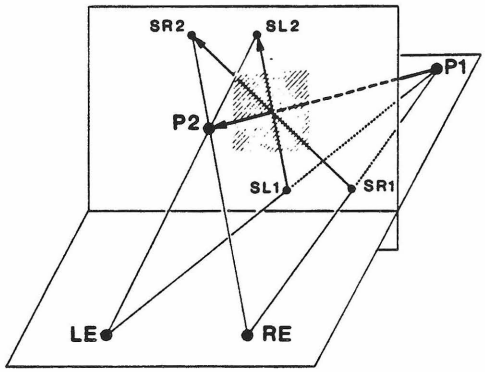
usually 10-20% of the receptive field width. This type of test will be referred to as a test for fixed disparity selectivity.

The second type of test was for selectivity for changing disparity. This was examined using sets of stimuli in which the rate of disparity change was varied systematically. Each set consisted of twelve stimuli which together simulated a complete range of trajectories from motion away, through fronto-parallel to motion toward, and back again to motion away. We will refer to this as a test for motion in depth. In the present context, fronto-parallel motion is not considered to be motion in depth, regardless of the disparity. It should be realized that no stimulus actually moved in depth, and changing disparity is only one of several cues for motion in depth.

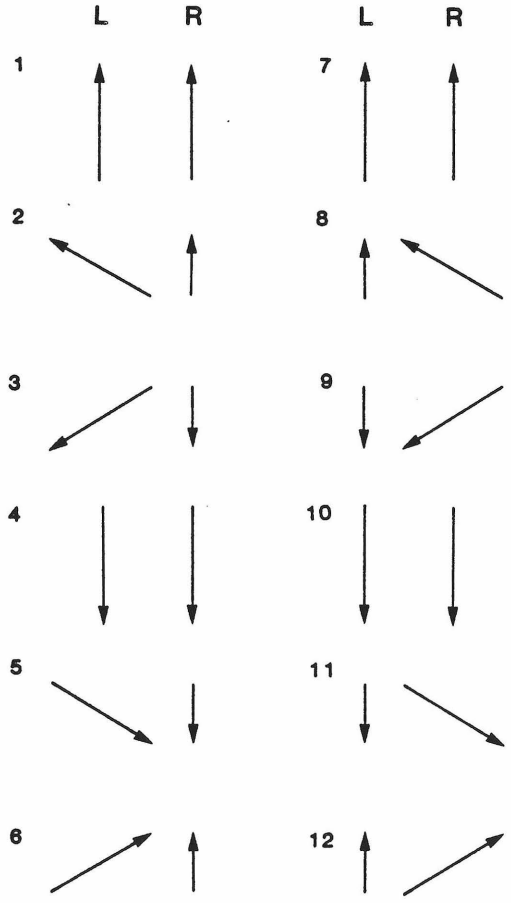
The technique of simulating arbitrary motions in depth using monocular stimuli is fairly straightforward, and is illustrated in Fig. 1A, which shows the simulation of a motion in depth which proceeds upward and to the left while approaching the animal. The movement starts at P1 behind the fixation plane and ends at P2 in front of it. In this example, the monocular stimuli move on the fixation plane, although in principle they could be on any surface. The correct positions for the monocular stimuli when simulating a given point in the movement can be found by projecting lines from the eyes to the point in question and then noting the intersection of these lines with the surface on which the stimuli move. Thus, the starting point of the movement (P1) is simulated with the stimulus for the right eye at SR1 and that for the left at SL1. For the complete motion, the right eye sees a stimulus moving from SR1 to SR2, while at the same time the left eye sees a stimulus moving from SL1 to SL2. In previous studies of motion in depth (Cynader and Regan 1978, Poggio and Talbot 1981), and also in the present experiments, the monocular stimuli moved at constant speeds on the projection screen, simulating a motion which, for geometric reasons, moved more slowly <u>through space</u> as it approaches the animal. Although for short excursions the

Figure 1. The simulation of motions in depth using monocular stimuli. See text for explanation.

A



B



actual three dimensional trajectory is approximately linear, it should be noted that linear motions of the monocular stimuli do not necessarily simulate linear three dimensional trajectories. Different motions in depth can be simulated with different pairs of monocular movements. In Fig. 1A the monocular stimuli meet at the center of the receptive field, but this need not be the case. For example, the movement in depth could be entirely in front or behind the fixation plane, in which case the monocular stimuli would never meet.

An important consideration for this type of stimulation is that there is a major constraint on the relative positions of the monocular stimuli on the screen if they are to correspond to a single stereoscopic image. Obviously, in the absence of abnormal disjunctive eye movements, no object can appear to be far superior in the left eye and far inferior in the right. In fact, a necessary condition for simulating a real object at some point in depth using monocular stimuli on a fronto-parallel screen is that both stimuli must be at the same vertical level on the screen at all times (see Appendix).

Previous studies of motion in depth have simulated motions in depth using stimuli in which each eye sees only horizontal motion (Cynader and Regan 1978, Poggio and Talbot 1981). Because neurons in MT have strong direction selectivity, only a minority could be expected to respond well to horizontal motion. To avoid excluding the majority from consideration, we decided to use trajectories for which at least one of the monocular stimuli moved along the axis of the unit's preferred direction.

The simplest case was when a unit did prefer a horizontal direction of movement on the projection screen. In this case the stimulation used was the same as in the aforementioned studies. It consisted of sets of stimuli in which the two monocular stimuli moved horizontally on the projection screen, but at different speeds and/or in different directions, so that the disparity changed at a constant rate during the movement. Each of these changing disparities simulated a different

trajectory in a plane which contained the two eyes and the receptive field center. Twelve different motions were tested, covering a complete circle of directions toward and away from the animal. As in the other studies, the different motions were separated by uniform increments in the rate of change of disparity. This biases the distribution of motions in depth in favor of motions directly toward or away from the animal's head (see Cynader and Regan 1978).

For units with non-horizontal direction preferences the situation is more complex, because it is not obvious what constitutes an appropriate surface within which trajectories should lie in order to provide an adequate test for motion in depth selectivity. For example, a unit preferring vertical motion might be tested with trajectories which were all within the median plane, but this would exclude motions directly toward or away from each eye. Instead of testing such units with trajectories confined to a single plane, we used sets of trajectories which lay in two planes; each of which contained the axis of preferred motion on the fronto-parallel plane and one of the eyes. These sets did not exclude motion toward the eyes, and, as in the tests for cells with horizontal direction preferences, consisted of stimuli in which at least one eye saw motion along the axis of the unit's preferred direction.

The procedure we used for generating these non-horizontal motions in depth is illustrated in Fig. 1B. The twelve stimulus pairs shown are those used when a unit preferred a vertical direction of motion. For each, one monocular stimulus is always directed along the axis of preferred direction (right eye for 1-6, left eye for 7-12); the other moves in directions that change in 60° increments. The relative speeds of the two monocular stimuli are adjusted so that there is never any vertical disparity on the screen, thus ensuring the simulation of real objects in visual space. The first six stimuli simulate motions in a vertical plane containing the right eye, the second six simulate motions in a vertical plane containing the left eye. Eight of the 12 stimuli simulate motion in depth, the other four (1, 4, 7, 10) fronto-parallel motion. Half of

the motions in depth are toward the animal, the other half are away. The sets of trajectories for units with other non-horizontal preferred directions were generated in the same way, only beginning from a different fronto-parallel direction. It should be noted that as the preferred direction approaches horizontal, the two imaginary planes in which the trajectories lie will collapse into a single horizontal plane, which is the same as that described for the tests of cells which preferred horizontal directions of motion.

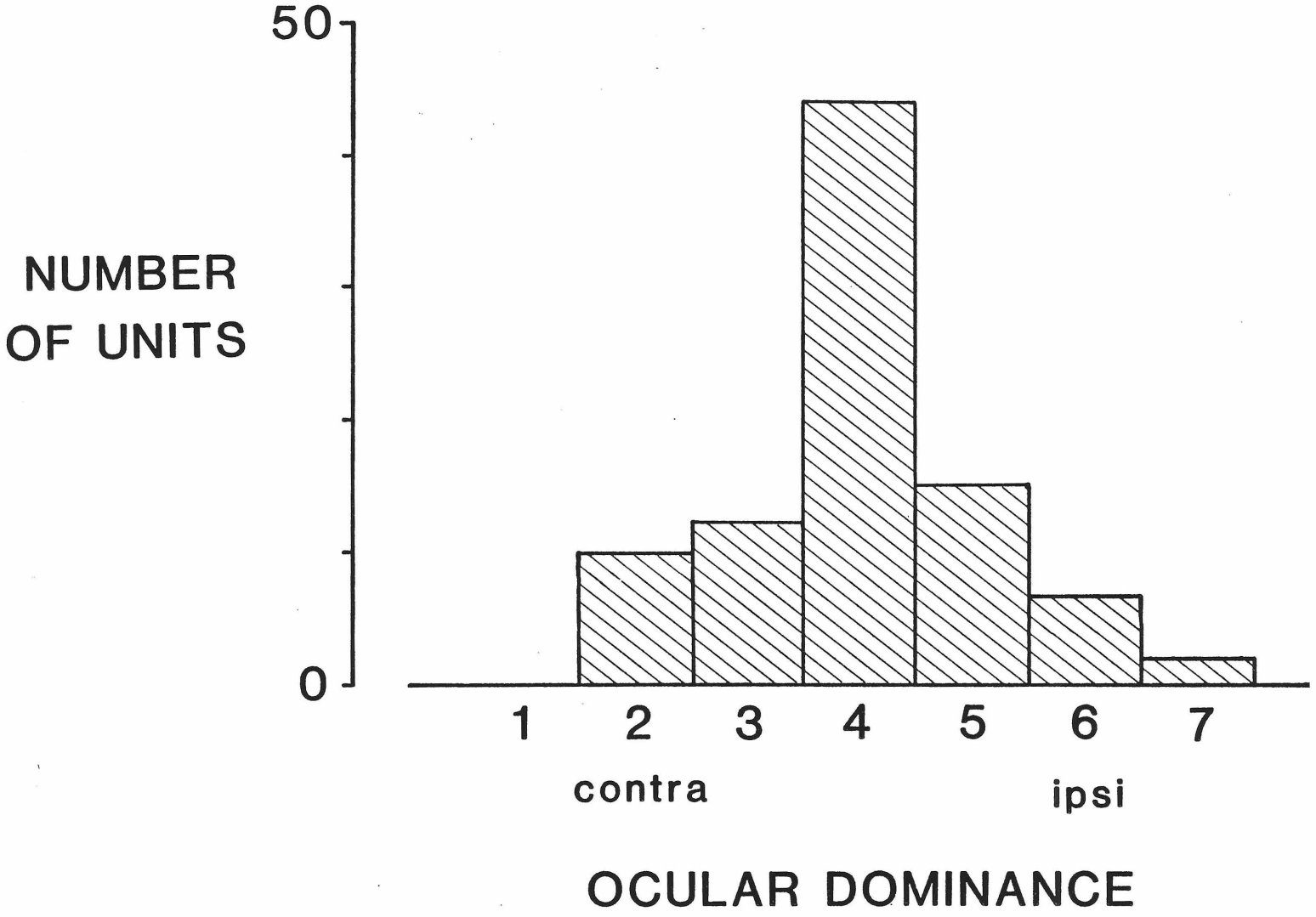
RESULTS

The results are drawn from 168 units in MT tested in 37 penetrations. All recording sites were in the right hemisphere and receptive fields were therefore centered in the left visual hemifield. Receptive field centers were between 0.6° and 22.7° eccentricity (average, 9.1°), and the most were in the inferior quadrant, reflecting the biased representation of the visual field in MT (Van Essen et al. 1981).

Binocular interactions

Most units in MT could be driven well through either eye alone, as has been previously reported (Zeki 1974a). Figure 2 is an ocular dominance histogram for 91 units based on the scheme introduced by Hubel and Wiesel (1962). Assignments are made according to the ratio of the quantitated response to several presentations of stimuli to each eye alone (see figure legend). The majority of cells received balanced inputs from the two eyes (ocular dominance group 4), and 79% were in groups 3-5. Cells showing ocular imbalance tended to be those which gave only a weak response to either eye alone. Conspicuously absent were neurons which gave a strong response to one eye and no response or inhibition to the other, although such monocular cells have been found in V1 (Hubel and Wiesel 1968, Poggio and Fischer 1977). Four of the 168 cells responded only to binocular stimulation.

Figure 2. The distribution of ocular dominance for 91 units in MT. The assignments are based on the quantitative ratio of response above background for stimulus presentations to each eye alone. Bins 1 and 7 contain those cells which were driven through one eye only, bins 2 and 6 contain cells for which the response to one eye was 3 or more times the response to the other, bins 3 and 5 contain cells for which the ratio of responses was between 1.5 and 3, and bin 4 contains cells whose monocular responses were within a factor of 1.5. By far most cells had roughly balanced inputs from the two eyes. Cells showing ocular imbalance generally responded weakly to either eye alone.


50
0
NUMBER
OF UNITS
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2
3
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5
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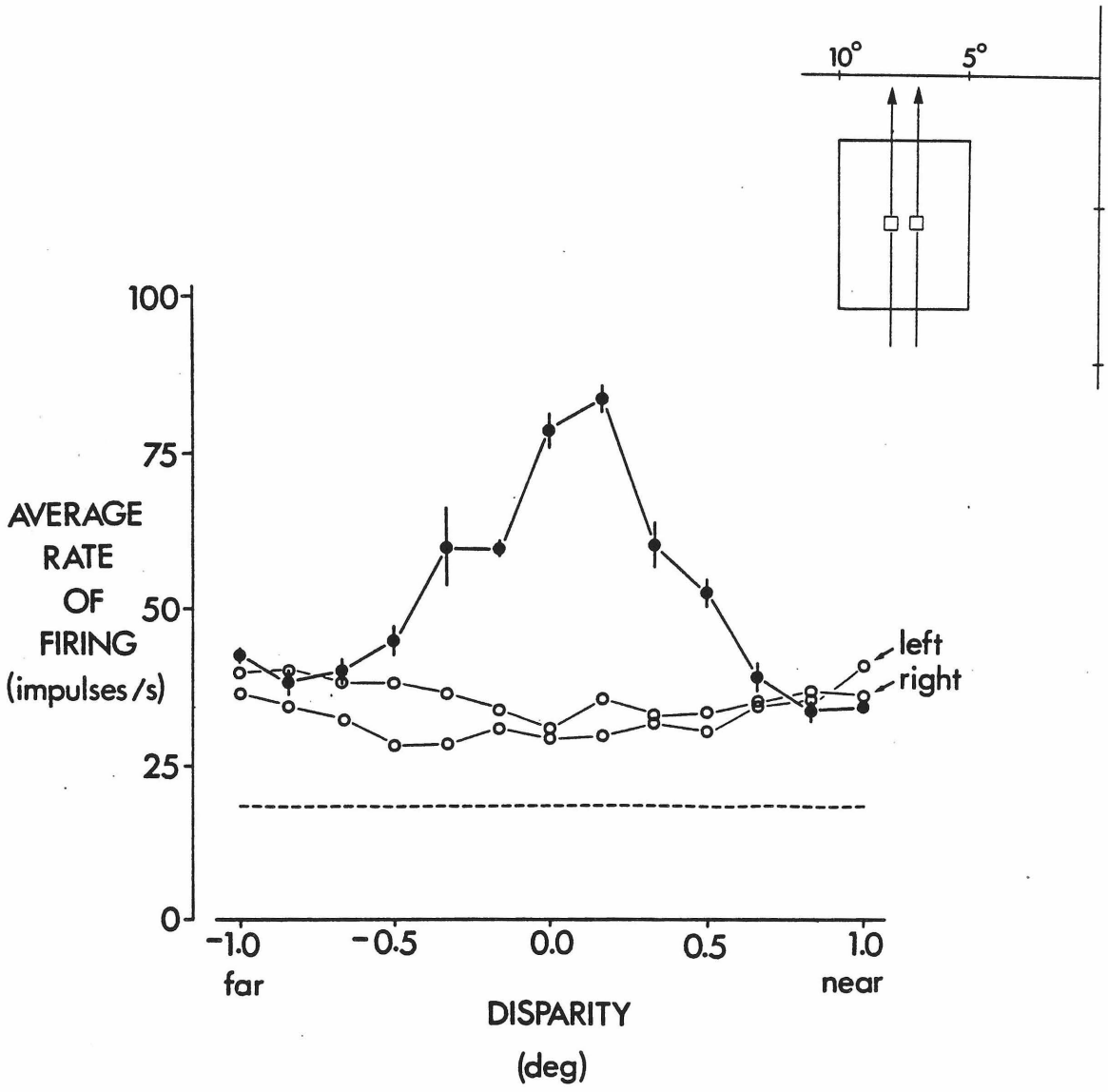
OCULAR DOMINANCE

Fixed disparity

Seventy-six units in MT were examined quantitatively for fixed disparity selectivity. Most tests were made using horizontal stimulus disparity alone (see Methods). The majority of neurons (52/76) showed striking sensitivity to horizontal disparity. Figure 3 illustrates the properties of one such neuron. It preferred upward movement, and the monocular stimuli used were small squares. Horizontal disparity was adjusted to simulate an object moving upward at different distances from the animal. The heavy solid line shows the average rate of firing for binocular stimulation at different disparities, and bars indicate the standard errors of the means. The dashed line is the background rate of firing. The inset shows the position and size of the receptive field, and the relative dimensions of the stimuli. The stimuli are drawn at their maximum disparity, at which they were well within the receptive field borders. The cell responded well only over a range of about 1° of disparity, which is a small fraction of the total receptive field width. Because the monocular stimuli moved upward, the parts of the receptive field that each stimulated changed as the horizontal disparity was adjusted. To ensure that the binocular disparity tuning was not due to the receptive field having a more excitable region which was stimulated at only a few disparity settings, monocular responses were measured at each. These are shown by the open circles. The monocular responses were uniform across the range of horizontal shifts tested, typical for all units examined in MT. In this and many other units we also used manual control of stimulus position and disparity, and qualitative assessment of responses to determine whether disparity preferences depended on the portion of the receptive field being stimulated. In all cases the results clearly showed that the preferred disparity and sharpness of disparity tuning were similar no matter what portion of the receptive field was being stimulated.

Poggio and Fischer (1977) described four classes of disparity tuning in V1 and V2 of the macaque: near, far, tuned excitatory, and tuned inhibitory. Subsequently it

Figure 3. Disparity tuning of a unit in MT. The unit was tested with stimuli with different fixed disparities, all of which moved directly upward. The inset shows the monocular stimuli at the maximum disparity examined in this test, at which they were well within the width of the receptive field. The closed circles show the responses to binocular stimulation, and bars indicate the standard errors of the means for five presentations. The dashed line is the background rate of firing. The unit responded well only over a narrow range of disparities. The open circles are the responses to monocular stimulation, and show that the disparity tuning is not due to inhomogeneity of the receptive field.


10°
5°
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RATE
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(impulses/s)
left
right
-1.0
far
-0.5
0.0
0.5
1.0
near
DISPARITY
(deg)

was found that disparity tuned neurons in cat V1 and V2 could be assigned to the same categories (Fischer and Krüger 1979, Ferster 1981). Most of our disparity tuning curves in MT also fell into the four categories described by Poggio and Fischer. The different types of responses found in MT are illustrated in Fig. 4.

The unit of Fig. 4A is typical of tuned excitatory cells, which included 22/76 units (see also Fig. 2). Near optimal responses were obtained only over a small range of disparities near zero. The tuning curves for these cells commonly resulted from a strong facilitation when the disparity was near zero. At disparities away from zero, responses were less than or equal to the sum of monocular responses, and sometimes were inhibited so that the response was less than that to one eye alone. These units could be expected to respond vigorously only to stimuli which were on or near the animal's horoptor.

Most tuned excitatory neurons in macaque V1 and V2 have tuning curves which peak within 0.1° of zero disparity (Poggio and Fischer 1977, Poggio and Talbot 1981). In our preparation the screen coordinates corresponding to zero disparity could be determined to only about $\pm 1°$ (see Methods). For the population of tuned excitatory neurons in MT, the apparent preferred disparity averaged $0.19° \pm 0.90°$ S.D. However, given the uncertainties in measurements of the peak and apparent zero disparity, this distribution is that which would be expected if all units gave their best response at the horoptor. Moreover, none of the tuned excitatory units had a preferred disparity which was clearly not on the horoptor. On the other hand, it is also possible that a substantial percentage of the tuned excitatory cells do indeed have small, but significant, non-zero disparities.

There were two classes of disparity selective neurons which responded over a broad range of disparities, but only on one side of zero disparity: one responsive to crossed disparities (18/76, Fig. 4B), equivalent to stimuli near to the animal, the other responsive to uncrossed disparities (10/76, Fig. 4C), equivalent to stimuli beyond the

Figure 4. Different classes of disparity tuning curves from units in MT. The inset for each plot shows the size of the receptive field and stimuli and the direction of motion. The monocular stimuli are drawn at the maximum disparity for which a response is plotted. The response curves are all to the same scale, and all disparities are horizontal, with positive values implying crossed (near) and negative uncrossed (far). Closed circles are responses to binocular stimulation, open circles are monocular responses. Dashed lines are background rates of firing. Bars are the standard errors of the means for five stimulus repetitions. The curves are normalized to their respective maximum responses, which are indicated beside each plot.

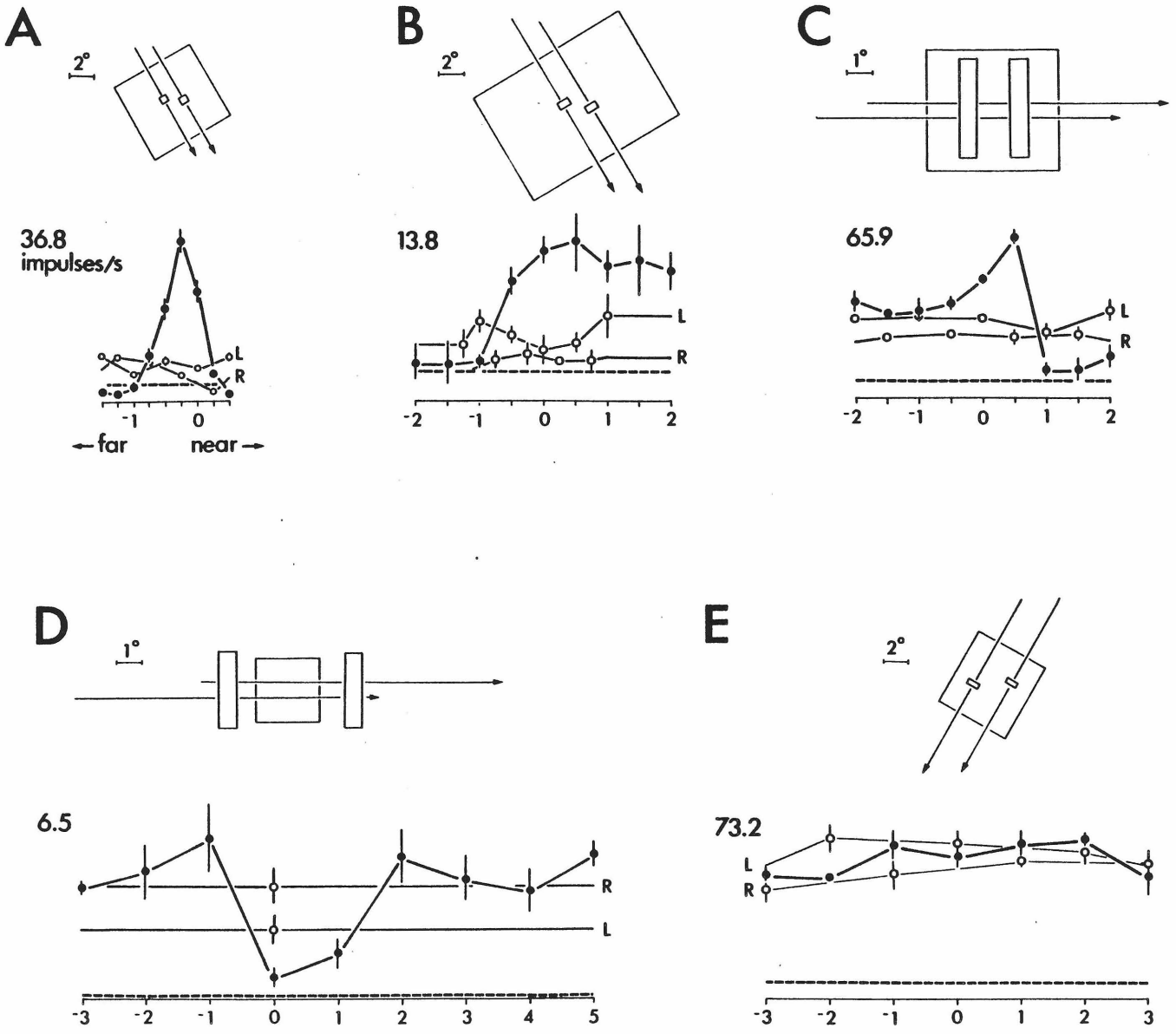
4A. A tuned excitatory response. This was one of 22/76 units which responded well only over a small range of disparities near zero. These units could be expected to respond well to stimuli on or near the horoptor.

4B. A near response. This unit gave good responses to a broad range of crossed disparities, with responsiveness falling off for uncrossed (negative) disparities. 18/76 units fell in this category.

4C. A far response. This neuron responded well to uncrossed stimuli. The response is complementary to that of a near cell. 10/76 cells tested had this type of tuning curve.

4D. A tuned inhibitory response. This response was seen for 2/76 units. These cells are complementary to tuned excitatory neurons, responding well to most disparities except a small range near zero. This unit could be expected to respond vigorously to stimuli in front of or behind, but not on, the horoptor. Because the direction of motion was horizontal, the monocular stimuli followed the same path across the receptive field as the disparity was changed. For this reason monocular responses were tested only once.

4E. A response lacking disparity selectivity. 24/76 units examined gave responses like this, which showed no obvious sensitivity to disparity.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2
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1°
65.9
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R
-2
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6.5
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-3
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E
2°
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L
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3

horoptor. For both types the transition from maximum to minimum responsiveness occurred near zero disparity, usually over a range of about 1°. The tuning resulted from facilitation or inhibition, and sometimes a combination of the two. These neurons are similar to the near and far cells described by Poggio and Fischer. Their tuning is much broader than that of tuned excitatory cells. In our preparation these neurons generally had broad peaks, and responded well over a range of several degrees of disparity.

A final class consisted of two neurons which responded well to a broad range of disparities excluding those near zero (Fig. 4D). These are complementary to tuned excitatory neurons and are similar to the tuned inhibitory neurons described by Poggio and Fischer. Such neurons could be expected to be responsive to stimuli which were in front of or behind, but not on, the horoptor. Finally, the response in Fig. 4E is typical of those 24 neurons which were insensitive to disparity.

Of the units with disparity tuning, most fell clearly into one or another of the four classes. The 6 which did not were on a border between two classes, usually having moderately broad tuning without a sharp transition near zero. These units were assigned individually to the class they most strongly resembled.

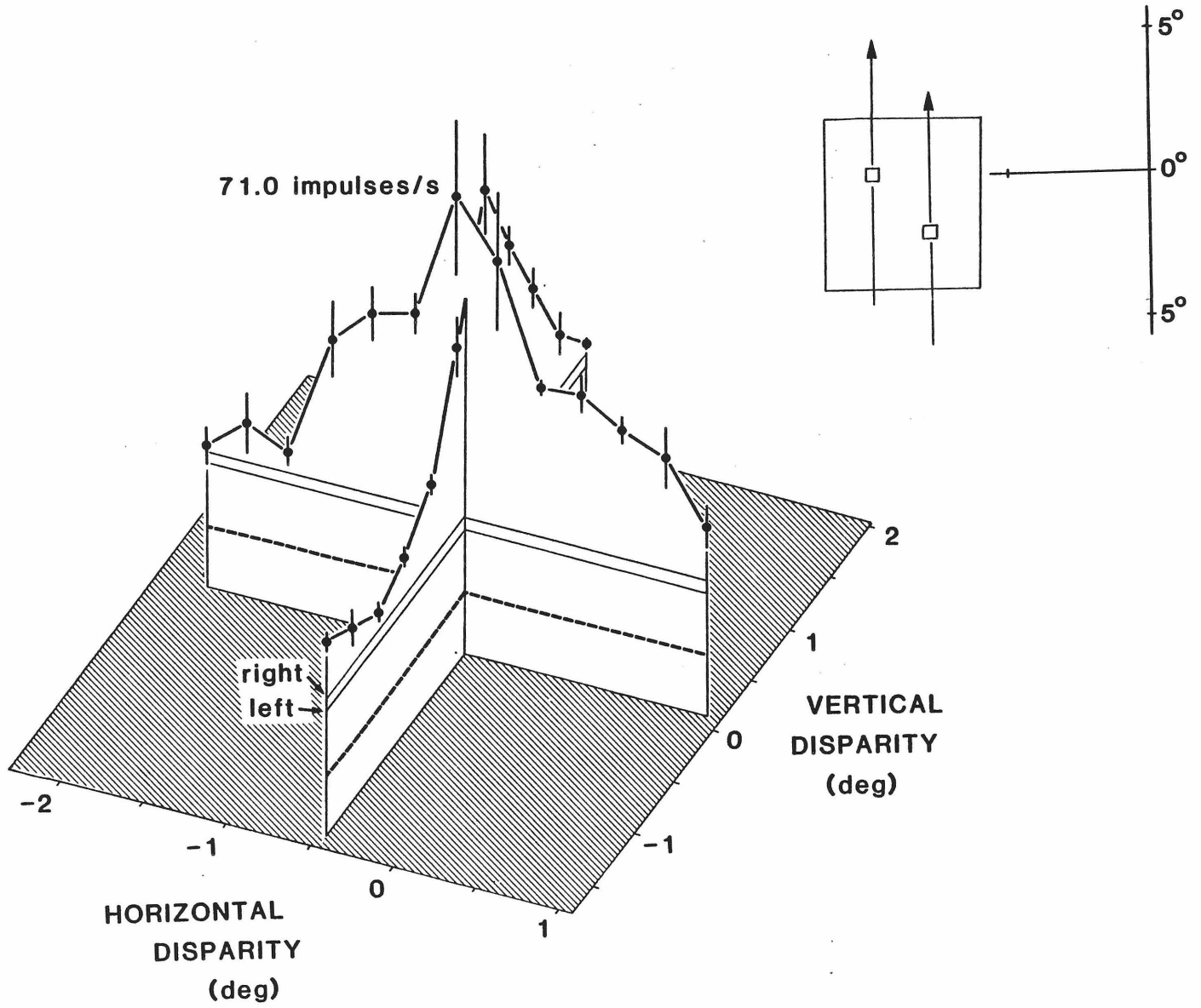
Studies of disparity tuning in other visual areas have found that tuned excitatory neurons typically have balanced inputs from the two eyes and tuning which arises from a strong binocular facilitation. In contrast, most near and far cells have imbalanced ocular inputs (Poggio and Fischer 1977, Poggio and Talbot 1981, Ferster 1981). In agreement with these investigations, binocular facilitation was important in the tuning of most tuned excitatory cells in MT. However, most disparity tuned cells of all classes had fairly balanced input from the two eyes, and those which did not were not associated with a particular type of tuning. This distinction is in keeping with the greater overall ocular balance in MT (c.f. Fig. 2 above and Hubel and Wiesel 1968).

Non-horizontal fixed disparity

Only horizontal stimulus disparity contributes to stereopsis (see Appendix). It is of interest to know whether neurons in MT which are tuned for fixed horizontal disparity are also sensitive to non-horizontal disparity, or, alternatively, if horizontal disparity is selectively emphasized at this level in the visual system. Several investigators have found units tuned for non-horizontal stimulus disparities in V1 and V2 of the cat (Bishop et al. 1971, Nelson et al. 1977, Ferster 1981), although individual units were not tested for both horizontal and non-horizontal disparity tuning. Von der Heydt et al. (1978) did test individual units in the cat with both types of disparity, and found that units sensitive to horizontal disparity were insensitive to vertical disparity. However, they examined only two units for this property, and varied vertical disparity at only one horizontal disparity. The question of disparity specificity is of interest for disparity tuned cells in any area, but those in MT are especially amenable for study because their large receptive fields make it easy to manipulate disparity without having stimuli missing the field altogether.

Figure 5 shows the results of two disparity tests run on a single unit. Disparity was varied along the horizontal axis in one, and along the vertical axis in the other. In both tests the stimuli moved in the preferred direction at the preferred speed. Responses are measured as the average rate of firing, and bars indicate standard errors of the means. A dashed line marks the average background rate of firing, and the responses to stimulation of each eye alone is indicated. The inset shows the size of the monocular stimuli and receptive field, and the position of the latter. The monocular stimuli are drawn at the maximum horizontal and vertical disparities tested (although this particular combination was not used). The maximum disparity in both cases was small compared to the size of the receptive field. Responses decreased about as rapidly with change in vertical disparity as they did to horizontal, indicating roughly equal selectivity for both. Note that the disparity tuning in this

Figure 5. Response of a unit in MT to vertical and horizontal disparities. This unit was tested with two disparity tests. One was a normal horizontal disparity test, the other involved changing the vertical disparity while the horizontal disparity remained constant. The stimuli always moved in the preferred direction at the preferred speed. The inset shows the monocular stimuli at their maximum horizontal and vertical disparities (this combination was not tested). The points mark the responses to binocular stimulation at different disparities, and bars are the standard errors of the means for five repetitions. Monocular responses and background rate of firing are also indicated. The responses fall off quickly when either horizontal or vertical disparities are changed from their optimum values.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HORIZONTAL
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VERTICAL
DISPARITY
(deg)
5°
0°
5°

cell results from facilitatory interactions over the preferred disparity range, and not from inhibitory interactions at non-preferred disparities. Thus the peak along the vertical axis is a result of specific facilitatory interactions near zero disparity. At large vertical disparities the binocular response is slightly greater than either monocular response, indicating minimal binocular interactions.

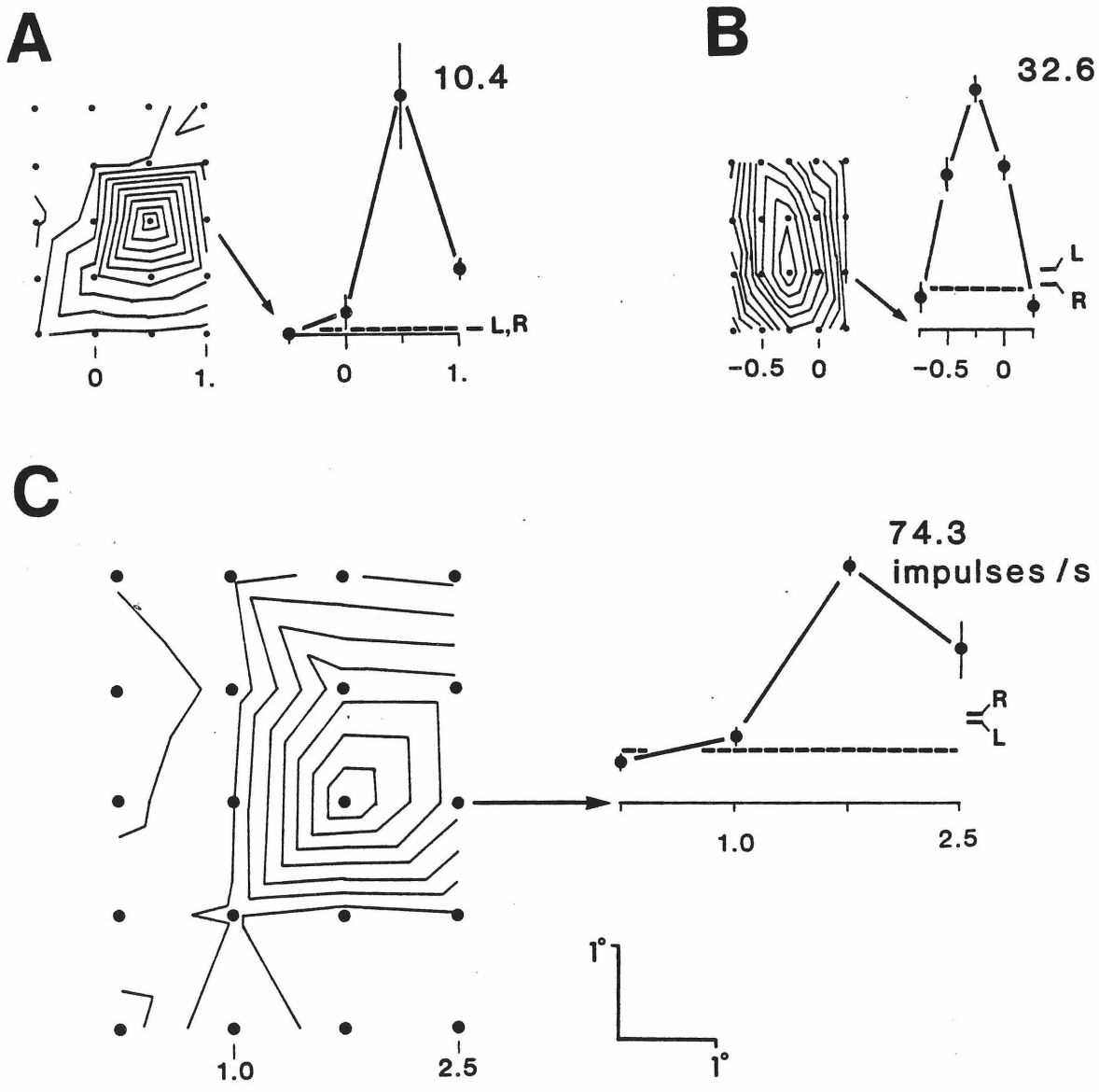
Nineteen units were tested for sensitivity to non-horizontal disparities in a systematic manner, using up to 24 interleaved combinations of horizontal and vertical disparities. The results were plotted on two-dimensional grids to show responses at different horizontal and vertical disparities. The responses from three units are displayed in Fig. 6, with all disparities plotted to the same scale. In each case the stimulus moved in the unit's preferred direction at the preferred speed. Dots mark the combinations of vertical and horizontal disparities at which responses were tested. The contours are response isograms, which were interpolated between neighboring points with a spacing equal to 10% of the maximum response above background (see figure legend). Tuning curves for horizontal disparity, taken from the row in the grid which contained the peak response, are plotted for each unit. Each tuning curve indicates the background rate of firing and the responses to monocular stimulation. Although there is some error in determining the precise positions of individual contours, the overall pattern of contours is sufficiently orderly to allow several significant conclusions. For example, if units were insensitive to vertical disparities, the contours would run more or less straight from top to bottom, which is clearly not the case for any of the units illustrated. All units have responses which changed substantially with vertical disparity. The responses of Figs. 6A and B are from tuned excitatory units. Fig. 6C is from a near cell which responded over a range of several degrees of crossed (near) disparities when tested for horizontal disparity. Only a portion of that range was tested for vertical disparity selectivity. The broadness of tuning of this unit and those of Figs. 6A and C is about equal for

Figure 6. Sensitivity of three units in MT to vertical disparity. Each unit was tested with 20 different combinations of horizontal and vertical disparities. The stimuli always moved in the preferred direction at the preferred speed. The plot to the right of each section shows the responses to different horizontal disparities at the vertical disparity which gave the best response. The grids to the left show the responses to different combinations of horizontal and vertical disparities. Points mark the combinations of horizontal and vertical disparity at which responses were measured. Contour lines show the responsiveness to different combinations of horizontal and vertical disparities. They were plotted by interpolating between the responses found at adjacent points, at a spacing equal to 10% of the maximum response above background. These responses, like all those examined, had pronounced sensitivity to vertical disparity.

6A. Responses of a tuned excitatory unit. Responses fell as disparity was changed in either the horizontal or vertical direction, and were near background (indicated by the dashed line the plot to the right) when disparity was about 1/2° from optimum.

6B. The responses of the unit with the most vertically elongated response pattern. Of 19 units tested, this one had the pattern of responses which was most vertically elongated, indicating less sensitivity to vertical disparity than to horizontal. Even so, this unit was not insensitive to vertical disparity. Other units had patterns which were slightly elongated along other axes.

6C. Responses of a near cell. This unit responded well over a broad range of crossed disparities, only part of which was examined in this test. Like the others, this unit also shows comparable sensitivity to horizontal and vertical disparities.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32.6
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-0.5
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74.3
impulses /s
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L
1.0
2.5
1°
1°
1.0
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vertical and horizontal disparity. The unit in Fig. 6B had the most vertically elongated pattern of the units examined, but even so it was not insensitive to vertical disparity. Several other units had slightly less regular patterns of response, but none was insensitive to vertical disparity.

Motion in depth

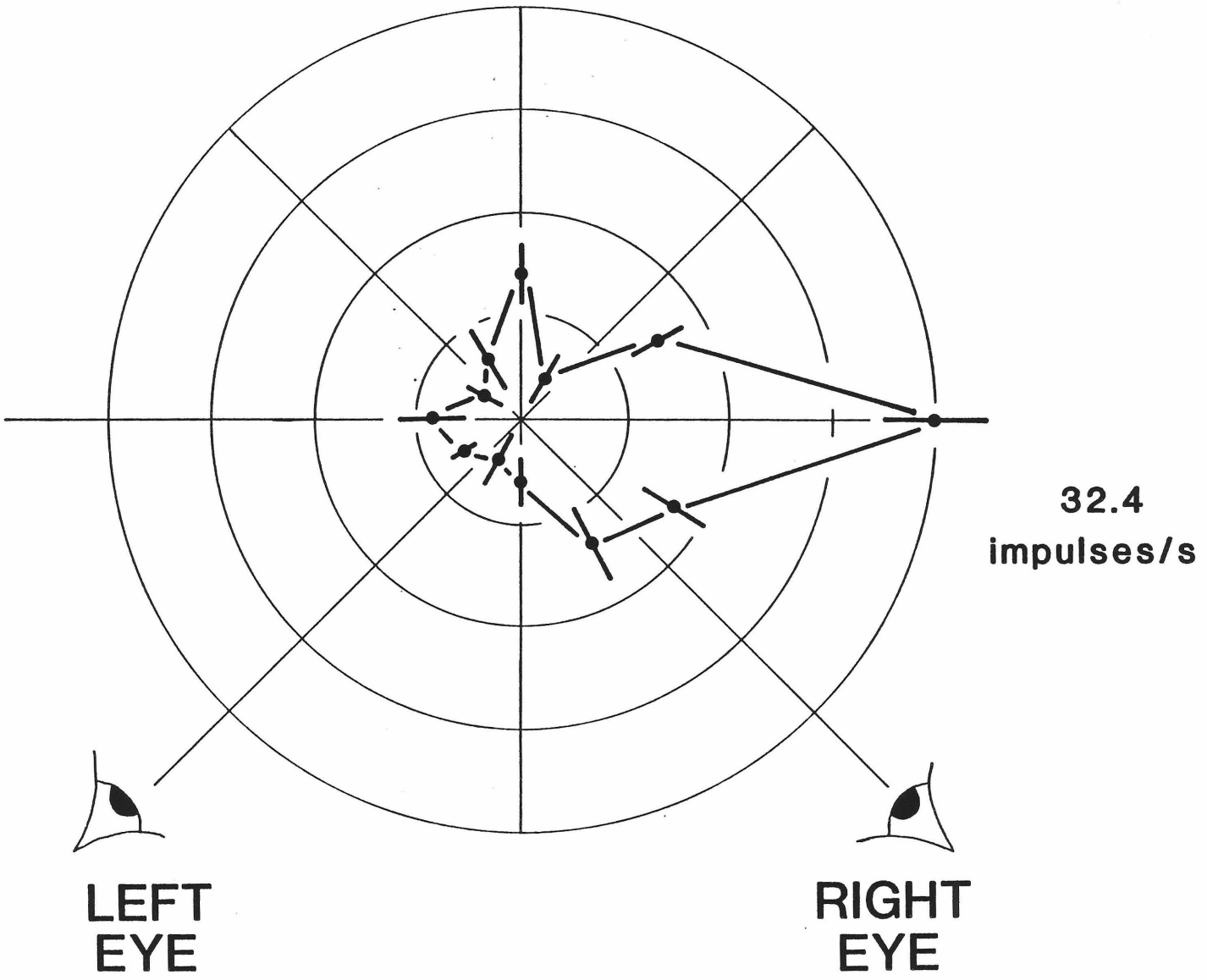
Motions in depth were simulated using stimuli whose disparity changed as they moved. The trajectories were not restricted to a horizontal plane, but instead were chosen so that at least one of the monocular stimuli moved along the axis of the unit's preferred direction (see Methods). Each test series examined the response to 12 simulated trajectories through space, including two which were fronto-parallel — one in the preferred direction, the other in the opposite (null) direction.

The trajectories of a test series all intersected at a common point midway through their traverse. This center point could be made to lie at the unit's best disparity, but could also be set at some other disparity. Whatever the disparity of the center point, though, its projection onto the screen was at the receptive field center. Initially, we anticipated that motion in depth selectivity, if found, would not be critically dependent on the center point of the trajectories. Hence for many cells only a single test series was carried out, with the center point at the best disparity (or on the horoptor if the best disparity was not known). Under these circumstances nearly all units preferred fronto-parallel movement over any of the motions in depth which were presented.

The responses of a typical unit to motions in depth with their center point of movement near its preferred disparity are shown in Fig. 7. The unit preferred horizontal movement to the right. Because of this, the motions in depth with which it was tested were all restricted to a single plane. Twelve different directions are arranged as if one is viewing the animal and the motions in depth from above, in a format identical to that used by others (Cynader and Regan 1978, Poggio and Talbot

Figure 7. Responses of a unit to motions in depth centered at its preferred disparity. Because this unit preferred a horizontal direction of motion, it was tested with stimuli which simulated trajectories confined to a single plane (see Methods), and the format of representation is identical to that used by others (Cynader and Regan 1978, Poggio and Talbot 1981). The arrangement is as if one is viewing the animal and trajectories from above. Points on the horizontal axis mark responses to fronto-parallel motions, those on the vertical axis are for motion directly toward or away from the animal. Increments of angle around the plot are not equivalent to increments in the angle into or out of the fixation plane, but instead correspond to increments in the rate of change of disparity. This biases the distribution in favor of trajectories close to directly into or out of the plane of fixation. Thus, the lines oriented at 45° are trajectories which are directly toward or away from each eye (see Cynader and Regan 1978 for further details).

The magnitude of response for each trajectory is indicated by the distance from the center. Bars are the standard errors of the means for five stimulus presentations. The best response is to fronto-parallel motion to the right. Responses fall quickly for other trajectories, where one or both eyes see motion in non-preferred directions and/or at non-preferred speeds.


32.4
impulses/s
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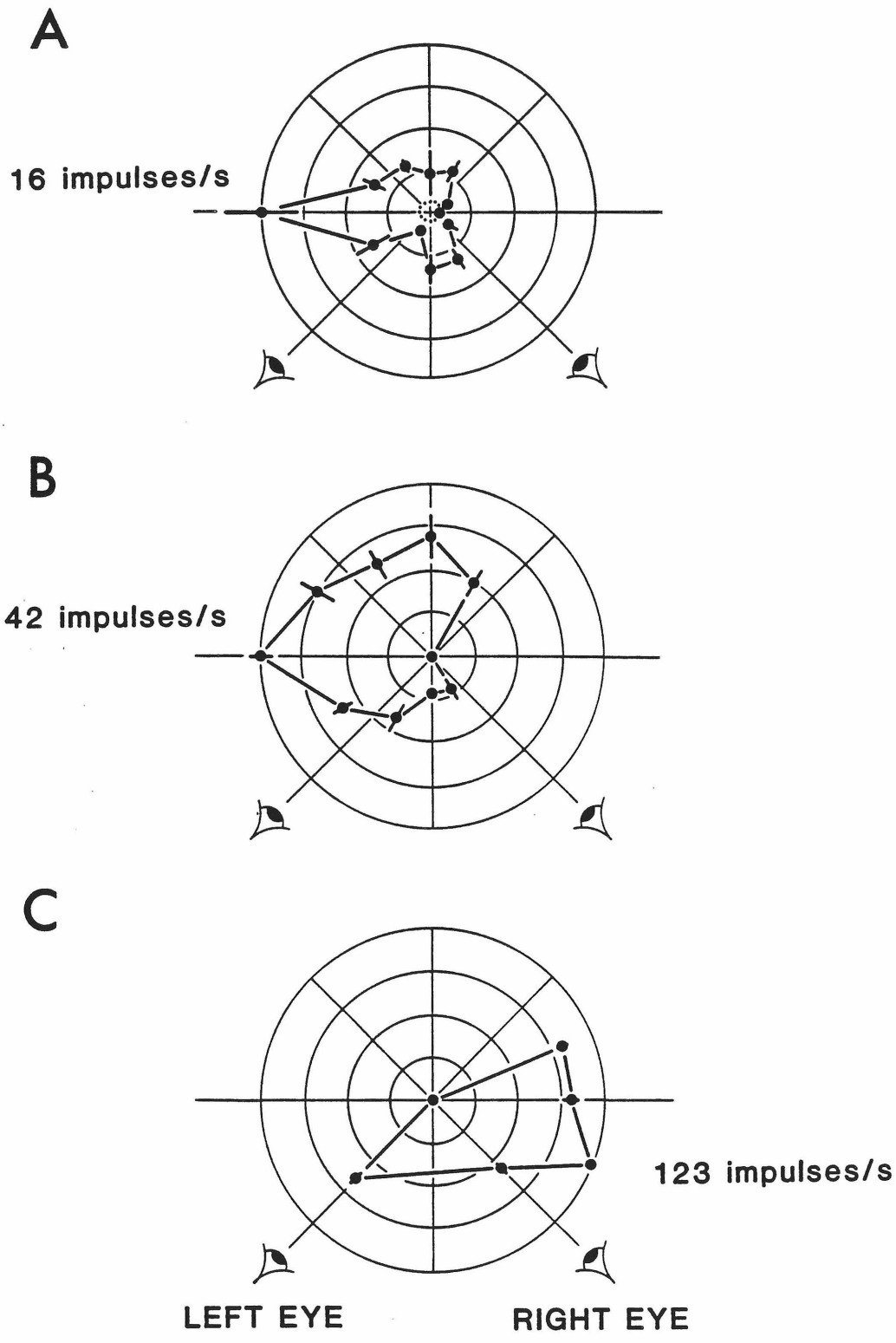
1981, see figure legend for details). The magnitude of response is indicated by the distance of points from the center of the plot, and bars show the standard error of the mean for each measurement. The best response is to fronto-parallel movement to the right. The response is slightly less for the two motions in depth on either side of the peak, for which both eyes see motion in the preferred direction, but with one stimulus moving at a slower speed. For other motions in depth, as the speed and direction of the monocular stimuli are further from optimal, the response continues to fall.

Other examples of responses to motion in depth centered at or near each unit's preferred disparity are shown in Fig. 8. The unit of Fig. 8C did not prefer a horizontal fronto-parallel direction, so the motions in depth were not confined to a single plane and this plot is not strictly equivalent to the others. However, it is analogous in indicating motions which were fronto-parallel, somewhat toward the animal, and directly toward each eye. Of 27 units tested in this manner, 24 (89%) preferred fronto-parallel motion over all others. Of the 3 in which the peak response was to some other motion, only one had a response which was significantly better than its fronto-parallel response ($p<0.05$, single-tailed t test). The responses of this unit are illustrated in Fig. 8C. It is apparent that this preference, although statistically significant, was not pronounced.

During the course of these experiments it became obvious that very different results could be obtained when disparity tuned units were tested with motions in depth whose center point was well in front of or behind the unit's preferred disparity. In this case the response to fronto-parallel motion was relatively weak, as expected, and the largest response within that set of trajectories was usually to some motion in depth. But in no case in which the appropriate tests had been made was the response to a motion in depth better than that to fronto-parallel motion at the best disparity. For reasons detailed below, we do not believe this type of response is correctly interpreted as selectivity for motion in depth.

Figure 8. The responses of three units in MT to motions in depth centered at their preferred disparities. The units in parts A and B were selected because they preferred horizontal directions of motion and the format of representation is therefore the same as that in Fig. 7. The unit in part C did not prefer a horizontal direction of motion on the fronto-parallel screen, and the representation is not identical to the others. However, it is analogous in its representation of trajectories which are fronto-parallel, directly toward or away from the eyes, and intermediate. The curves are normalized to their best responses and bars indicate the standard errors of the means for five presentations of each stimulus. The units in parts A and B, like 24 of the 27 units tested in this manner, preferred fronto-parallel motion over all others. The response in part C was from the only unit tested which had a statistically significant preference for a non-fronto-parallel trajectory when tested with motions centered at its preferred disparity. It is clear that while this preference is statistically significant, it is not pronounced.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16 impulses/s
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LEFT EYE
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Figure 9 illustrates how changing the center point of movement can dramatically affect the responses of a disparity tuned unit. Figure 9A shows the fixed disparity tuning curve for the unit. It preferred crossed (near) disparities, and responded over a broad range. Fig. 9B shows a set of summed responses histograms to motions with different fixed disparities. The disparities to which they correspond are indicated by one axis of the plane. If these disparities are interpreted as distances from the animal, it can be seen that the effect of the disparity tuning is to limit the extent of the receptive field in depth, restricting responses to the part of space near to the animal (positive disparities).

Two tests of motion in depth selectivity for this unit are shown in Fig. 9C and 9D. The test series in 9C had its center point at a non-preferred (far) disparity (indicated by the arrow labeled C in Fig. 9A). The responses in Fig. 9D are to motions in depth with a center point near the preferred disparity (arrow D in Fig. 9A). Both plots are to the same scale. With the center point near the preferred disparity (Fig. 9D) there is clear preference for fronto-parallel motion. In the other case (Fig. 9C) the response to the first motion in depth clockwise from fronto-parallel (labeled 4) is significantly better than that to fronto-parallel motion (labeled 3), but less than half the magnitude of the best response obtained from the same unit in the other test series (labeled 2 in Fig. 9D).

The responses of this unit are readily explained by its fixed disparity tuning. When the center point is far from the preferred disparity, only stimuli with changing disparity can approach the preferred disparity. Further evidence for this explanation comes from examination of the timing of responses in relation to the three-dimensional stimulus trajectories. Fig. 9E shows that the response to fronto-parallel motion at the preferred disparity (trajectory 2) is near maximal throughout the time the stimulus is in the receptive field. The response to fronto-parallel motion at the non-preferred disparity is uniformly low (trajectory 3). In contrast, the stimuli with

changing disparity have sharp peaks in response during specific portions of their trajectories—early for trajectory 4 and late for trajectory 1. The significance of these interactions can best be appreciated by replotting the same data on spatial coordinates rather than as response vs. time. Figure 9F shows the response histograms for the same four trajectories, plotted as a function of disparity in the horizontal plane, as in Fig. 9B. The two fronto-parallel trajectories are oriented directly from left to right, while the two motions in depth cut across disparities on the horizontal plane. What is strikingly clear from this figure is that a significant response occurs only when the simulated trajectory enters a restricted zone within the horizontal plane, starting at about the fixation plane and extending over several degrees of disparity toward the animal. Within this zone, response is good to any stimulus having a component of motion in the left to right direction, irrespective of whether it is moving in depth. The smaller <u>average</u> response to motion in depth is attributable simply to a reduced time within the responsive zone. Viewed in this way, it is natural for a unit tuned for fixed disparity to show an apparent preference for motion in depth when tested with a set of motions centered at a non-preferred disparity.

The motions in depth shown in Fig. 9E cut across a large range of disparities. It is important to realize that this is not an exaggeration of the usual case, and that motions in depth generally do cover a wide range of disparities relative to receptive field dimensions. For example, if the monocular stimuli start and stop their motion outside the receptive field, then to simulate a motion directly toward or away from the animal they must cover a range of disparities which is twice the width of the receptive field.

We found that most disparity selective units displayed apparent motion in depth selectivity when the center point of the test series was far from the preferred disparity. Twelve units were tested for motion in depth selectivity both with motions

Figure 9. The effect of changing the center point of movements on the responses of a single disparity tuned cell.

9A. The fixed disparity tuning curve for a unit in MT. The unit responded well over a broad range of crossed (near) disparities.

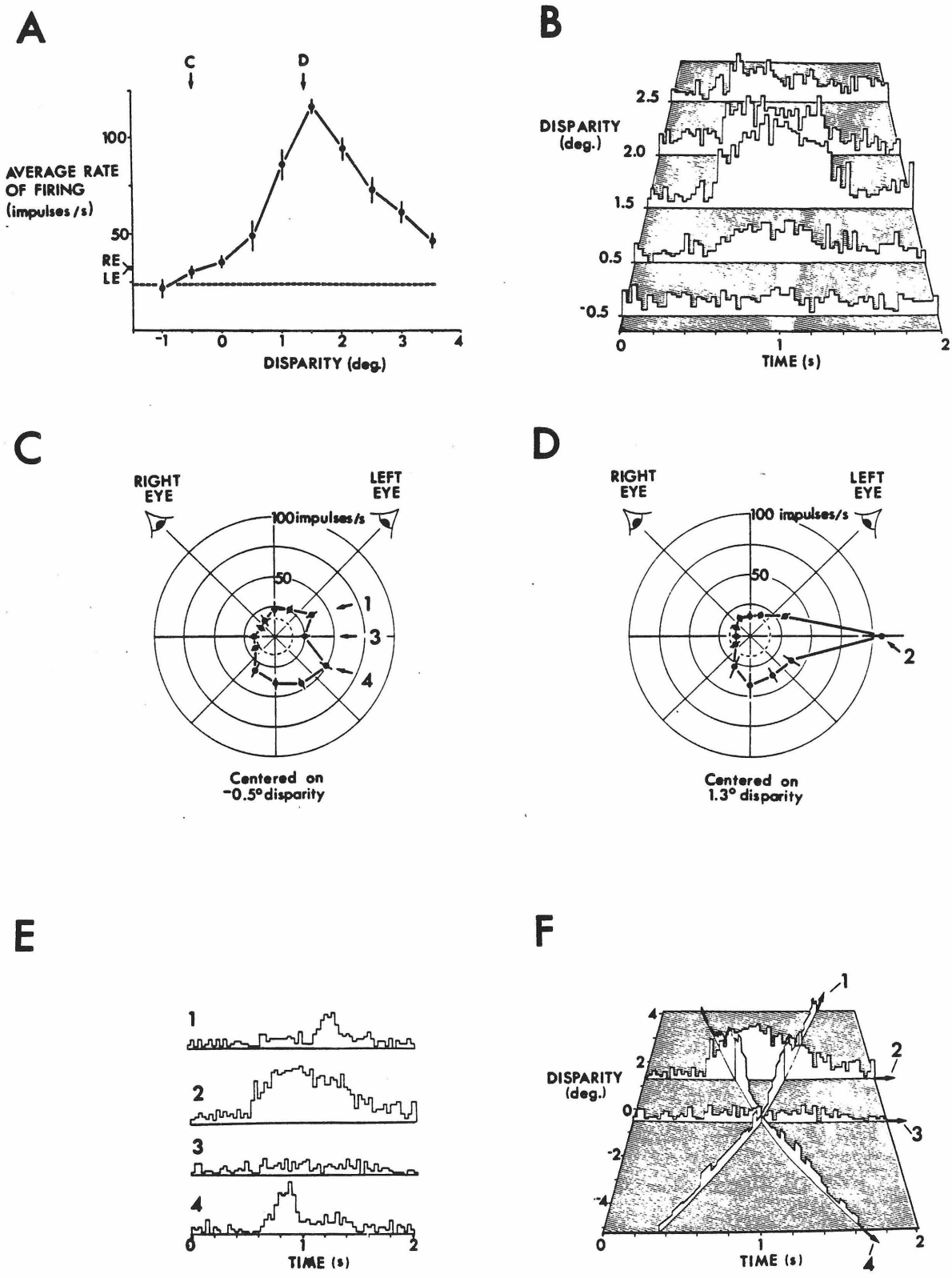
9B. Summed response histograms to motion at different fixed disparities. The summed response histograms from the test of part A are plotted at the appropriate positions on a plane where disparity is represented along one axis. If disparity is interpreted as distance from the animal, it can be seen that the effect of the disparity tuning is to limit the extent of the receptive field in depth. Robust responses are evoked only in the part of space near to the animal (positive disparities).

9C. The responses of the unit to a test for motion in depth selectivity centered far from the preferred disparity. The trajectories were centered at -0.5° of disparity (indicated by arrow C in part A). The response to fronto-parallel motion (#3) was less than that to several of the motions in depth (e.g. #1, 4).

9D. The responses of the unit to a test for motion in depth selectivity centered close to the preferred disparity. The trajectories were centered at 1.3° of disparity (indicated by arrow D in part A). The response to fronto-parallel motion (#2) was clearly best. The scale for this plot is the same as that in part C, for which the responses were all relatively weak.

9E. Differences in the timing of responses to different trajectories. The summed response histograms for four trajectories from the tests in parts C and D are shown. The response to fronto-parallel motion at the best disparity (#2) was uniformly high during stimulus presentation, while that for fronto-parallel motion at the non-preferred disparity (#3) was uniformly weak. The responses to motions at depth centered at the non-preferred disparity have pronounced peaks which occur at different times. That for trajectory 1, which begins far from the animal and approaches, is late in the movement. That for trajectory 4, which begins near to the animal and moves away, is early in the movement.

9F. Spatial relationships of peaks in response histograms. The four response histograms from part E have been plotted on a plane where disparity is represented along one axis, as in part B of this figure. The scale of the disparity axis is different than that in part B. Trajectories 2 and 3, which were fronto-parallel, are plotted running straight from left to right at their respective disparities. Trajectories 1 and 4, which moved in depth, cut across disparities as they move. It is obvious that the peaks in the response histograms for the motions in depth occur at the time when the stimuli have a disparity close to the preferred disparity (parts A, B).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whose center point was at the preferred disparity and with motions centered elsewhere. Ten were like the unit shown in Fig. 9, preferring fronto-parallel motion when the center point was near the preferred disparity, and having a peak response to a motion in depth when the center point was far from the preferred disparity. The remaining 2 preferred fronto-parallel motion in both cases. For these units the center point was shifted a relatively short distance between test series; they might well have preferred motion in depth over fronto-parallel had the center point been further from their preferred disparities.

Thirteen additional units were tested with motions in depth centered away from their preferred disparity. Of the total 25 units tested in this way, 4 had a peak at a fronto-parallel motion. Of the remaining 21, which had peak responses to some motion in depth, 13 had responses which were significantly better than fronto-parallel motion ($p<0.05$, single-tailed t test). However, when compared with the results of tests of fixed disparity tuning, none of the units tested with motions centered away from their preferred disparity had a response which was better than their response to fronto-parallel motion at the preferred disparity.

These results indicate that a disparity tuned unit may appear to prefer motion in depth if the center point of the motions is set away from the preferred disparity. However, if the responses of such a cell can be explained in terms of fixed disparity selectivity, and if the best overall response is to a particular fronto-parallel stimulus, we believe it is inappropriate to describe the cell as having selectivity for motion in depth.

DISCUSSION

Disparity selectivity in MT

This study, in conjunction with the preceding one (Maunsell and Van Essen 1982) shows that the majority of neurons in MT are selective for disparity in addition to

having direction and speed selectivity. Thus MT appears to be very well adapted to analyzing the movements of visual stimuli through space. This specialization is accented by the relative indifference of most neurons in MT toward stimulus form and color (Dubner and Zeki 1971, Zeki 1974a, Maunsell and Van Essen 1982). The only detailed studies of binocular interactions in extrastriate visual areas, prior to this report, have been on V2, where there also is a high incidence of disparity selective cells (Poggio and Fischer 1977, Poggio and Talbot 1981). Information on other areas is more fragmentary. Zeki (1978) reported occasional cells with strong binocular interactions in all five extrastriate visual areas he studied. The percentage of disparity selectivity has now been shown to be high in two of these areas, V2 and MT, and it would not be surprising if this were also the case for the other three: V3, V3A, and V4. Recent recordings in our laboratory from ventral extrastriate visual areas in the macaque (Burkhalter and Van Essen, unpublished data) also support the idea that disparity selectivity is widespread, if not universal.

The width of disparity tuning in cat V1 and V2 is closely correlated with receptive field size (Pettigrew et al. 1968, Ferster 1981). In a detailed examination of the mechanisms of binocular interactions, Ferster (1981) demonstrated that the spatial arrangement of excitatory and inhibitory subfields could be used to predict the disparity tuning of most cells with reasonable accuracy. This question has not been addressed directly in macaque V1 and V2, but the width of disparity tuning curves is related to receptive field size (Poggio and Talbot 1981) and there is a correlation between types of disparity tuning curves and ocular imbalance (Poggio and Fischer 1977), suggesting that the same may be true in these areas. However, there is nothing in the substructure of receptive fields in MT to suggest a basis for disparity tuning. Although we have not examined receptive field structure exhaustively, most units seem to have large, uniform receptive fields when tested with stationary or moving stimuli (e.g. Figs. 3, 4). Disparity tuning is found within these apparently homogeneous fields, and the tuning curve widths are narrow relative to receptive

field dimensions. However, it seems very likely that disparity tuning is already established in the V1 and V2 cells which project to MT, and it is therefore possible that receptive field structure at these lower levels gives rise to disparity selectivity in MT. If this is so, then the cells providing input to a neuron in MT could share not only a common direction preference, but also the same disparity tuning. In this regard it is interesting that about one half of the disparity tuned neurons in V1 and V2 are direction selective (Poggio and Talbot 1981). However, much less is known about the properties of the specific cells in V1, such as those in layers IVb and VI, which give rise to the projection to MT (Lund et al. 1976).

There are other differences between the disparity tuning of MT and that in V1 and V2. Although tuning curves in MT were narrow compared to receptive field dimensions, the absolute width of tuning curves was broader than those reported for macaque V1 and V2. In these areas, tuned excitatory neurons respond well only over a range of about 0.25° (Poggio and Talbot 1981), while the narrowest tuning seen in our data is about 1.0°. This might reflect a genuine difference between visual areas, but it may be due to other factors. The majority of tests for disparity selectivity in V1 and V2 were done in or near the foveal representation (<3° eccentricity), while recording in the present study was at an average eccentricity of about 10°. It may be that tuning curves in V1 are correspondingly broader at this eccentricity. It could also be that the broadness of tuning is due to differences between the anesthetized and paralyzed preparation used in the present study and the alert preparation used by others. Another difference was that our sample had almost twice as many near cells as far. The inverse relation has been found in V1 and V2 of both the macaque and cat (Poggio and Fischer 1977, Ferster 1981). Ferster (1981) found that while V1 of the cat has twice as many tuned excitatory as near and far cells, the ratio was reversed in V2 of this animal.

Regan and Beverly (1973b) reported that selective adaptation in humans can demonstrate a class of disparity detectors which are selective for the direction of

stimulus motion. More recently, Fox et al. (1982) have found that the motion aftereffect (the waterfall illusion) is dependent on the disparity of the adapting movement. Peterson et al. (1981) have found neural correlates of the motion aftereffect in MT of the owl monkey. Our finding that MT neurons are both disparity and direction selective is consistent with the psychophysical results of Fox et al. It would be interesting to know if the motion effects in humans are dependent on stimulus speed, as are the neurons in MT.

Sensitivity to non-horizontal disparities

The large receptive fields in MT facilitated the examination of selectivity for non-horizontal stimulus disparities, which do not contribute to stereopsis. Those neurons examined were apparently not specialized for detecting horizontal disparities, but instead were comparably sensitive to disparity changes along all axes. Data on the specialization of the mammalian visual system for disparities which are significant to stereopsis are not conclusive. Receptive field incongruities with greater horizontal scatter than vertical have been reported in V1 of the cat (Barlow et al. 1967, Blakemore 1970), and a prevalence of cells selective for horizontal disparities has been seen in V2 of the macaque (Hubel and Wiesel 1970) and sheep (Clarke and Whitteridge 1976). However, investigations which carefully controlled for residual eye movements have found no bias in central receptive field incongruities in cat V1 (Nikara et al. 1968, Joshua and Bishop 1970, Hubel and Wiesel 1973, von der Heydt et al. 1978) or measured disparity preferences in cat V1 and V2 (Bishop et al. 1971, Nelson et al. 1977, Ferster 1981).

Two types of hypothesis can be advanced to explain why neurons in MT (and elsewhere) are selective for both vertical and horizontal stimulus disparities. One possibility is that the neural circuitry which is used to generate selectivity for horizontal disparities automatically provides selectivity for vertical disparity as well, and that it would require additional, unnecessary circuitry to avoid selectivity in this

second dimension. It also seems possible that selectivity for vertical stimulus disparity provides useful information to the animal. If disparity tuning were important for controlling alignment of the eyes, then information about non-horizontal disparities would clearly be needed. Also, it is conceivable that sensitivity to non-horizontal disparities may be important for cases when the head is not upright. With small head tilts there is a compensatory cyclorotation of the eyes, causing disparities of objects in space which are not strictly horizontal. Equal sensitivity to all axes of disparities is consistent with the observation that Panum's fusional area is equal in horizontal and vertical extent (Mitchell 1966).

Motion in depth

Determining whether any particular neuron is selective for motion in depth is in certain respects a more complicated issue than determining whether the same neuron is selective for other commonly considered parameters (e.g. color, intensity, orientation, speed, length). In essence, this is because changing the direction of motion in depth necessarily involves changes in other basic parameters, including binocular disparity and the speed and direction of movement seen by each eye. The general problem of confounding one type of selectivity with another has previously been brought up in connection with orientation vs. direction selectivity in the visual cortex. In that case it was pointed out that testing with moving slits of various orientation can, at least in principle, make a direction selective cell appear also to be orientation selective (see Henry et al. 1974). An analogous situation holds for the present case. Poggio and Talbot (1981) found in V1 and V2, and we have found in MT, that neurons tuned for fixed disparity can show apparent selectivity for motion in depth when tested only with motions whose center was at a non-preferred disparity (see Fig. 9).

The question of whether a neuron is selective for fixed disparity and not motion in depth, rather than the reverse, is of course an important one. Our argument that

the selectivity is indeed for fixed disparity for the MT neurons in the present study is based on several objective criteria. First, for cells that were tested over a range of fixed disparities and with multiple sets of motions in depth at different center points, the most effective stimulus was consistently a trajectory parallel to the frontal plane. Second, the preferred trajectory was generally different in sets of motions in depth with different center points (e.g. frontoparallel motion best at one disparity and motion toward the animal at another). Thus the best motion in depth within a set was very much dependent on the choice of center point. In contrast, the best disparity, and hence the best position in space was largely independent of the particular center point. A response was elicited along that portion of a trajectory which brought the simulated object to the appropriate region of space. A neuron with fixed disparity selectivity can be considered to have a three-dimensional receptive field of limited extent. This, coupled with its direction selectivity in the fronto-parallel plane is sufficient to account for the responses to a wide variety of motions in depth. While tuning for motion in depth is not a necessary consequence for a neuron which has fixed disparity tuning, elaborate neuronal circuitry would be necessary to prevent it.

On the other hand, there have been several previous reports suggesting that there is motion in depth processing in extrastriate visual cortex. Perhaps the most striking have been the opposed movement cells, which have been seen in several areas in the visual cortex of the cat and monkey, including MT (Zeki 1974b). Such cells, with opposite preferred directions for the two eyes, cannot be simply selective for fixed disparity. However, only those neurons with horizontal direction preferences are suitable for analyzing motion in depth (see Appendix). These cells could signal motion straight toward or away from the animal. Others, with non-horizontal direction preferences, might be useful in controlling eye alignment (Pettigrew 1973). In any event, the overall incidence of such cells is very low, especially if only those

with horizontal direction preferences are considered. Nonetheless, it would be valuable to know more about their response properties, for example, whether responses were independent of the center point of motions in depth.

A somewhat larger class of possible motion in depth cells was studied by Cynader and Regan (1978). However, as noted by Poggio and Talbot (1981), many of these cells were tested with trajectories centered at a non-preferred disparity, which would make responses to fronto-parallel motion weak relative to some motions in depth. Some of the cells illustrated by Cynader and Regan gave their best overall response to fronto-parallel motion at the preferred disparity. We can therefore regard such cells as selective for fixed disparity. Others are ambiguous, as not enough information is available. However, aside from the aforementioned opposed movement cells, we are not aware of any examples of tuning for motion in depth which has been adequately shown not to be a simple consequence of fixed disparity selectivity. A convincing demonstration of genuine motion in depth selectivity would include 1) an overall maximum response for a non-fronto-parallel trajectory, and 2) best trajectories in test series with different center points which were more or less parallel. From this it would follow that there would be no well-defined restricted three-dimensional receptive field for such cells.

It is intriguing that neurons with true selectivity for motion in depth have not yet been found in reasonable numbers. Given the tremendous increase in form selectivity between the V1 (Hubel and Wiesel 1968) and inferotemporal cortex (Gross et al. 1972), it is perhaps natural to expect that extrastriate cortex should also contain a population of neurons selective for complex motions, such as motion in depth. The existence of such a population has by no means been ruled out, since most of extrastriate cortex has not been explored for this property. Subcortical centers could also play an important role in motion analysis. On the other hand, it is worth recognizing that the capacity for fine analysis of motions in depth does not

necessarily require the existence of individual neurons with motion in depth selectivity. It is at least possible that this capability arises only from the interaction of a large number of neurons, no one of which is individually selective for motion in depth.

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APPENDIX

Points in space which do not lie on an animal's horoptor will have retinal images which fall on non-corresponding positions on the two retinas. This disparity provides a powerful cue for the perception of the depth in space (Wheatstone, 1838). The perception of a point at a given depth can be produced by stimulating each eye separately with stimuli. Monocular stimuli projected on a fronto-parallel screen can be used to create stimulation which simulates objects at any distance from the animal.

It is not true, however, that any pair of monocular stimuli on a screen will correspond to a single real stimulus at some position in depth. It will be shown that when binocular perceptions are to be produced with monocular stimuli on a fronto-parallel screen, no vertical disparity should exist between the stimuli. Figure 10 is a schematic of a viewing situation in which the left eye (LE) and right eye (RE) are stimulated individually to create a perception of a point at P in space. The image of each of the monocular stimuli (S_R and S_L) must be in the correct retinal position, but the distance of the stimuli from their respective eyes is not important for stereopsis. For these reasons, each stimulus might lie anywhere along the line connecting its corresponding eye with the point P. If the eyes are at (-a, 0, 0) and (a, 0, 0) and the point P arbitrarily taken to be at (x_p, y_p, z_p), these two lines will be:

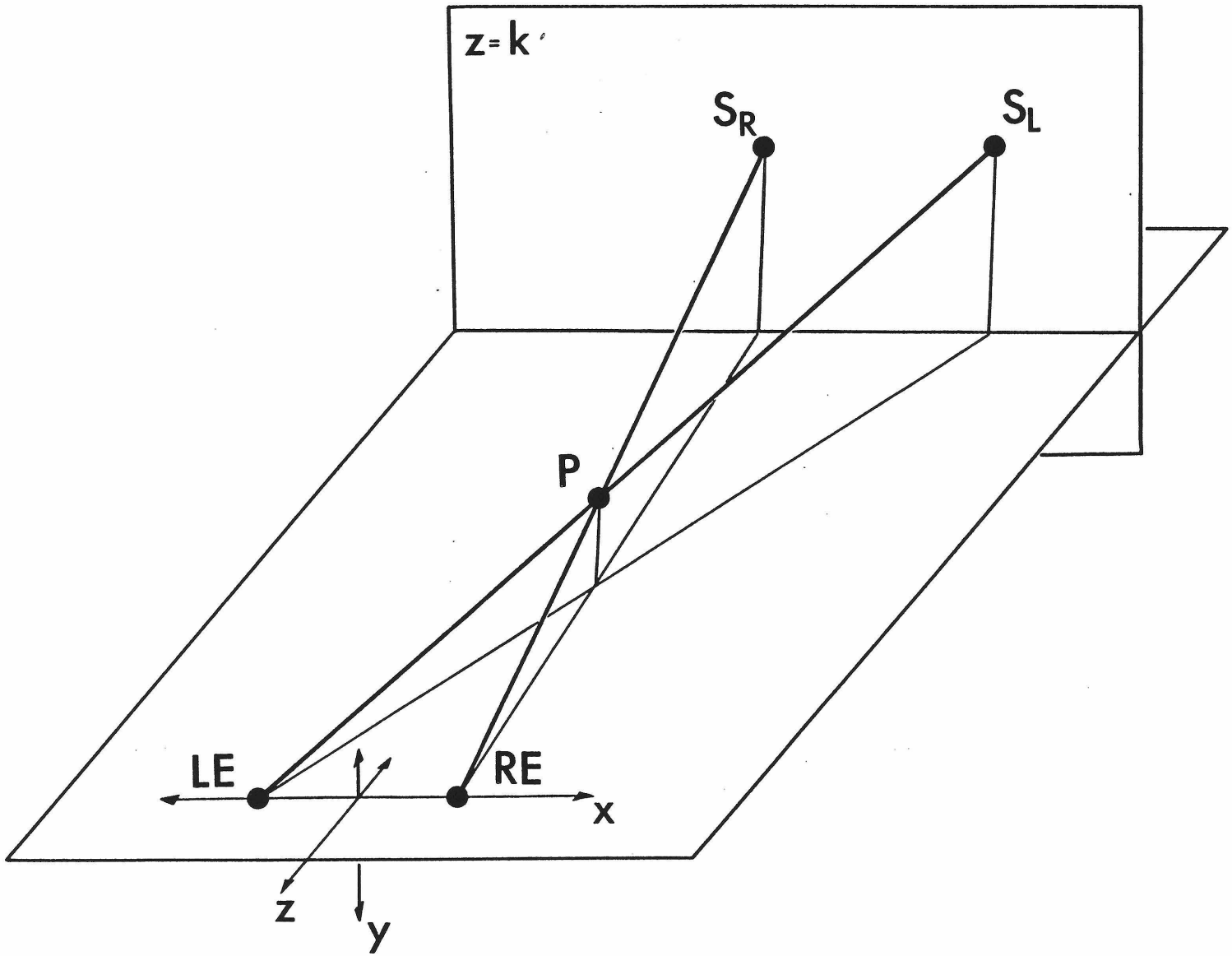
$$(x+a)/(x_p+a) = y/y_p = z/z_p \qquad \text{and} \qquad (x-a)/(x_p-a) = y/y_p = z/z_p$$

For both lines:

$$y = zy_p/z_p \qquad \text{and} \qquad \delta y/\delta z = y_p/z_p$$

Since both lines are at z=0 when y=0, the intersection of both lines with any fronto-parallel plane z=k will be at a vertical level of $y = ky_p/z_p$, and no vertical disparity will exist between the stimuli. Since this applies for all points P in space, monocular stimuli on a fronto-parallel screen should always maintain zero vertical disparity even if they are simulating a binocular stimulus moving through space.

Figure 10. Simulation of a point in space using monocular stimuli confined to a fronto-parallel surface. If the stimuli are to simulate a real object at some point in depth, they most always have the same vertical level. See text for details.


z = k
S_R
S_L
P
LE
RE
x
z
y

These monocular stimuli may create retinal images which do have a vertical disparity, since the distances from each eye to its stimulus may be different (see Ogle 1950). The vertical disparity of the retinal images will be that which would exist between the retinal images of a binocularly viewed point at P, and for most points is small compared to horizontal disparity.

It is interesting that neurons responding to monocular stimuli with changing vertical disparity have been reported in area 17 (Bishop et al. 1971) and 18 (Pettigrew 1973) of the cat, and V1 and V2 (Poggio and Talbot 1981), and MT in the macaque (Zeki 1974b). The above considerations support the suggestion of Pettigrew (1973) that these units might be involved in detecting errors in eye alignment rather than binocular detection of motion in depth.

Chapter 3

INTRODUCTION

The finding of a large number of intricately connected cortical and subcortical visual areas in higher mammals makes it clear that there is a very complex network involved in the processing of visual information. Anatomical tracing techniques have been instrumental in demonstrating that there are at least ten visual areas in the cerebral cortex of the macaque (see Van Essen et al. 1982a), and in suggesting how information is distributed among them (see Weller and Kaas 1981).

This report concerns the anatomical connections of one of the extrastriate visual areas in the macaque, the middle temporal area (MT). MT is a small area lying in the posterior bank of the superior temporal sulcus and receiving a direct input from V1 (striate cortex) (Cragg 1969, Zeki 1969). It has a high percentage of neurons which are selective for the direction, speed, and binocular disparity of moving stimuli, suggesting it is important in the analysis of visual motion (Dubner and Zeki 1971, Zeki 1974, Maunsell and Van Essen 1982a,b). It is obviously of interest to know exactly what inputs it gets, which centers receive its output, and whether these targets are also specialized for motion.

We have studied the anatomical connections of MT using anterograde and retrograde tracers. MT has reciprocal connections with a large number of identifiable cortical areas, and also extensive connections with subcortical centers. However, there is considerable order in the system of connections and it is possible to delineate a clear hierarchy of cortical visual areas based on objective anatomical criteria. Also, the connections of MT provide evidence contributing to the identification of two previously unrecognized extrastriate visual areas. Finally, by analyzing the fine pattern of connections with individual visual areas, we have obtained intriguing clues pertaining to the functional hetereogeneity of certain cortical areas.

METHODS

Anatomical tracers were injected into MT in the right hemisphere of three Macaca fascicularis which weighed between 3.1 and 3.7 kg. Because MT is small and there is considerable individual variability in its position within the superior temporal sulcus (Van Essen et al. 1981), it was necessary to establish the location of MT in each animal with physiological recordings before the injection. All the animals had been used for semi-chronic recordings of MT, the results of which have been reported elsewhere. In the course of these recordings the extent and topography of MT was largely established in each of the experimental hemispheres, and this mapping was used as a guide for determining where to make the injections. With this technique it was possible to make injections which were entirely confined to MT and which involved the representation of a particular part of the visual field.

Injections were made using a 1 µl syringe (Hamilton) containing 25 µCi of ^{3}H-proline in 150 nl of a 20% solution of horseradish peroxidase (HRP; Boehringer Mannheim). To reduce damage by the syringe, the original barrel was replaced with a 30 ga. syringe needle (300 µm O.D.). Leakage of tracers was minimized by loading 30 nl of a 30% sucrose solution into the syringe both in front and behind the tracers. The approach to MT was horizontal, running through striate cortex and the lunate sulcus to reach MT from the white matter. For two injections the syringe needle was coated with a thin layer of insulating varnish everywhere except the tip. Multi-unit recordings were made to confirm the depth of MT and the visual field representation before the injection. For the other injection, a microelectrode penetration to identify MT was made immediately before the syringe was inserted. Injections were made at a rate of about 120 nl/hr, and there was a 15 min pause between the end of the injection and the retraction of the syringe. For the two injections made with the recording syringe, the animal was paralyzed and respired with nitrous oxide. For the other injection, the animal was sedated with ketamine (IM).

The splenium of the corpus callosum (posterior 1 cm) was transected to provide an anatomical marker for the boundaries of some of the extrastriate visual areas (Zeki 1970, Van Essen et al. 1982a). The callosum was cut three to four days after the tracers were injected to allow time for label to be transported to the opposite cerebral hemisphere. This surgery was performed in aseptic conditions with sodium pentothal anesthesia.

Four or five days after the corpus callosum was cut, an acute recording session was made to map receptive fields in MT and the surrounding cortex in the left (uninjected) hemisphere. The recording techniques used for this session have been described in detail elsewhere (Van Essen et al. 1981). This session lasted from 1.5 to 2 days. At the end of this session the animal was deeply anesthetized with sodium pentobarbitol and perfused through the heart with a phosphate buffer rinse (0.1 M, pH 7.4) followed by a series of buffered 4% formaldehyde solutions containing 0%, 10% and 20% sucrose. The brain was then removed, photographed, blocked, and allowed to equilibrate with phosphate buffer containing 30% sucrose.

The blocks were sectioned at 31 μm. Sections every 0.25 mm (1 in 8) were reacted for HRP using a modification of the tetramethyl-benzidine method (Mesulam 1978) suggested to us by C. Schatz. Sections were lightly counterstained with neutral red before scanning for labeled cells with brightfield microscopy. Other series of sections at 0.25 mm spacing were processed for autoradiography (Cowan et al. 1972), and fiber degeneration (Wiitanen 1969). Autoradiographic sections were exposed for three to six weeks. A final series of sections was stained for myelin (Gallyas 1979) and was used to determine the borders of MT (Van Essen et al. 1981). All histological data were scored on 8x photographic enlargements of the individual sections and subsequently transferred to two-dimensional maps of the cortex for analysis (Van Essen and Maunsell 1980).

The survival time for these experiments was long, and there were fewer HRP labeled cells than we have seen for smaller injections with shorter survival times.

The long survival time is likely to have affected the reactivity of the HRP, and it is quite possible that minor inputs to MT were missed.

RESULTS

Location of injection sites

The location of three MT injections is shown in photomicrographs of sections in Fig. 1. Those for injections 1 and 2 were cut in the parasagittal plane, and that of injection 3 was cut horizontally. Each is within 0.5 mm of the center of its injection. The borders of MT could be determined to an accuracy of about 1 mm on nearby sections stained for myelin, and the range of uncertainty for the location of each border is indicated by a black line below cortex in the photographs of Fig. 1.

Injections 1 and 2 were centered near layer IV and restricted to MT, and there was no significant leakage of tracers along the syringe tracks. Injection 3 was centered in white matter below MT, but it extended well into the infragranular layers. Unlike the others, this injection resulted in HRP labeled cells over most of the prelunate gyrus, presumably as a result of uptake by damaged axons in the white matter around the injection site (Grob et al. 1982). For this reason the HRP data for this animal were discounted. Fortunately, the autoradiography showed a more restricted distribution of transported label. This indicates that substantial proline uptake did not occur in white matter, just as has been found in control experiments in our lab (unpublished results).

Figure 2A contains two-dimensional maps of MT in which the locations and approximate sizes of the injection sites have been marked. These maps include only cortex in and immediately surrounding MT; they were made by aligning adjacent contours of layer IV taken from histological sections (Van Essen and Maunsell 1980). The representation is as though one were looking at the superior temporal sulcus after it had been opened by unfolding. The dashed line is the fundus of the sulcus, and the

Figure 1. Photomicrographs of the injections of MT. These sections were taken from within 0.5 mm of the center of each injection and processed for autoradiography. The plane of section for injections 1 and 2 was parasagittally, that for injection 3 is horizontal. The black lines below cortex indicate the range of uncertainty in assigning the borders of MT on nearby sections stained for myelin. Injection 3 was centered in white matter below MT, but extended well into the infragranular layers. The HRP data from this injection were discounted. The sections for injections 1 and 2 were exposed for three weeks, that for injection 3 was exposed for six weeks.

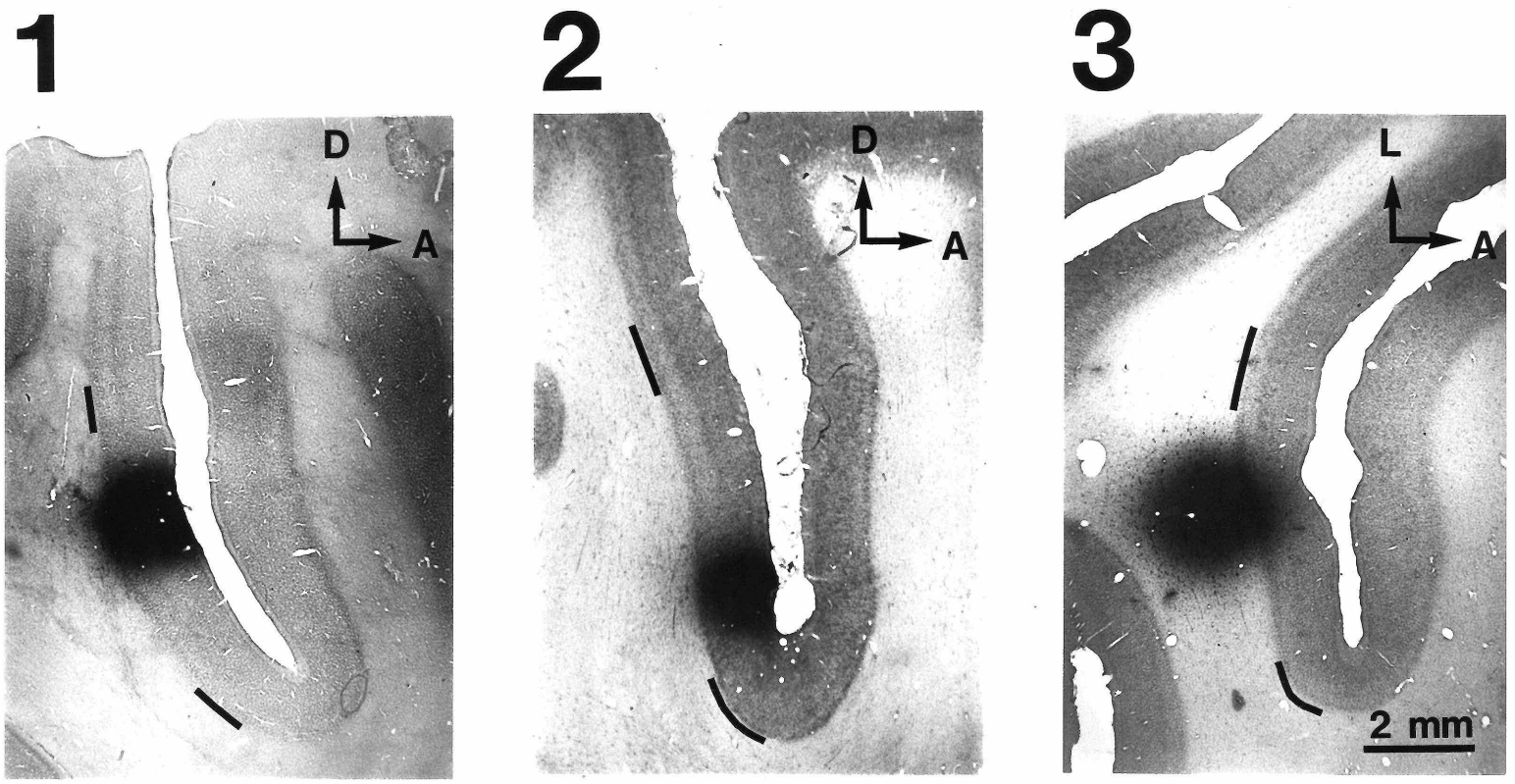
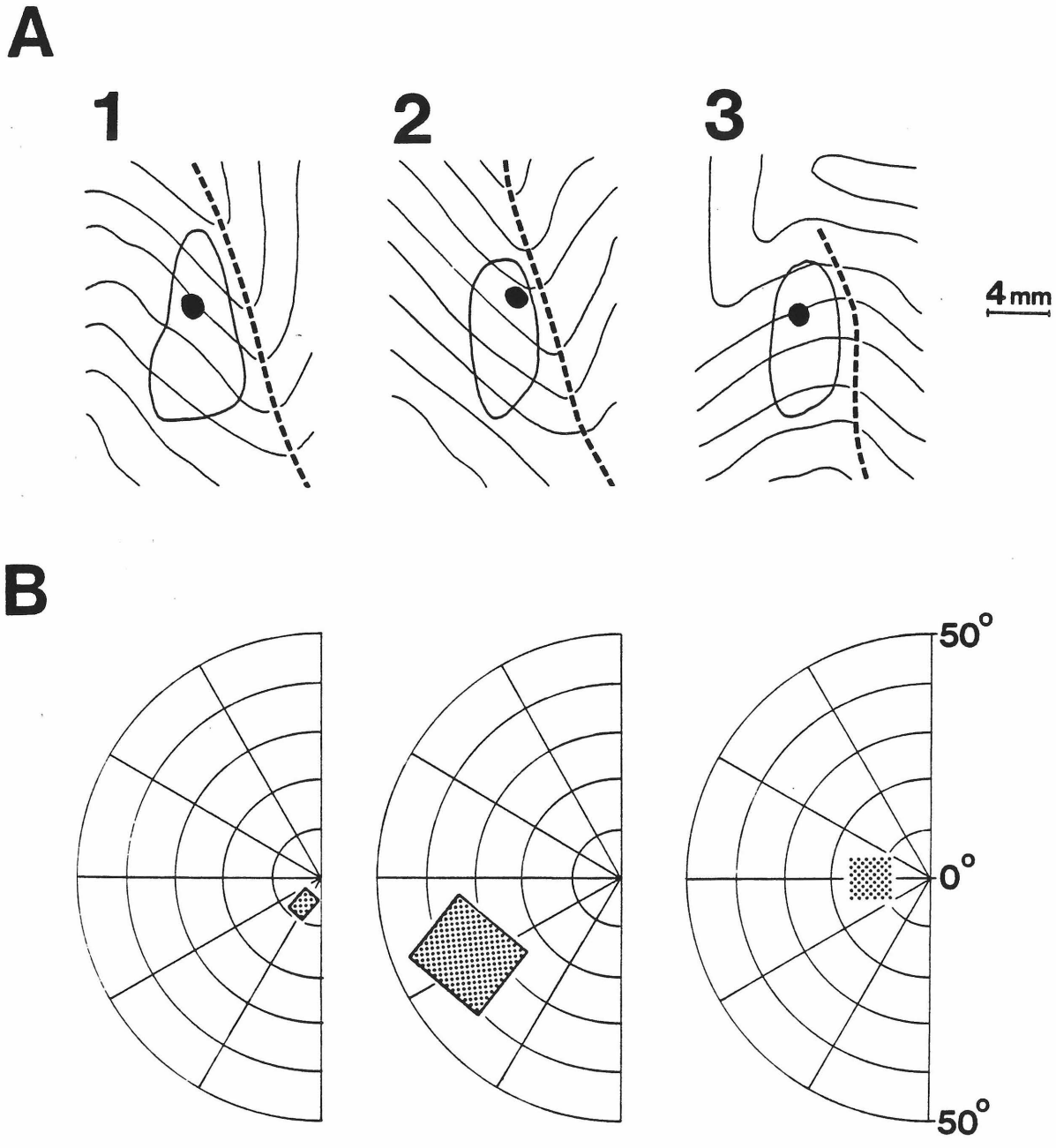

1
D
A
2
D
A
3
L
A
2 mm

Figure 2A. Two-dimensional maps of the injections. The location and size of the injections are shown in two-dimensional maps of the cortex in and around MT in the superior temporal sulcus. The perspective is as if one is looking down on the cortex after the sulcus has been unfolded. The dashed line is the fundus of the sulcus, and the posterior bank is to its left. The border of MT is drawn as a solid line. Each injection was confined to the cortex within MT, and involved a small fraction of its total area.

2B. The locations of the receptive fields of cells at or near the injection sites. The receptive fields for injections 1 and 2 were plotted at the time of the injection using a syringe modified for recording. Although no recording was made at the time of injection 3, the position of the receptive field representation at this site can be assigned with confidence based on prior recordings in the vicinity and the location of label in visual areas with well defined topographies.


A
1
2
3
4mm
B
50°
0°
50°

posterior bank is to its left. The borders of MT are marked by drawing smooth lines through the regions of uncertainty for the borders on each section. All injections were in the more dorsal half of MT, where the more peripheral parts of the visual field are represented (Van Essen et al. 1981).

The receptive fields of cells at or near each of the injections sites are drawn in Fig. 2B. The receptive fields for injections 1 and 2 were plotted at the time of the injections using a syringe which had been modified for recording. Both injections were in the representation of the inferior quadrant, with injection 1 at an eccentricity of 6-7° and close to the representation of the vertical meridian, and injection 2 more peripheral (35° eccentricity) and away from both the horizontal and vertical meridians. Recordings were not made at the time of injection 3, but the approximate location can be confidently assigned to the region of the horizontal meridian representation at about 12° eccentricity based on previous recordings made in the immediate vicinity of the injection site, and also on the distribution of projections to V1 and V2. The absence of a strong correlation between injection position within MT and receptive field location among these cases is consistent with the irregular topography and individual variability found in MT (Van Essen et al. 1981).

Cortical connections

Assignment of cortical connections. All three experiments resulted in an extensive, complex pattern of connections with at least six cortical visual areas, and one of the injections indicated that there are connections with one or more additional areas. Most of these connections can be assigned with confidence to specific visual areas. This section will deal with the identification of the visual areas with which MT is connected. Subsequent sections will address the topographic order of these conenctions, the uniformity or patchiness of label distribution in different areas, and the intrinsic connections of MT.

The overall connections and their relationship to established visual areas are best appreciated by considering one case in detail. The complete pattern of cortical connections for injection 1 is shown on two-dimensional cortical maps in Fig. 3A (^{3}H-proline) and Fig. 3B (HRP). The map unfolds the convoluted cortex into a flat sheet with relatively little areal distortion (Van Essen and Maunsell 1980). The obvious advantage of this type of representation is that the entire pattern of projections, and the size, shape, and local relationships of labeled regions can be seen at a glance on a single plot, whereas it is difficult to discern these features from the positions of label on a series of sections. The maps are similar to those in Fig. 2A, except the representation is expanded to include all of visual cortex. More anterior regions of cortex are represented mainly to the right, and dorsal and ventral regions respectively are on upper and lower parts of the map. Striate cortex is represented by the elliptical region on the left; it has been separated from extrastriate cortex by a discontinuity to reduce distortions. Dashed lines mark fundi of sulci, and MT has been outlined and lies roughly in the middle-right of the extrastriate portion of the map near the fundus of the superior temporal sulcus. In Fig. 3A anterogradely transported label is indicated by hatching, and the locations of HRP labeled cells are marked with dots in Fig. 3B.

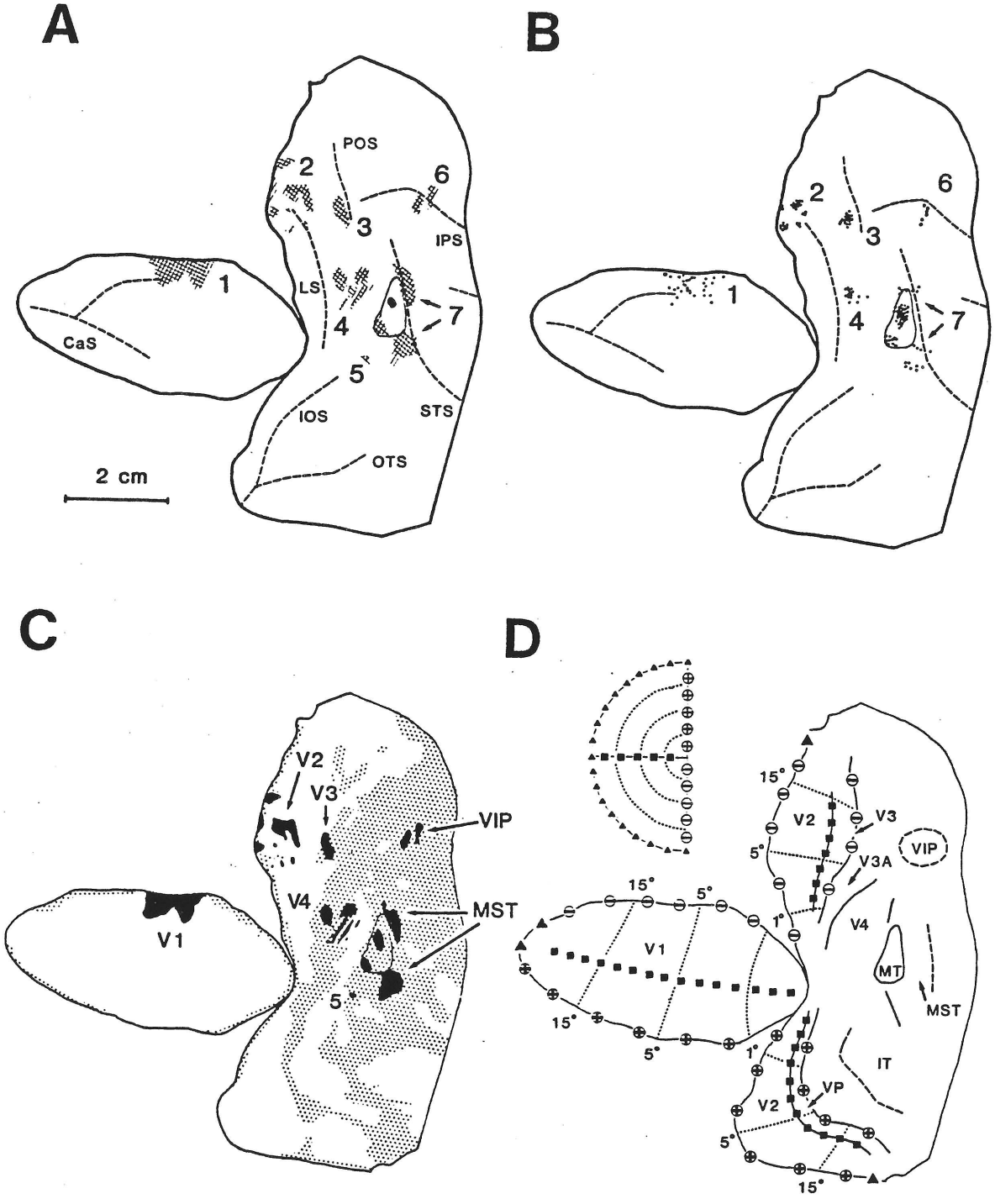
The connections revealed by this injection were mostly in the dorsal part of the hemisphere (upper portion of the cortical map). This is not surprising, given that the injection was within the representation of the inferior quadrant, and that inferior fields are represented predominantly in the dorsal part of the occipital lobe. Connections with many distinct regions can be seen for both the HRP and the proline injections. The patterns are remarkably similar, and for convenience corresponding connections have been labeled with the same number. The correspondence of anterograde and retrograde transport implies that the cortical pathways to and from MT are reciprocal and also that the fine patterns are largely overlapping. The only substantial difference is that no retrogradely labeled cells are visible in some of the

Figure 3A. A two-dimensional map of anterogradely transported label in visual cortex following injection 1. The location and extent of anterogradely transported label is indicated by hatching on a two-dimensional, unfolded map of visual cortex. For convenience, the different labeled regions have been numbered. The fundus of each sulcus is marked with a dashed line, and labeled using the following abbreviations: CaS, calcarine sulcus; IOS, inferior occipital sulcus; IPS, intra-parietal sulcus; LS, lunate sulcus; OTS, occipito-temporal sulcus; POS, parieto-occipital sulcus; STS, superior temporal sulcus.

3B. A two-dimensional map of retrogradely transported label in visual cortex following injection 1. The location of HRP filled cells is shown by dots on a map of visual cortex. The numbering scheme is the same as that in part A. The position of retrogradely transported label largely coincides with that of anterograde label, indicating that most cortical pathways to MT are reciprocal.

3C. The pattern of callosal inputs. Stippling indicates the location of degenerating axon terminals following transection of the splenium of the corpus callosum. For clarity, the fundi of the sulci have not been marked. The pattern of callosal inputs can be used to identify the position of several extrastriate visual areas. The locations of transported label are marked in solid black on this map, and most can be unambiguously assigned to specific visual areas on the basis of the callosal inputs.

3D. The location of established visual areas based on the pattern of callosal inputs. The locations of 10 visual areas in this hemisphere are indicated. These assignments are based on the pattern of callosal inputs in part C. The approximate positions of horizontal and vertical meridian representations, and selected eccentricities, have been indicated for those areas with known topographic representations.


A
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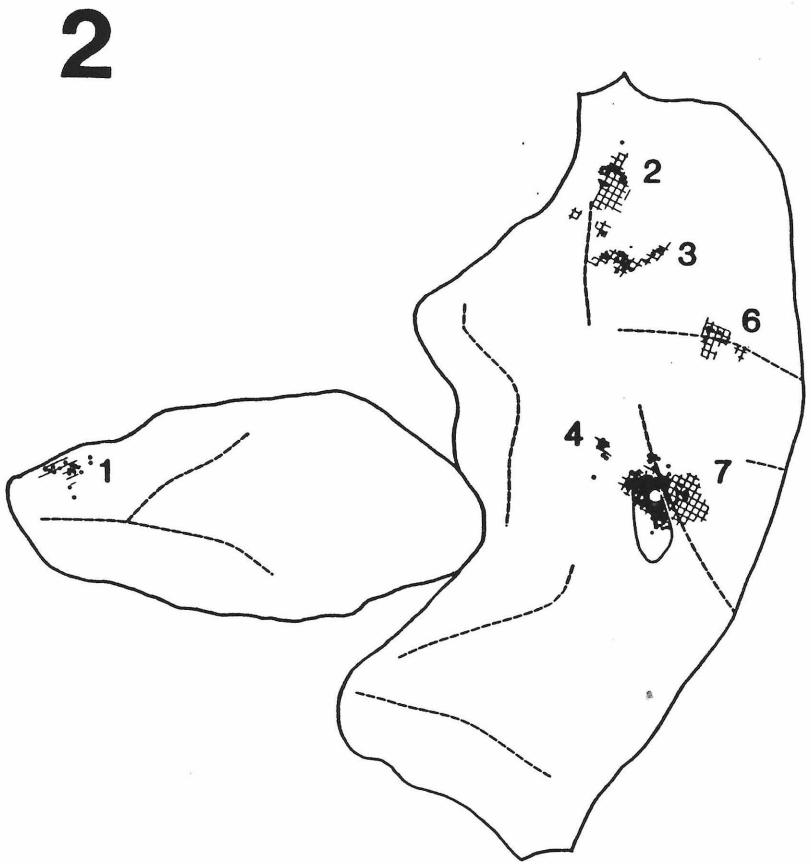
V2
V3
VIP
V4
MST
V1
5
D
15°
V2
V3
5°
VIP
V3A
15°
5°
1°
V4
V1
MT
MST
15°
5°
1°
IT
VP
V2
5°
15°

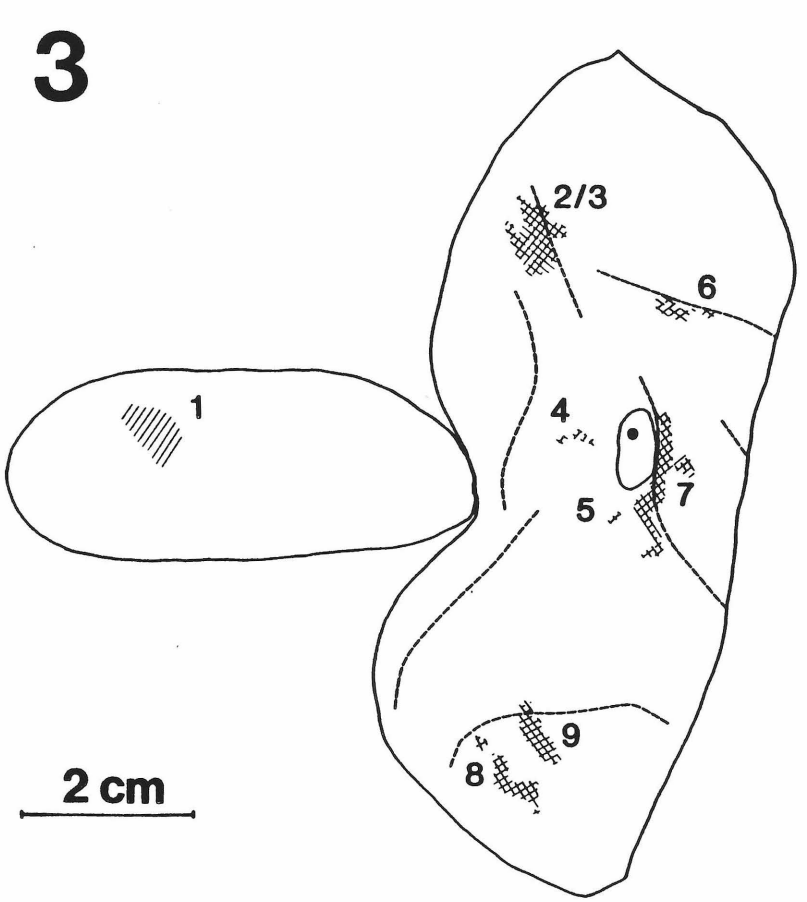
regions with weak anterograde label. However, this is most likely attributable to the long survival time (see Methods).

The projections to V1 and V2 can be identified very easily on the basis of their relationship to the sharply defined architectonic border of striate cortex. The other assignments are less certain, however, and it is important to have an independent marker for the location of particular visual areas. The marker we used was callosal inputs which were visualized by means of cutting the corpus callosum and staining sections for degenerating terminals. The pattern of degeneration in this hemisphere is shown by stippling in Fig. 3C. Regions labeled by the HRP and proline injections are marked in solid black. Fig. 3D is a map of the same hemisphere on which the borders of visual areas have been marked. The positions of these borders are based on the relationship between these borders and the pattern of callosal degeneration, which has been described in detail elsewhere (Van Essen et al. 1982a). Figure 3D also shows the approximate topography expected in the various visual areas (Van Essen et al. 1981, Gattass et al. 1981, Van Essen and Zeki 1978, Newsome et al. 1980). In brief, there are 10 distinct areas, most of which contain clear topographic representations of part or all of the contralateral visual hemifield. In general, the foveal representation of these areas is near the center of the map (lateral cortex), with inferior fields dorsal and superior fields generally ventral (V3A and MT are exceptions). Several areas lack obvious topography, including two (MST and VIP) not previously recognized and identified in large part on the basis of results of the present study (see below).

With the aid of the pattern of callosal inputs, it is possible to assign most of the connections of MT to specific visual areas, as indicated by labels in Fig. 3C. One connection (#5) has not been assigned to a visual area (see below). Figure 4 contains cortical maps for the other two injections. As for injection 1, the pattern of label was extensive and complex, but there was a remarkably consistent superposition of

Figure 4. Two-dimensional maps of transported label for injections 2 and 3. Transported anterograde (hatched) and retrograde (dots) label are shown on two-dimensional maps of the visual cortex for injections 2 and 3. The labeled regions have been numbered with the same conventions used in Figure 3. Injection 3, unlike the other two, resulted in two patches of label in ventral cortex (zones #8 and #9).

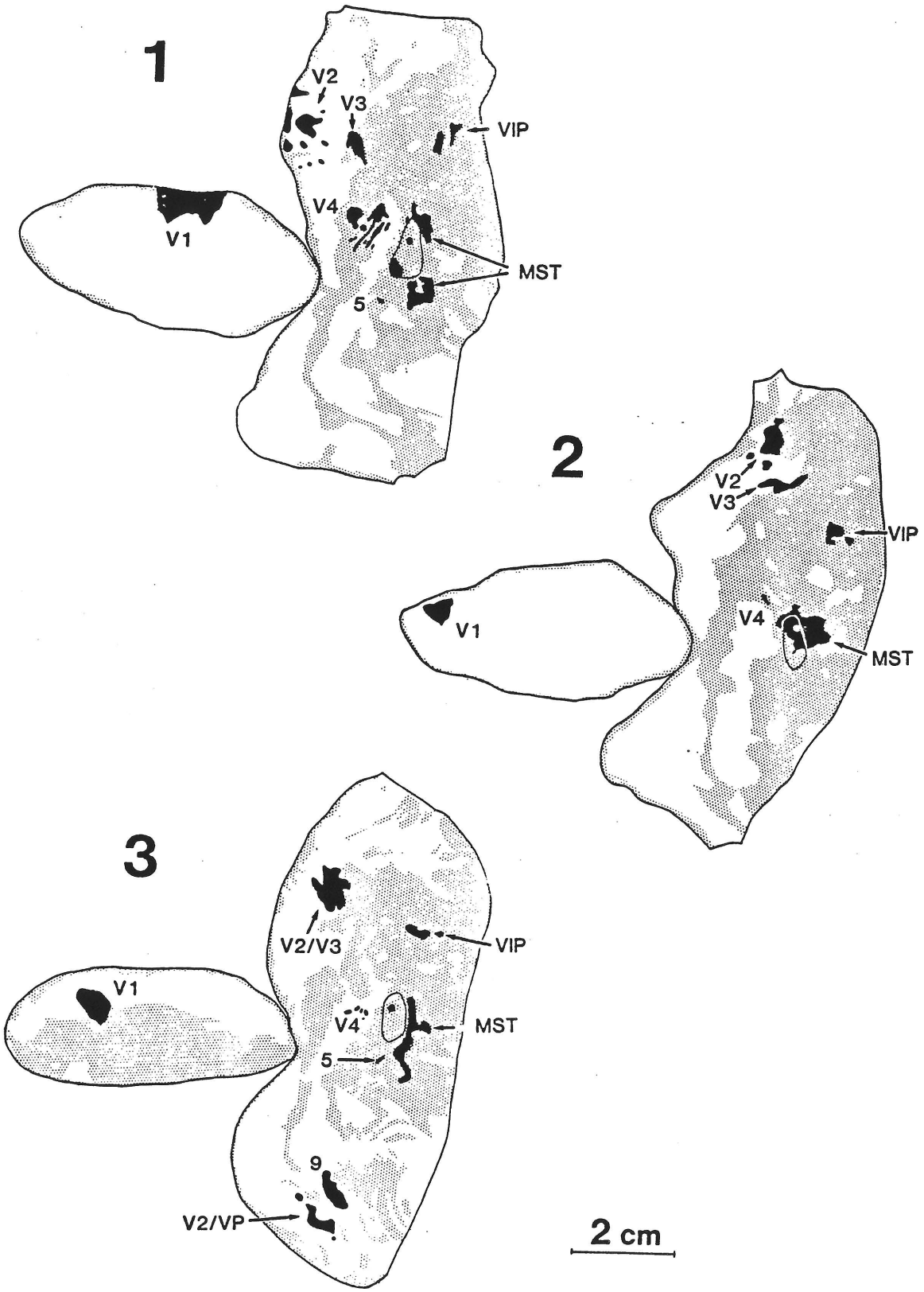

2
1
2
3
6
4
7


3
1
2/3
6
4
5
7
9
8
2 cm

anterograde and retrograde label. Labeled regions have been numbered as in Figs. 3A and B. Injection 3, at the representation of the horizontal meridian, resulted in two patches of label ventrally, numbered 8 and 9, which were not seen in the other cases. The pattern of degeneration for all three hemispheres is shown in Fig. 5. The individual patterns of degeneration have been used to make assignments of the labeled regions to visual areas. The pattern of degeneration of injection 3 had unexpected degeneration covering the ventral half of V1. The optic radiation of this hemisphere was found to contain a small lesion, presumably resulting from a vascular accident incurred about the time the corpus callosum was cut. Fortunately, this lesion did not affect the pattern of degeneration in extrastriate cortex.

The maps of Fig. 5 show that MT is connected with a substantial number of visual areas. Given this degree of connection (which is only part of the greater overall interconnections of cortical visual areas), there is great value in defining a simplifying structure within the network of connections. One of the striking features in the results of these experiments was systematic differences in the laminar organization of connections of MT with other areas. The pattern is like that seen for many other reciprocal pathways—namely, in one direction a projection originates from primarily superficial layers and terminates mainly in layer IV, while the projection in the other direction originates in substantial part from infragranular layers and terminates mainly outside layer IV. In all instances in which a clear hierarchical relationship can be inferred on other grounds, the first pattern is associated with forward projections, and the second is associated with feedback (see Discussion). This correlation also fits well with the present results for MT, and we will use the notion in the following descriptions of the connections of MT. These considerations allow the grouping of areas which connect with MT into those which provide input, those which receive output, and a single area which occupies an intermediate position.

Figure 5. The pattern of callosal inputs on two-dimensional maps for all three injections. Stippling marks the location of callosal input in each map. The three patterns are similar. Transported label is marked in solid black. By using the pattern of callosal inputs, most of the label can be assigned to specific visual areas. Labeled zones which have not been assigned to specific visual areas are numbered as in previous figures.


1
V2
V3
VIP
V4
V1
MST
5
2
V2
V3
VIP
V1
V4
MST
3
V2/V3
VIP
V1
V4
MST
5
9
V2/VP
2 cm

Inputs to MT. It is known from previous studies that V1 and MT in the macaque are reciprocally connected, and that the projection from V1 to MT arises from layer IVb and, to a lesser extent, layer VI (Zeki, 1969, Lund et al. 1976, Weller and Kaas 1978, Wong-Riley 1979). The present experiments confirmed these observations, and in addition show that the projection from MT back to V1 terminates in IVb and VI (Fig. 5, Table 1). Both projections were weak, and it was necessary to double the exposure time to see the projection to layer VI clearly. Although the injections in MT were reasonably focal (<2 mm diameter), retrograde and anterograde label occurred in large, roughly circular regions of V1. For the case of injection 1, the labeled region was about 12 by 5 mm in extent. Based on a magnification factor of 1.5 mm/deg (Daniel and Whitteridge 1961), the extent of label in V1 would correspond to 27 deg^2 of visual field, which is about the size of the receptive field recorded at the injection site (Fig. 2B). The extent of label in V1 for the other two injections was also consistent with the magnification factor for V1.

It has previously been shown that V2 projects to MT (Zeki 1971). It was also suggested that V3 projects to MT, but this pathway was less convincing due to uncertainties in the identification of V3. We have found that both areas indeed do have a major projection to MT. In both cases the projections arise mainly from layer III, but a few HRP labeled cells were also seen in the lower half of layer II (Table 1). V2 and V3 each had about twice as many HRP labeled cells as were seen in V1, suggesting that they are as important as V1, if not more so, in providing visual inputs to MT. The pathways from V2 and V3 to MT are reciprocal, and the laminar distribution of anterograde label was similar in both. The density of label was greatest in layers I and VI, with less in layers II, V, and III (Fig. 6). Virtually no label was seen in layer IV. The distribution of proline in both these areas is patchy, as will be discussed further in another section.

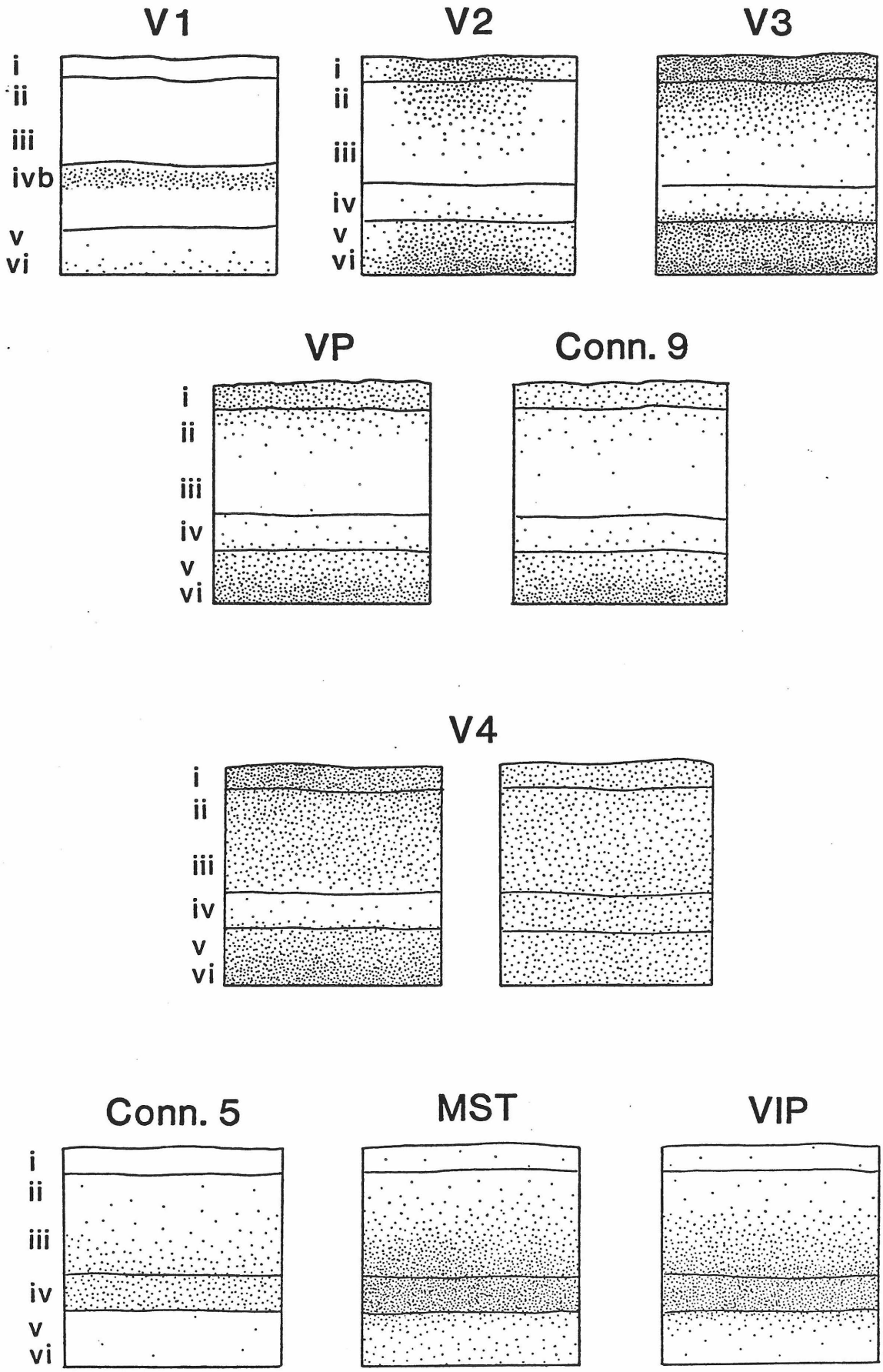
While all the injections revealed connections with V2 and V3 dorsally, only injection 3 also produced label at the border between V2 and VP in ventral

TABLE 1

Laminar Distributions of MT Connections

	Laminar Origins of Projections to MT	Laminar Terminations of Projections from MT
V1	IVb, VI	IVb, VI
V2	III, II	I, VI, V, II, III
V3	III, II	I, VI, V, II, III
VP		VI, I, V, II
Conn. 9		VI, V, I, II
V4	III, II	I, VI, II, III, V I, II, III, IV, V, VI
Conn. 5		IV, III, II
MST	III, V, VI	IV, III, II, V, VI
VIP	III, V, VI	IV, III, II

Figure 6. The laminar distribution of anterogradely transported label. The laminar distribution of label is shown for each of the cortical targets of MT. Feedback projections from MT are characterized by terminating largely in layers I and VI and sparing layer IV. Forward projections terminate mainly in layers IV and III. The label in V4 did not fit cleanly into either class, in some cases sparing layer IV, but in others labeling all layers equally.


V1
i
ii
iii
ivb
v
vi
V2
i
ii
iii
iv
v
vi
V3
VP
i
ii
iii
iv
v
vi
Conn. 9
V4
i
ii
iii
iv
v
vi
Conn. 5
i
ii
iii
iv
v
vi
MST
VIP

extrastriate cortex. As mentioned above, this additional label is attributable to the injection site being centered on the horizontal meridian and extending into the superior field representation. The label extends from about 1 mm of the center of the strip of callosal input at its closest to about 5 mm at its furthest. Since this strip demarcates the anterior border of VP (Van Essen et al. 1982a) and since VP is only 2-3 mm wide (Newsome et al. 1980), the projection is likely to include both V2 and VP. However, we do not consider this to be a conclusive interpretation. An injection confined to the representation of superior fields would resolve this question, but would be difficult to achieve since the superior fields are under-represented in MT (Van Essen et al. 1981). The laminar distribution of autoradiographic label at the V2/VP border was found principally in layer VI and I, with some spread into layer V. Unfortunately, the HRP injection was not successful in this animal, so we have no direct evidence that this connection is reciprocated.

Injection 3 also labeled cortex in a second region of ventral extrastriate cortex (Zone #9, Fig. 5). This label was within a degeneration-free zone which is a regular feature in the pattern of callosal degeneration (Van Essen et al. 1982a). This region has not as yet been identified as a distinct visual area; for the purposes of discussion we will refer to it as connection 9 from MT. The laminar distribution of radioactive label differed from the others in that there was little involvement of the superficial layers. Most of the label was in layer VI with some spread into layer V.

Outputs of MT: visual areas MST and VIP. Three cortical connections could be classified as outputs of MT on the basis of the laminar distribution of anterograde and retrograde label. The major output of MT is to a region immediately medial to it, along the fundus of the superior temporal sulcus and in places extending up to several millimeters onto the anterior bank. This region is known to contain a high percentage of direction selective neurons with receptive fields far larger than those in MT (Van Essen et al. 1981, Newsome and Wurtz 1981). In addition, this region has been

shown to project to area 7a (Barbas and Mesulam 1981) and to the frontal eye fields (Mesulam et al. 1977). In one of the three injections the projections medial to MT terminated in discrete patches about 6 mm apart. However, since distinct foci are not a consistent feature of either the input or the outputs of this region, there is not sufficient justification for subdividing it into multiple areas. We therefore consider MT-recipient cortex medial to MT to be a single area, which we have designated the medial superior temporal visual area (MST).

Autoradiographic label in MST was found primarily in IV with less in layers II and III, then V and VI. HRP labeled cells were mainly in layers III, V, VI. These laminar distributions were consistent with assigning the projection from MT to MST as forward, and that from MST to MT as feedback.

Another target of MT was a region of cortex in the lateral bank of the intraparietal sulcus near its fundus. There is also a weak projection to this region from V1 (Ungerleider and Mishkin 1979) and a stronger projection from ventral V2 (unpublished observations). It appears to be distinct from V3 and V3A, which lie posterior to it (Van Essen and Zeki 1978) and from POa, which lies dorsal to it (Seltzer and Pandya 1980). Although little else is known about this region, these features appear sufficiently distinctive to regard it as a distinct cortical area, and we have designated it the ventral intraparietal area (VIP). The laminar distribution of label in VIP was similar to that in MST, the only difference that VIP had even less anterograde transport in layers V and VI than did MST (Fig. 6).

The third output of MT was to a region of cortex lying lateral and ventral to MT (Zone #5 in Fig. 5). It is not clear to what area this projection belongs. Because of the uncertainty of assignment for this projection we will simply refer to it as connection 5 for the remainder of the manuscript. The anterograde label in this projection was very weak, and there were no HRP labeled cells associated with it. It was not found following injection 2, which had the weakest labeling in other areas.

As in MST and VIP, the proline was found mainly in layer IV with much less in layers III and II. There was no obvious label in the other layers.

A connection of MT with V4. There was one connection of MT whose laminar distribution did not fit clearly into either the input or output class: the connection with V4. Although some of the patches of anterograde label avoided layer IV, like feedback projections, many had label across the entire thickness of cortex, without concentration in any layer. HRP labeled cells were found mainly in layer III, with a few in the lower half of layer II. Because the labeling in V4 does not correspond well with the typical distributions for input or output, we provisionally regard this connection as lateral, rather than forward or feedback.

There is evidence to suggest that V4 actually consists of more than one visual area (Zeki 1971, Schein et al. 1982). It is possible that the different laminar distributions in V4 could belong to distinct subdivisions.

Topographic order of MT connections

One would expect a priori that any given site within MT would have its strongest connections with topographically corresponding portions of other visual areas. Since we knew the location and size of receptive fields for the injection sites in MT, it was possible to address several questions pertaining to the location and extent of the connection with other areas. In all cases the labeled pathways to and from visual areas already known to be topographically organized (V1, V2, V3, and VP) connected portions of these areas containing the representation of the same part of the visual field as that at the injection.

The orderliness of these connections can be seen in Fig. 5. In V1, increasing eccentricity at the injection site (inj. 1 < inj. 3 < inj. 2) was coupled with label progressively further from the foveal representation (at the right), each case corresponding well with the expected representation of its eccentricity in V1 (Daniel and Whitteridge 1961, Van Essen et al. 1982b). Also, injections at representations

further from the vertical meridian resulted in label further from the dorsal border of V1, where the vertical meridian is found in this area.

Similar orderliness existed in the connections with V2 and V3. Injection 3 resulted in label further from the foveal representation than injection 1, and that from injection 2 was further still. Injection 1 was near the representation of the vertical meridian, and resulted in label at the posterior (left) border of V2 and the anterior (right) border of V3, where the vertical meridian is found in each area. For injection 2, further from the vertical meridian, label was found in each area that was closer to their common border, at the representation of the horizontal meridian. Finally, injection 3, which included the representation of the horizontal meridian resulted in label in the expected locations at the V2/V3 border dorsally and the V2/VP border ventrally.

It is naturally of interest to know if this set of injections provides evidence for topographic order in other, less well characterized, visual areas. One area whose connections did show topographic order was V4. The exact position and extent of V4 is not known, but it is associated with a callosal-free zone following callosal section (Van Essen et al. 1982a). One possibility which has been suggested is that V4 comprises most of this callosal-free zone, plus a surrounding strip of callosal input, where a representation of the vertical meridian is expected. The results of the present experiments are in agreement with this suggestion. Label in V4 following injection 1 was along the dorsal margin of the degeneration-free zone, implying that the inferior vertical meridian is represented there. Injection 3, at the horizontal meridian, resulted in label in the middle of the callosal-free zone. Injection 2, in the inferior periphery, labeled the part of the V4 near MT dorsally. Together, these injections suggest a topography in which inferior fields are represented dorsally, superior fields are found ventrally, with the fovea posterior and the periphery anterior. The label in V4 was not found in a discrete focus, however, and the numerous patches could indicate complexities in the representation.

Only injection 3 labeled ventral cortex in the degeneration-free zone anterior to VP. Although it is not possible to establish a topography directly by comparing the position of label from different injections, it is nonetheless possible to propose a likely topographic order for this region. The absence of connections with the other injection sites suggests that only the superior quadrant is represented, as is true for other parts of ventral cortex. Because callosal degeneration is associated with representations of the vertical meridian, it is likely that the superior vertical meridian is represented at the anterior and posterior borders of the degeneration-free zone. These observations, together with a likely representation of the horizontal meridian in the center of the zone, suggest that this degeneration-free zone contains two representations of the superior quadrant, with a topographic arrangement analogous to V2 and VP.

The projections to MST were to different places in each case, but there is no obvious topographic structure consistent with the results. It is possible that this area, like MT itself, shows considerable variability in its topography among individuals. The connections with VIP were all approximately in the same geographic position.

Connections with contralateral cerebral cortex. The corpus callosum was cut about three days after the injections were made, allowing time for transport of label to the contralateral hemisphere. Only injection 1 resulted in label in the contralateral hemisphere. Faint radioactive label was seen in the opposite MT and MST, but no HRP reaction product was found. A reciprocal projection presumably exists, but was not detected due to the consistently lower degree of retrograde labeling in these experiments. The laminar distribution of label in the contralateral MST was the same as that in the ipsilateral MST, namely, densest in layers IV and III. The contralateral MT had faint label extending the full thickness of the cortex, with no obvious concentration in any particular layer.

The labeling in the contralateral hemisphere following injection 1 is illustrated on a cortical map in Fig. 7A. The map has been transposed so that it has the same

configuration as the map of the injection site in the other hemisphere, which is shown in Fig. 7B. The label in the contralateral MT is in a position similar to that of the injection site in the other hemisphere. The contralateral MST has a projection to a location corresponding to a patch of label in the opposite MST. However, the topography of MT is known to be disorderly and that for MST is not established. An acute physiology session was performed in this animal in the hope of plotting receptive fields in and around sites of transported label. Relevant recording sites from this session are shown as dots on the map in Fig. 7A, and the associated receptive fields are drawn in Fig. 7C. The receptive field recorded at the time of injection is cross-hatched in the left hemifield; its mirror image across the vertical meridian is hatched in the right hemifield.

The two most likely relationships for connections between opposite MTs is to link either representations of nearby parts of the visual field, or representations of points mirror symmetrically opposed across the vertical meridian. Although the results are not absolutely unequivocable, we believe that the pathway preferentially links representations of similar parts of the visual field. Receptive field 1 in Fig. 7C was recorded within the labeled region, while receptive field 2 was taken further away. Field 1 crosses the vertical meridian and contains parts of the visual field represented in both the receptive field at the injection and its mirror image. Field 2 overlaps as much or more of the mirror image, but not the receptive field at the injection. Since recording site 1, but not 2 was closely associated with labeled cortex, it is more likely that the labeled pathway connects representations of the visual field near the vertical meridian, which are found in both hemispheres. This conjecture is supported by the fact that neither of the other injections, which did not involve representations of the vertical meridians, resulted in contralateral labeling.

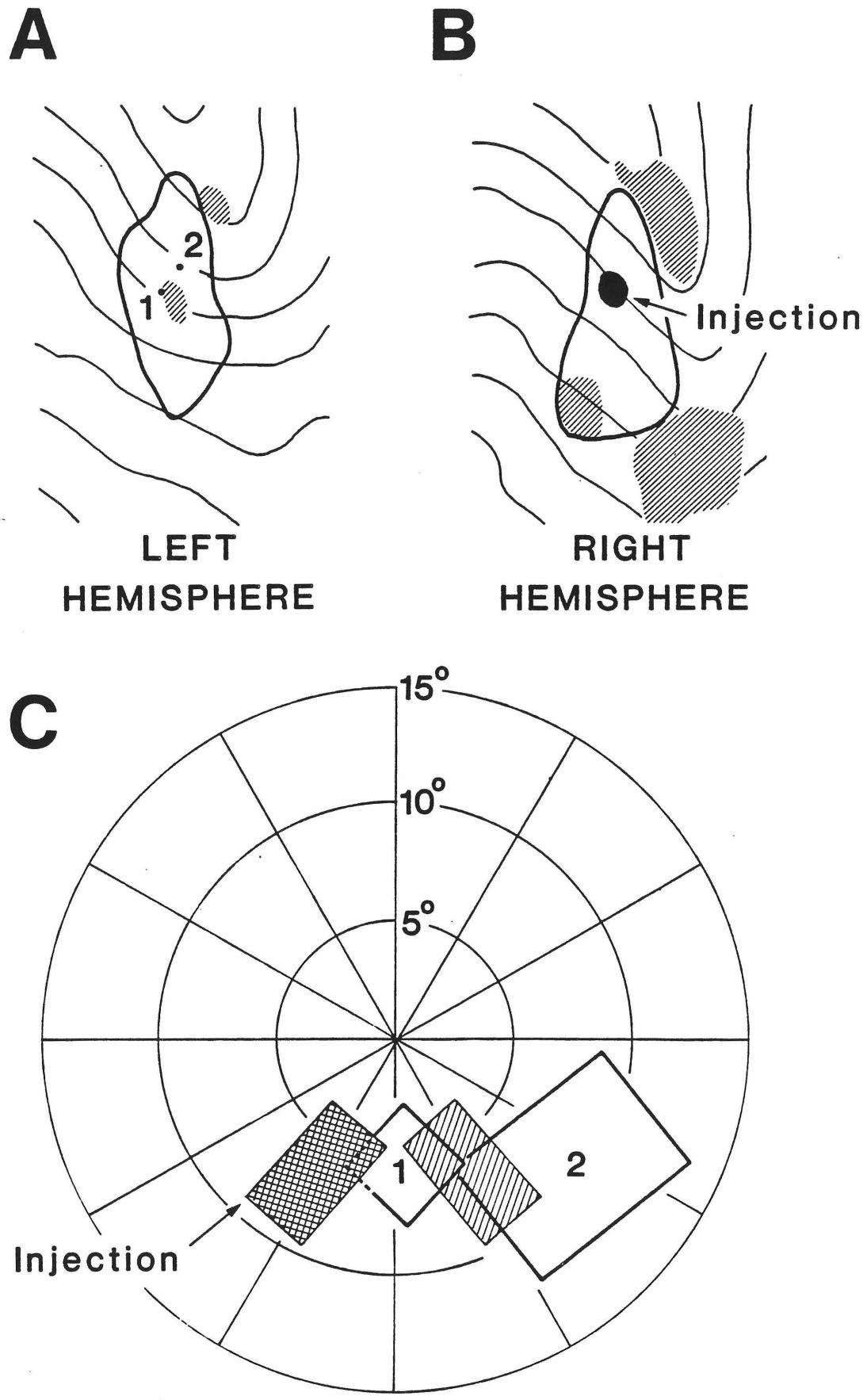
Intrinsic connections of MT. The tracer injections also revealed extensive connections within MT. The distribution of label was different in each case, perhaps as a result of differences in the particular layers injected. Injection 1 resulted in a

Figure 7. Contralateral transport of label following injection 1.

7A. A two-dimensional map of MT in the hemisphere contralateral to the injection. The map has been transposed so that it has the same orientation as maps of the other hemisphere. The border of MT is marked with a solid line, and the location of transported label is shown with hatching. Dots indicate two sites at which receptive fields were plotted in a physiological recording session.

7B. The location of the injection site and nearby transport of label for injection 1. The injection site and one of the patches of label in MST (to the right of the top of MT) occupy positions corresponding to the location of label in the contralateral hemisphere (part A).

7C. The locations of receptive fields for cells near the injection site and in the contralateral MT. The receptive field plotted at the time of the injection is cross-hatched in the left visual hemifield. Its mirror image across the vertical meridian is hatched in the right hemifield. The receptive field recorded at points 1 and 2 in MT contralateral to the injection are also drawn. Since recording site 1, but not 2, was associated with transported label, the contralateral pathway is likely to link representations of similar parts of the visual field near the vertical meridian. Because receptive fields were plotted as rectangles, the left corner of the field plotted at site 1 may extend slightly further into the left hemifield than did the response. On the other hand, the corpus callosum was cut before fields 1 and 2 were plotted, and the receptive field at site 1 may have extended even further into the left hemifield before this operation.


A
B
2
1
Injection
LEFT
HEMISPHERE
RIGHT
HEMISPHERE
C
15°
10°
5°
1
2
Injection

conspicuous patch of retrograde and anterograde label near the ventral tip of MT, separated from the injection site by a region with very little label (Fig. 3). The heavily labeled patch was clearly within the architectonic border of MT. It is not clear what purpose this internal connection might serve, since the patch is near the foveal representation.

Neither of the other two injections resulted in a discrete patch of label within MT. Injection 2 was surrounded by label whose density decreased steadily with distance, and which was not obviously concentrated in any layer. However, injection 3 had a different and striking pattern of intrinsic connections. This injection was centered in the white matter directly below MT and involved mainly the deep layers. The label is pictured in Fig. 8A. Figure 8B is a photomicrograph of a nearby section which has been stained for myelin. The borders of MT can be seen in the section, and the range of uncertainty in their positions is indicated by white lines below cortex. There is heavy label in layer VI and lighter label in the superficial layers across the width of MT. The label in layer VI extends beyond the lateral (upper) border, and in other sections superficial layers were also labeled lateral to MT.

This pattern of labeling was seen for a dorso-ventral extent of 4 mm around the injection site. This particular section is 1 mm below the injection center. One explanation for this type of labeling being seen only in this case is that the injection involved mainly the infragranular layers. Labeling of this type has also been seen in somatosensory cortex (Jones et al. 1978).

Patchiness of cortical connections. The label within individual cortical visual areas was often distributed in patches, and the degree of patchiness varied from one area to the next. The two extremes were V1, in which the label was almost uniformly distributed, and V2, in which small, intensely labeled patches were separated by wide regions with little or no label. Figure 9 shows this contrast in a photomicrograph of a section from the hemisphere of injection 1, which has been processed for autoradiography. Faint, evenly distributed label is visible in layer IVb of V1 to the left, while

Figure 8. Intrinsic connections of MT following injection 3. Part A is a dark-field photomicrograph of a horizontal section which has been processed for autoradiography. There is heavy labeling of layer VI and lighter labeling of superficial layers extending a long distance from the injection. Part B shows a nearby section which was stained for myelin and which was used to find the borders of MT. White bars below cortex indicate the range of uncertainty in the position of each border on this section. The transition in myelination is visible for the lateral (upper) border, but on this section the medial border is not obvious at this magnification. White bars have been drawn on the section in part A to indicate the corresponding positions. The label in layer VI extends beyond the lateral border of MT. On other sections both the superficial and deep label crossed this border.

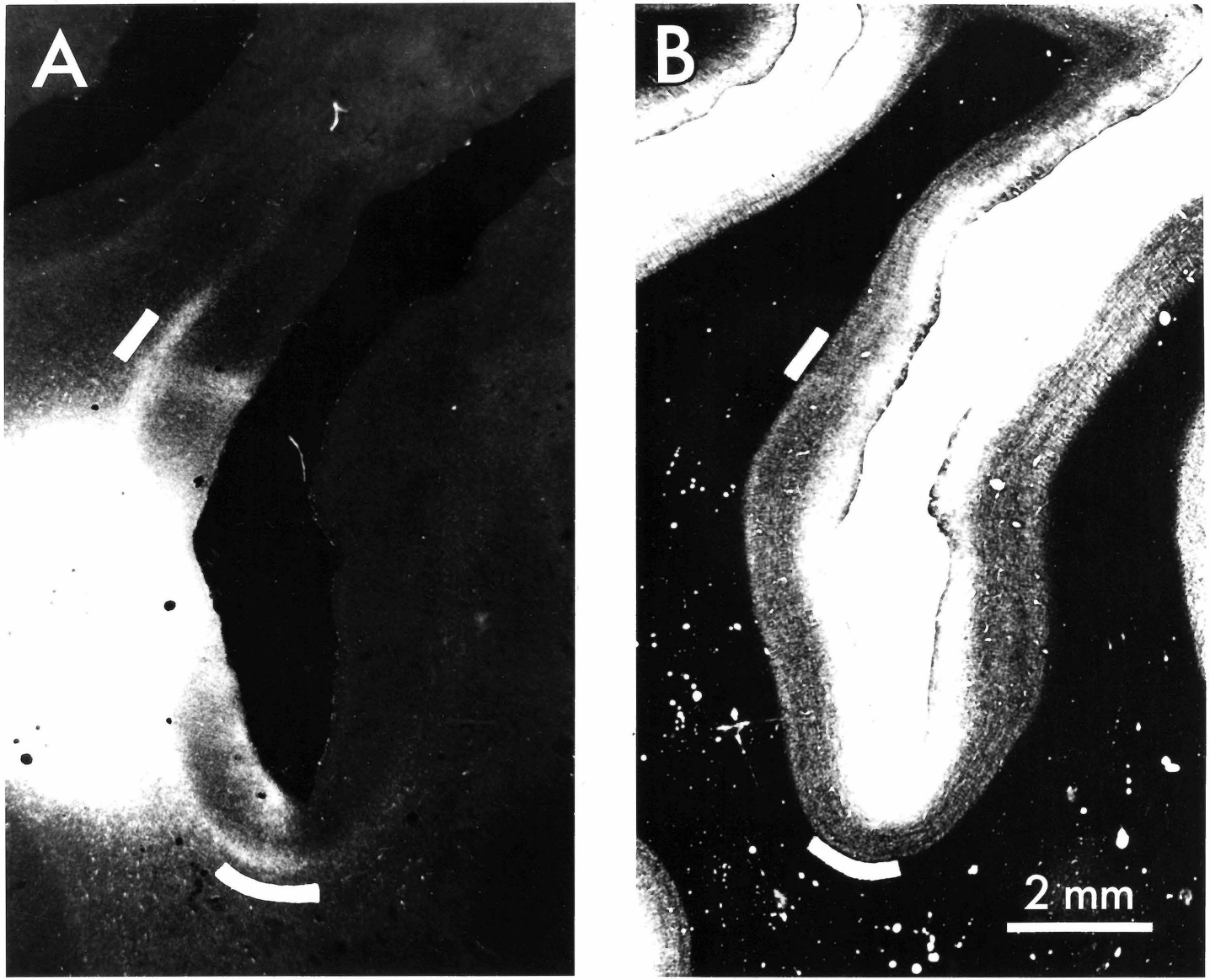
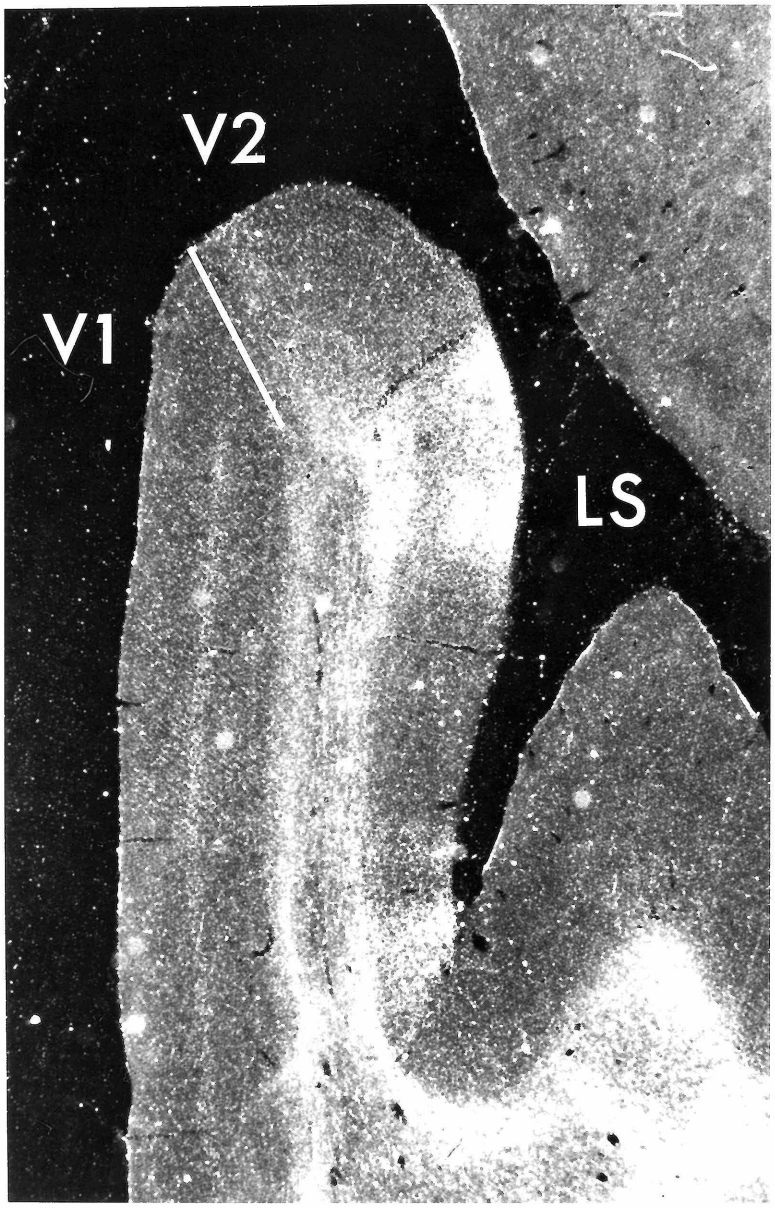

A
B
2 mm

Figure 9. A dark-field photomicrograph of label in V1 and V2 following injection 1 in MT. Faint, uniform labeling of layer IVb is visible in V1. V2, in the lunate sulcus (LS) has two widely separated patches of label. Label in V2 is mainly superficial and deep, and does not extensively involve layer IV. The label in layer VI of V1 is too faint to be readily visible in this photograph.


V2
V1
LS

V2, in the lunate sulcus (LS), has two widely separated patches of label. Cortical maps illustrate the full extent of HRP labeled cells for these areas in Fig. 10. The labeled cells in V2 were found in five distinct patches, which together covered roughly the same extent as that which was uniformly labeled in V1.

Pronounced patches were also seen in V4. Less dramatic patches were obvious in all the remaining ipsilateral connections (Fig. 5), with the exception of connection 5. The label in this projection was sufficiently weak that fine structure could have been undetected.

The significance of patches in cortico-cortical connections is not clear. Lund et al. (1981) have suggested that they may represent a functional inhomogeneity within visual areas. If this is true, then the patches of label in V2 and other areas following MT injections might contain pockets of neurons whose properties were appropriate for input to MT (i.e. direction, speed, and disparity selective), while other neurons in these areas might have other properties. Patchiness has previously been seen in the projections from V1 to V2 (Wong-Riley 1979, Maunsell et al. 1980) and MT (Montero 1980), but not in the projection from V2 to V1 (Maunsell et al. 1980).

Sub-cortical connections

Descending projections were seen to eight ipsilateral subcortical centers. No contralateral subcortical projections were identified, and only one pathway, that to the pulvinar, had detectable reciprocal connections with MT.

Claustrum and basal ganglia. Projections were seen to the claustrum, caudate nucleus, and putamen. The strongest projection was to the claustrum. Label was found in several small patches (0.5 to 1 mm diameter) which were distributed over about 5 mm along its posterior margin. The location of this label for injection 3 is shown diagramatically in Fig. 11B. The absence of HRP labeled cells in the claustrum was unexpected in view of its projection to MT in the marmoset (Spatz 1975), but it may be that the injections were too small to pick up minor subcortical inputs.

Figure 10. Two-dimensional maps of the distribution of HRP labeled cells in V1 and V2 after injection 1. The label in V1 is evenly distributed over a large region. The label in V2 is found in five discrete patches, which collectively cover about the same extent as the label in V1.

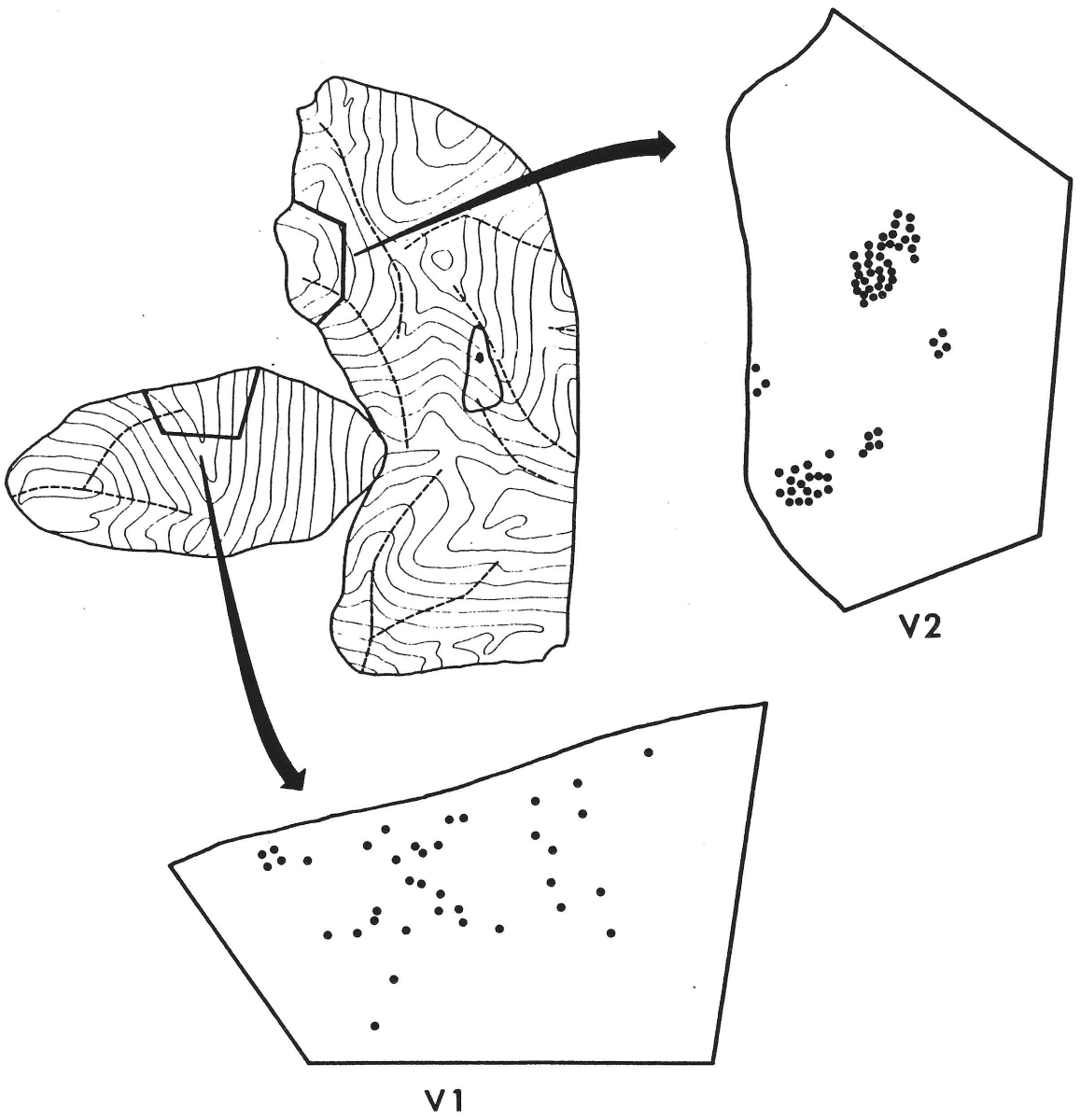
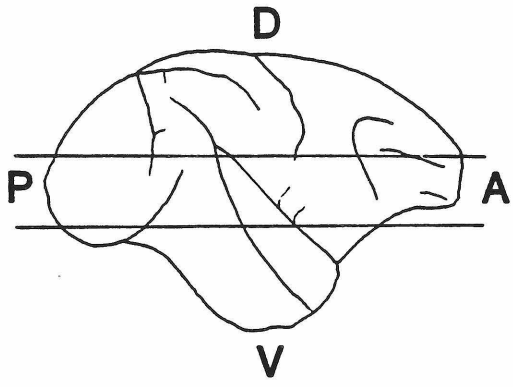
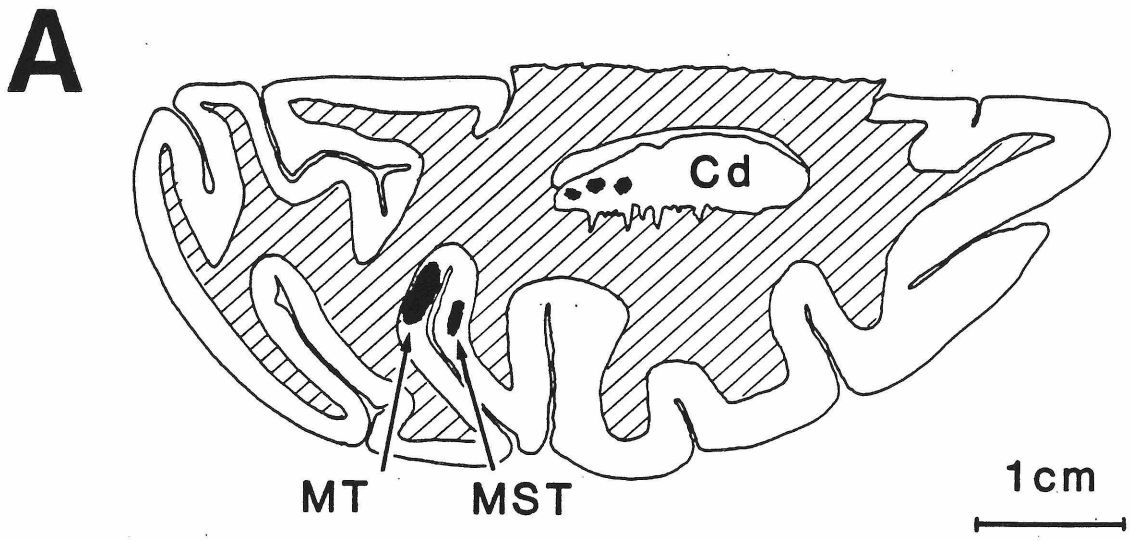

V2
V1

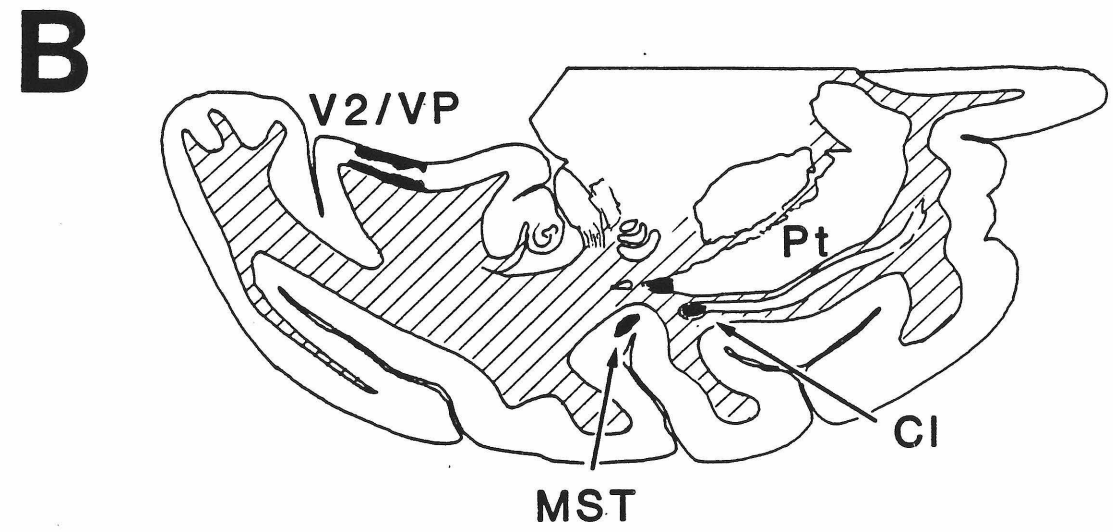
Figure 11. Labeling of the claustrum and basal ganglia following an injection of MT. An inset shows the level of two horizontal sections from the hemisphere of injection 3.

11A. The projection to the caudate nucleus. The caudate nucleus (Cd) contained small patches of anterogradely transported label over an extent of 7 mm.

11B. The projections to the claustrum and putamen. Several small patches of anterogradely transported label were found in the claustrum (Cl) for about 5 mm along its posterior margin. There was very faint radioactive label in the putamen (Pt) close to its posterior limit at this level. There was also label in several cortical visual areas at this level.


D
2cm
P
A
V


A
Cd
MT
MST
1cm

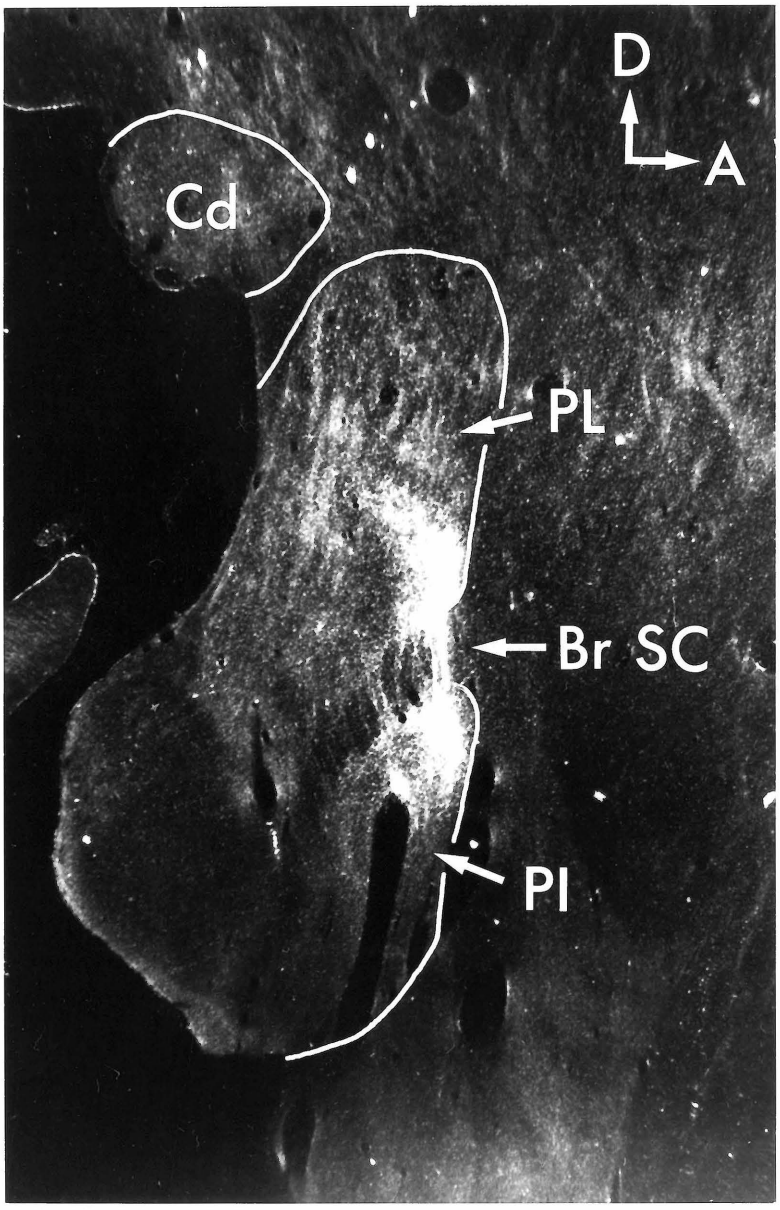

B
V2/VP
Pt
Cl
MST

Patches of similar size, but less intensely labeled were found over about a 7 mm extent in the tail of caudate nucleus. A section from the hemisphere of injection 3 which had label in the caudate is shown in Fig. 11A. Very weak label was seen in the posterior part of the putamen (Fig. 11B). This label covered about 1.5 mm, and was not obviously subdivided into patches.

Thalamus. All injections demonstrated anterograde projections from MT to the pulvinar, the ventral lateral geniculate nucleus (pregeniculate nucleus), and the thalamic reticular nucleus. By far the densest thalamic label was in the pulvinar, and, as mentioned above, this was the only reciprocally organized pathway. Label was found only in the inferior (PI) and lateral (PL) subdivisions (terminology of Olszewski 1952). Figure 12 is a dark-field microphotograph of an autoradiography section from the hemisphere in injection 1. The plane of sectioning is parasagittal. Figure 13 is an outline diagram of the nuclei visible in the section. Dense patches of label are present in front of and behind the brachium of the superior colliculus, in PI and PL, respectively. Dots on the outline figure show the distribution of HRP labeled cells, which coincided with the anterograde projection, as was the case throughout the pulvinar. The irregular patches of label are typical of what was seen on most sections. The label in PL was confined to the portion nearest PI. This portion of PL has been designated PLα (Rezak and Benevento 1977) and has been shown to have connections similar to PI, unlike the rest of PL (Rezak and Benevento 1979, Standage Benevento 1980). The same subdivisions of the pulvinar were labeled by the other two injections.

In all three cases the label was extended along a roughly antero-posterior axis. This fits with the topographic organization of the pulvinar, which in this region has lines of iso-representation parallel to this axis (Bender 1981). The position of the label within the subdivisions was also consistent with their known topography. Injection 1, which involves the representation of vertical meridian, led to label which was adjacent to the border between PI and PLα (Figs. 9A, B). Injections 2 and 3,

Figure 12. A dark-field photomicrograph of the projection from MT to the pulvinar. The section shown is from the hemisphere of injection 1 and the plane of sectioning is parasagittal. Clumps of label can be seen near the brachium of the superior colliculus (Br) in both the inferior (PI) and lateral (PL) subdivisions of the pulvinar.


D
A
Cd
PL
Br SC
Pl

which were made at representations away from the vertical meridian, resulted in label which was mostly away from the PI/PLα border. The topographic order indicated by these injections is in good agreement with that found by Benevento and Rezak (1976), who also showed a projection to MT from the pulvinar which arose from the same subdivisions. They found the vertical meridian to be represented at the border between PI and PLα, and that representations moved toward the horizontal meridian as one moved away from this border. A similar topography was described by Bender (1981), except he found that the border between the anatomical subdivisions did not correspond with the topographic border, which was shifted dorsally to lie entirely within PL at most levels. Our results are not consistent with this scheme, however. It may be that there is significant individual variability in the relative locations of topographic and architectonic borders.

The thalamic reticular nucleus also receives a projection from MT. Axon terminations were found mainly in the region where this nucleus was pierced by labeled axons heading to the pulvinar. Termination in the reticular nucleus around bundles of axons of cortical origin passing through it has been seen in other projections in primates (Lin and Kaas 1977, Spatz and Tigges 1973).

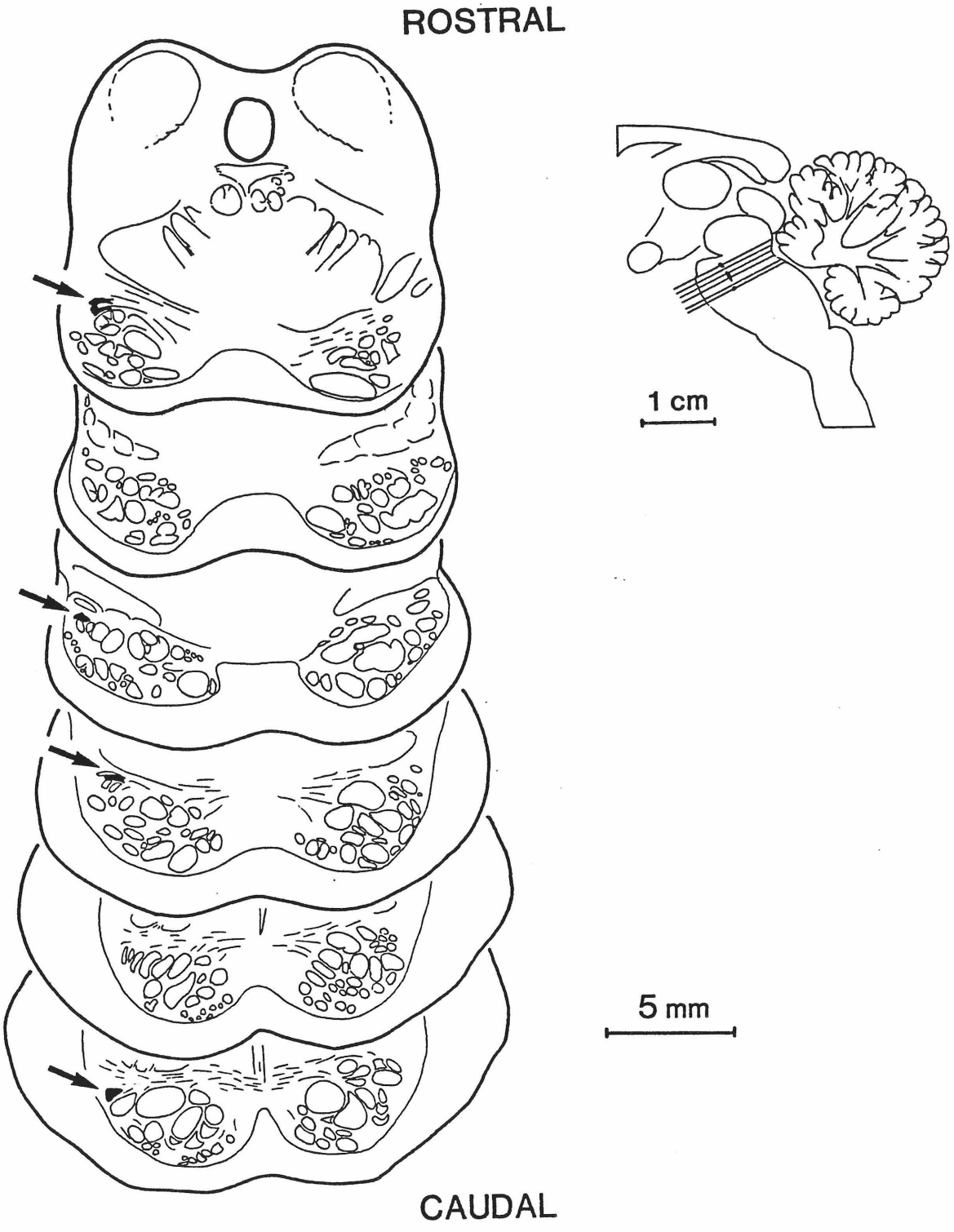
The third diencephalic target of MT is the caudal subdivision of the ventral lateral geniculate nucleus (Olszewski 1952). The caudal subdivision is the portion which does not receive a direct retinal input (Hendrickson et al. 1970). Label was confined to a small part of this subdivision.

The dorsal lateral geniculate (dLGN) was carefully examined for label, but none was found in any case. The dLGN receives a projection from MT in the owl monkey (Graham et al. 1979, Lin and Kaas 1977), but not in the marmoset (Spatz and Tigges 1973). Although a direct projection from the dLGN to extrastriate cortex exists in the macaque (Yukie and Iwai 1981, Fries 1981a), this projection does not include the part of the posterior bank of the superior temporal sulcus where MT is found (Benevento and Yoshida 1981).

Mesencephalon and pons. There was a moderate projection from MT to the ipsilateral superior colliculus. The label was confined to a single patch about 1.5 mm diameter and was primarily in the stratium griseum superficiale, which also receives direct input from the retina and other cortical visual areas (see Rodieck 1979). The position of the label within the superior colliculus was different in each case, and corresponded well with the known topography (Cynader and Berman 1972).

MT also sent a strong projection to the pontine nuclei. Radioactive label was seen in a rostro-caudally oriented column about 500 µm in diameter and 4 mm in length (Fig. 13). The label was not continuous within this column, but was broken into irregular clumps. Clumps of labeled cells are also found in the pontine nuclei following HRP injections of the cerebellum (Brodal 1982). Rostrally the proline was in the lateral part of the nucleus peduncularis and caudally it was near the border between the nucleus lateralis and the nucleus dorsolateralis (Nyby and Jansen 1951). This part of the pontine nuclei is known to receive cortical input primarily from visual cortex (Brodal 1978), and it is this same part of the pons that receives a projection from MT in other primates (Spatz and Tigges 1973, Graham et al. 1979). Projections to this part of the pons have previously been demonstrated by lesions (Glickstein et al. 1980) and ^{3}H-proline injections (Fries 1981b) in the superior temporal sulcus, which, however, were not obviously restricted to MT. The response properties of visual neurons in the pons of the monkey are not known, but in the cat (Baker et al. 1976), visually responsive cells in the pons are almost all direction selective and largely unselective for stimulus form, as are the neurons in macaque MT.

Figure 13. Termination of the projection from MT to the pontine nuclei. An inset shows the level of the sections and the plane of sectioning. Anterogradely transported label was found as small, dense clumps along a rostro-caudally oriented column in the rostro-lateral region of the pontine nuclei.


ROSTRAL
1 cm
5 mm
CAUDAL

DISCUSSION

Hierarchical organization of visual cortex

MT in the macaque has been shown to have a rich set of reciprocal connections with other areas in visual cortex. On the basis of the laminar distributions of connections, we have suggested that these areas consist of at least four and perhaps as many as six which send forward projections to MT, three which receive forward projections from MT and one which appears to be intermediate. The idea that forward and feedback projections can be differentiated on the basis of laminar distributions is certainly not new (Tigges et al. 1977, Jones and Wise 1977, Kaas et al. 1977, Rockland and Pandya 1979, Van Essen et al. 1982a). There are two major points we wish to emphasize here. Firstly, there is now sufficient evidence to support this as a strong principle of cortical organization in primates. Secondly, it is possible, using these relationships as objective anatomical criteria, to delineate a well-defined hierarchical order among a large number of visual areas.

Ideally, the validity of laminar distributions for assigning relative positions should be tested by comparing assignments based on these distributions with those indicated by other, independent, criteria. One relationship which is suggested by independent criteria is that V1 occupies a lower level in the processing of visual information than all extrastriate areas. This assertion is strongly supported by several arguments. In primates, V1 is clearly the main recipient of the geniculo-cortical projection (Wilson and Cragg 1967), and sends output to extrastriate cortex (Cragg 1969, Zeki 1969). While there are alternate routes to extrastriate cortex through direct geniculate projections (Yukie and Iwai 1981) and the colliculo-pulvinar pathway, these are not as influential on extrastriate responses as input from V1. For example, they do not sustain responses in V2 when V1 is inactivated (Schiller and Malpeli 1977). In contrast, inactivation of V2 affects, but does not eliminate, the responsiveness of the majority of neurons in V1 (Sandell and Schiller 1981). On the

basis of this, and the relatively simple response properties of its neurons, V1 can be considered to occupy a primary position in the visual cortex of primates (although this may not be the case in other species, e.g. the cat).

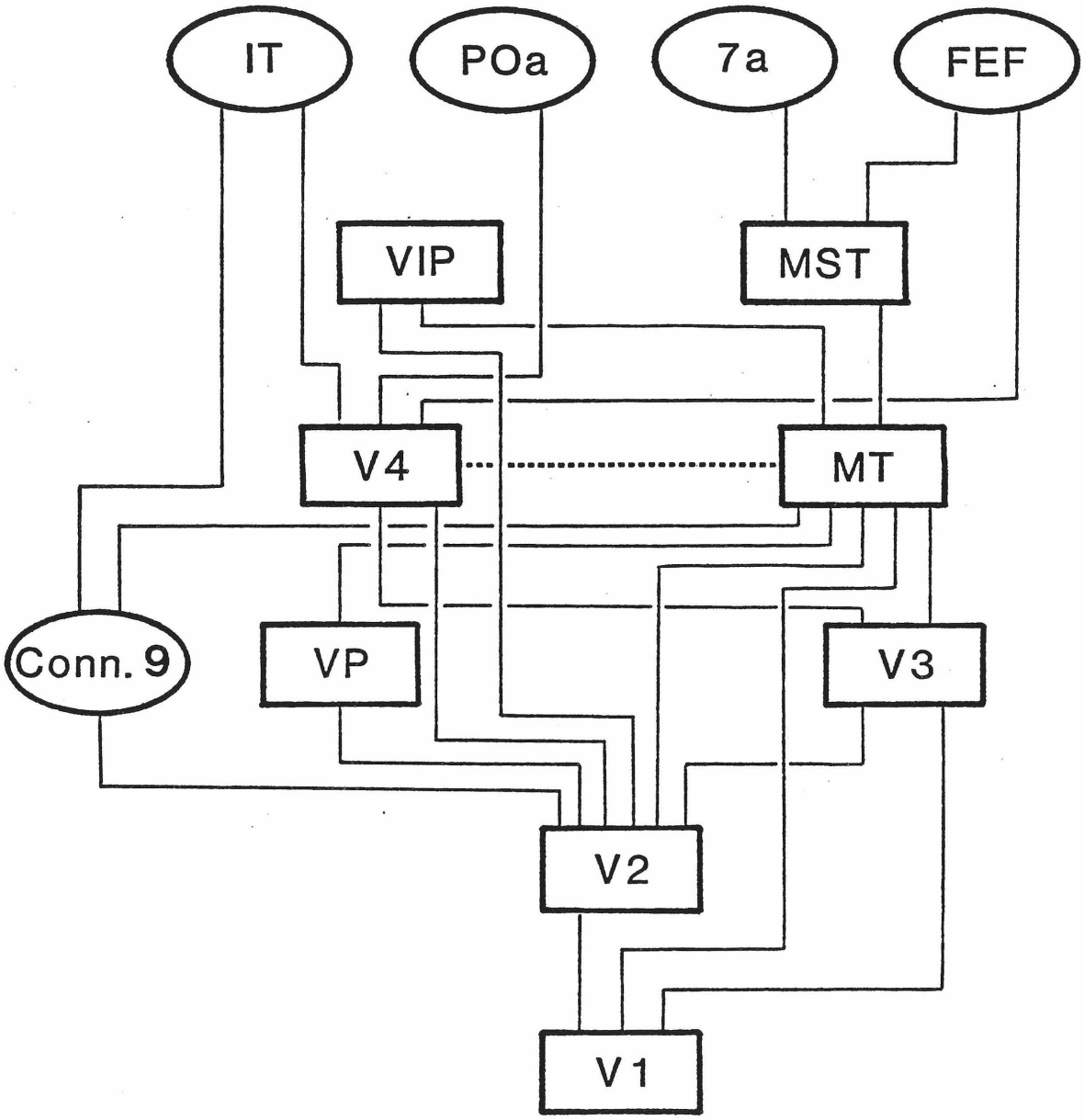
Another relationship which is suggested on the basis of independent criteria is that V2 represents a lower stage of processing than other extrastriate areas. V2 receives a substantial input from V1 (Cragg 1969, Zeki 1969), which occupies the lowest position among the cortical areas. Its neurons also have the smallest receptive fields in extrastriate cortex (Van Essen and Zeki 1978), making it unlikely to receive substantial excitatory drive from extrastriate cortex. While arguments can be made for other relationships among the cortical visual areas, none is as compelling as the two mentioned. Thus, if laminar distributions are an accurate indication of rank among visual areas, they should describe a hierarchy in which V1 is below V2 which in turn is below the remaining areas.

The vast majority of cortical projections from V1 originates in the supragranular layers (including IVb) with a much smaller contribution from the infragranular layers (Rockland and Pandya 1979, Maunsell et al. 1980, Lund et al. 1981). These projections terminate most densely in layers IV, III and II of V2, V3, and MT (Rockland and Pandya 1979, Weller and Kaas 1978, Montero 1980). The reciprocal projections from these areas to V1 originate in the supra- and infragranular layers and terminate outside the granular layers of V1 (Rockland and Pandya 1979, Lund et al. 1981). The projections of V2 to V3, V4, VP, and MT terminate mainly in layers IV and III. Feedback projections from MT (and unspecified locations in area 19) avoid layer IV in V2 (present study, Rockland and Pandya 1979). The laminar distributions of these connections support the general hypothesis that forward projections originate mainly or exclusively in supragranular layers and terminate mainly in layers IV and III, and that feedback projections arise in substantial degree from infragranular layers and terminate predominantly outside layer IV. Within this general structure, there may be some variation in the precise distribution of label (see Fig. 6).

Two observations on the available data add further support to this premise. The first is that if, within a reciprocal pathway, one projection has a distribution that implies it is forward, the other has a distribution of the feedback type. The second is that the known connections among visual cortex of the macaque show transitivity, so that if area B is forward relative to A, and C is forward relative to B, and if A projects to C, then this projection is also forward. If these two findings were not generally true, there would be major ambiguities in any attempt to assign different areas as higher or lower than others. Because they are, it is possible to order the visual areas into a hierarchy in which each occupies a level above all areas which send it forward projections and below all those from which it receives a feedback projection. This hierarchy is illustrated in Fig. 14, and is based on data from many sources, including the present study (see figure legend). Each visual area is simply assigned to the level immediately above the uppermost level from which it receives a forward projection. Note that the three V1-recipient areas (V2, V3, and MT) are at different levels, with MT surprisingly high.

The uppermost members of this hierarchy are those areas which are known to have some of the most complex response properties (Hyvärinen 1981, Mountcastle et al. 1981, Gross 1972), supporting the idea that this hierarchy of connections corresponds with functional properties. A hierarchical organization does not mean that there is a single direction for the flow of information, since feedback projections are present and visual areas at all levels have connections with subcortical structures. But it does suggest that the cortex respects some ranking in the pattern of connections which might have functional, phylogenetic, or ontogenetic significance. It is also possible that similar hierarchies exist for the cortical areas subserving different sensory modalities, and that hierarchies for different sensory systems could meet at polysensory areas, such as area 7. If this were the case, then cerebral cortex could be described in a single hierarchy of areas.

Figure 14. The hierarchy of cortical visual areas based on the laminar distributions of projection. Each visual area is assigned to the level immediately above the highest area from which it receives a forward projection. Rectangles indicate established visual areas. There are undoubtedly more connections which have not yet been identified, and levels containing two or more areas may ultimately be split. Very weak projections, such as that from V1 to VIP, have been excluded. The dashed line connection MT and V4 reflects the uncertainty in the relationship between them, and a connection from MT to VP has been tentatively included. The connections shown, and the laminar distributions used to assign levels in the hierarchy, are from the present study and other investigations (Cragg 1969, Zeki 1969, 1971, Mesulam et al. 1977, Rockland and Pandya 1979, Desimone et al. 1980, Seltzer and Pandya 1980, Barbas and Mesulam 1981, unpublished observation).


IT
POa
7a
FEF
VIP
MST
V4
MT
Conn. 9
VP
V3
V2
V1

Topographic order of MT connections

The representation of the visual field in MT is not entirely orderly. An electrode penetration through MT may encounter a sequence of receptive fields which deviate from a smooth progression by an amount greater than that accounted for by normal scatter (Van Essen et al. 1981). Yet for all three injections the label in areas with known topographies was in positions corresponding to representations of the part of the visual field found at the injection sites. This suggests that despite the disorder in the topography within MT, its connections obey the widely observed principle of joining representations of the same part of the visual field (see Tigges et al. 1981). Further support for this idea comes from the fact that trans-callosal projections were found only for injection 1, which was the only injection near the representation of the vertical meridian.

However, this does not explain the widespread intrinsic connections of MT, which included connections with distant parts of the area and labeling across the full width of MT. The extent of some of these internal connections makes it unlikely that they are providing a major excitatory drive. It is possible that they serve some role in far-reaching surround inhibitory effects, as have been seen in MT of the owl monkey (J. Allman, personal communication).

Comparisons with other species

MT in the owl monkey (Aotus) is known to have connections with five ipsilateral cortical areas (see Weller and Kaas 1981). The connections of MT with V1 and V2 in this animal clearly correspond to those in the macaque. The dorsolateral area (DL), which lies adjacent to MT in the owl monkey and is in connection with it, may be related to V4 in the macaque (Van Essen et al. 1982a). The correlation between other MT recipient areas in the owl monkey and macaque is not clear.

For the most part, there is good agreement between the subcortical projections of MT in the macaque and owl monkey. However, there are some differences

between the species. In the owl monkey, MT has a weak projection to the magnocellular layers and layer S of the dLGN (Lin and Kaas 1977). Although the dLGN was carefully examined, no such projection was seen in the macaque. MT in the owl monkey also projects to the pretectum (Graham et al. 1979), which was not demonstrated to receive input from MT in the macaque. Finally, MT in the owl monkey does not project to the claustrum, although this projection exists in the macaque.

The afferent and efferent connections of MT in the marmoset (Callithrix) have been examined using lesions and HRP injections (Spatz and Tigges 1972, 1973, Spatz 1975). These connections are consistent in most respects with those of the present study. The arrangement of cortical visual areas in the marmoset is not well known, but MT in this animal has cortico-cortical connections which are likely to be equivalent to those of MT in the macaque (Spatz and Tigges 1972). However, while marmoset MT appears to project to ventral V2, there is no projection further anterior in ventral cortex which could be equated to the projection from MT to ventral visual cortex in the macaque. Furthermore, marmoset MT sends a substantial projection to the frontal eye fields. No such projection has been found in the macaque.

All subcortical projections for MT seen in the macaque were also seen in the marmoset (Spatz and Tigges 1973). Additional subcortical targets of marmoset MT which were not seen in the macaque were the pretectum, and the nucleus subthalamicus of Luys. Finally, faint reciprocal projections to marmoset MT, not demonstrated in the present experiments, arise from the nucleus centralis medialis and paracentralis of the intralaminar group of the thalamus, the claustrum, and the pontine reticular formation (Spatz 1975).

The medial superior temporal visual area

An important result of these experiments has been the demonstration of a projection from MT to the cortex immediately medial to it in the superior temporal

sulcus. The area is known to contain neurons which respond to visual stimuli, and which have direction selectivity much like that in MT (Van Essen et al. 1981). We have called this the medial superior temporal area (MST) and define it as the MT-recipient cortex in the medial part of the superior temporal sulcus which contains a high proportion of direction selective neurons.

Previous anatomical and physiological experiments have demonstrated other connections of MST. HRP labeled cells are found in MST following injections of area 7a (Barbas and Mesulam 1981) or the frontal eye fields (Mesulam et al. 1977). A recent study by Newsome and Wurtz (1981) in alert monkeys suggests that neurons in MST may differ from those in MT in their responses to visual motions caused by eye movements. While the large majority of cells in MT respond similarly to equivalent retinal motions whether they are caused by stimulus or eye movements, many cells in MST respond during smooth eye movements in ways which are not explained by their responses to stimulus movements during stationary fixation. These anatomical and physiological results support the idea that MST may represent a further stage in the processing of motion by the cortical visual system.

Functional considerations of MT connections

The high proportion of neurons in MT which are selective for direction, speed and disparity suggest that it is important in the analysis of visual motion. The anatomical outputs of MT give further insight into how this type of information is used in the nervous system.

MT projects to MST, which is also concerned with motion, and which in turn projects to area 7 (see above). Area 7 has been implicated in certain forms of complex behavior, including "attention" (Mountcastle et al. 1981). MT may provide an important sensory contribution to these functions, since any given stimulus is in general more likely to attract attention if it is moving than if it is stationary.

MT also projects to areas associated with the generation and control of eye movements, notably the superior colliculus and pontine nuclei. The superior colliculus in the macaque is known to contain a motor map of saccades (Schiller and Koerner 1971). The MT-recipient part of the pons gives rise to a substantial projection to the part of the cerebellum around lobule VII (Brodal 1978, 1982), which contained another motor map of eye movements (Ron and Robinson 1973), and also neurons which signal eye speed and retinal slip speed (Suzuki et al. 1981).

As yet there is no evidence for a major input from MT to inferotemporal cortex. This part of cortex has been shown to contain neurons with a high degree of shape specificity (Gross et al. 1972) and is important for visual discrimination of form (see Gross 1972). It would not be surprising if such a connection did not exist, since information from MT would be of little direct value for discrimination of form. The overall pattern of outputs from MT is consistent with the notion that extrastriate cortex contains relatively independent subsystems serving the analysis of motion and form discrimination. Further anatomical studies will be needed to determine whether such a functional segregation actually exists.

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