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Direction and Orientation Selectivity of Neurons in Visual Area MT of the Macaque

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SUMMARY AND CONCLUSIONS

1. We recorded from single neurons in the middle temporal visual area (MT) of the macaque monkey and studied their direction and orientation selectivity. We also recorded from single striate cortex (V1) neurons in order to make direct comparisons with our observations in area MT. All animals were immobilized and anesthetized with nitrous oxide.

2. Direction selectivity of 110 MT neurons was studied with three types of moving stimuli: slits, single spots, and random-dot fields. All of the MT neurons were found to be directionally selective using one or more of these stimuli. MT neurons exhibited a broad range of direction-tuning bandwidths to all stimuli (minimum = 32°, maximum = 186°, mean = 95°). On average, responses were strongly unidirectional and of similar magnitude for all three stimulus types.

3. Orientation selectivity of 89 MT neurons was studied with stationary flashed slits. Eighty-three percent were found to be orientation selective. Overall, orientation-tuning bandwidths were significantly narrower (mean = 64°) than direction-tuning bandwidths for moving stimuli. Moreover, responses to stationary-oriented stimuli were generally smaller than those to moving stimuli.

4. Direction selectivity of 55 V1 neurons was studied with moving slits; orientation selectivity of 52 V1 neurons was studied with stationary flashed slits. In V1, compared with MT, direction-tuning bandwidths were narrower (mean = 68°). Moreover, V1 responses to moving stimuli were weaker, and bidirectional tuning was more common. The mean orientation-tuning bandwidth in V1 was also significantly narrower than that in MT (mean = 52°), but the responses to stationary-oriented stimuli were of similar magnitude in the two areas.

5. We examined the relationship between optimal direction and optimal orientation for MT neurons and found that 61% had an orientation preference nearly perpendicular to the preferred direction of motion, as is the case for all V1 neurons. However, another 29% of MT neurons had an orientation preference roughly parallel to the preferred direction. These observations, when considered together with recent reports claiming sensitivity of some MT neurons to moving visual patterns (39), suggest specific neural mechanisms underlying pattern-motion sensitivity in area MT.

6. These results support the notion that area MT represents a further specialization over area V1 for stimulus motion processing. Furthermore, the marked similarities between direction and orientation tuning in area MT in macaque and owl monkey support the suggestion that these areas are homologues.

INTRODUCTION

In primates and other mammals, there are several extrastriate visual areas, each of which contains a systematic representation of the contralateral visual field. The suggestion has been made that each of these areas is specialized for the analysis of some basic feature of the visual stimulus, such as motion, color, or size (6, 22, 28, 38, 65, 75).

In macaques, the most extensively studied of the extrastriate visual areas has been area MT. This area lies along the posterior bank of the superior temporal sulcus (17, 64, 66, 70). It contains a topographic representation of the contralateral visual field (17, 66) and

receives direct projections from V1 and V2 (33, 37, 64, 66, 73). Area MT has a high incidence of neurons sensitive to stimulus motion and an apparent lack of sensitivity to other stimulus properties, such as color or form (3, 34, 66, 71). MT neurons are organized into cortical columns of similar direction selectivity (3, 10).

In the present experiment, we have examined some of the ways in which area MT is specialized for motion processing relative to primary visual cortex. Can the high degree of motion sensitivity in area MT be simply the result of an input exclusively or primarily from motion-sensitive neurons in V1? Are there any significant transformations of motion sensitivity between V1 neurons and those in area MT? To examine these questions, we compared the response properties of single MT neurons with those of V1 neurons using identical stimulus conditions.

METHODS

Animal preparation and maintenance

Eight male *Macaca fascicularis* weighing between 4 and 5 kg were each recorded 8–10 times over a 4- to 8-week period. During recording, animals were immobilized and anesthetized with nitrous oxide. The surgical preparation and recording procedures were similar to those described in an earlier report (3).

Recording

Varnish-coated tungsten microelectrodes with exposed tips of 10 μm or less were used to record extracellular potentials from single isolated cells. In four animals, cells in area MT were sampled along microelectrode penetrations entering nearly normal to the cortical surface of MT. To accomplish this, the electrodes were angled 30° from vertical in the parasagittal plane passing dorsoanteriorally to ventroposteriorally. These penetrations passed through the lateral surface of area 7 and through the anterior bank of the superior temporal sulcus before reaching area MT. In all four animals, recordings were confined to the cortex representing an area of the visual field within ~20° of the center of gaze.

In another four animals, cells in area V1 were sampled from a region on the dorsolateral cortical surface within the representation of the central 7° of the lower contralateral visual field. In these animals, the penetrations were made vertically in the frontal plane.

In both MT and V1, single neurons were recorded at ~200-μm intervals along each penetration. Spikes were determined to be arising from an isolated single neuron if they were of constant amplitude and waveform.

Visual stimulation

Visual stimuli were presented on a rear-projection tangent screen subtending 60 × 60° with a background luminance of 2 cd/m^2. Stimulus intensity was ~1.5 log units above background intensity. Once a cell was isolated, several observations were made before rigorous quantitative testing was begun. These observations were made using a hand-held tungsten filament projector and an audio monitor of single-unit activity. First, the optimal values of parameters, such as stimulus size, contrast, and speed of motion, were estimated monocularly for each isolated unit. The optimal stimulus was then used in each eye separately to measure receptive-field size and to make a preliminary estimate of preferred direction of motion and tuning range.

A quantitative study of unit properties was then carried out with the assistance of a PDP-11/34A computer testing only the eye yielding the strongest driven activity. The computer controlled stimulus presentation and accumulated spikes for peristimulus time histograms. Stimuli were presented by an optical bench fitted with x- and y-axis mirror galvanometers, a stepping motor controlled rotation device, and an electronic shutter.

The moving stimuli were of three types: *1)* moving slit (MSL). These stimuli always extended several degrees beyond the borders of the receptive field. The optimal width was determined by hand testing and generally ranged from 0.25 to 1°. *2)* Moving spot (MSP). These stimuli were single small squares, and the optimal size was estimated by hand testing. A maximum width of 0.5° was used. *3)* Moving random-dot field (MRD). These stimuli were projected from a high-contrast black-and-white 35-mm slide and subtended a visual angle of 40 × 30°. The dots in the pattern varied from 0.25 to 1° diameter with a density of 40%. Some cells were also tested with similar stimuli presented on an X-Y CRT display (HP1300A) centered on the receptive field and subtending a visual angle of 15 × 15°. The dots in this pattern varied from 0.10 to 0.25° diameter with a density of 5%. The results were identical to those obtained with the projected random-dot stimuli.

All moving stimuli were presented at the speed that was estimated to be optimal with hand testing. The single slits and spots were swept 30° across the tangent screen along a path centered on the neuron's receptive field. Each of the three types of moving stimuli was presented in 16 directions of motion with equal deviations between directions (22.5°). The same 16 directions were used for all tests on all neurons. Each test consisted of a series

of 5 pseudorandomly interleaved presentations of each direction.

Stationary flashed slits (SSL) were used to test orientation selectivity. These stimuli always extended several degrees beyond the receptive-field borders. For each neuron, the stimulus dimensions were identical to those used for the moving-slit test. These stimuli were positioned within the receptive field such that they elicited the maximum response for each orientation. Each stimulus was flashed on in eight orientations with equal deviations between orientations (22.5°). The same eight orientations were used for all tests on all neurons. Each test consisted of a series of five pseudorandomly interleaved presentations of each orientation.

Most neurons were studied for at least 2–3 h. Some neurons, however, became injured or poorly isolated during the course of testing. For this reason, we were unable to apply all tests of direction and orientation tuning to every neuron.

Data collection

Intertrial intervals for all moving and stationary stimuli were a minimum of 3 s. The spontaneous firing rate was estimated from periods immediately preceding the onset of each stimulus (equal to 50% of the stimulus presentation interval). Peristimulus time histograms were displayed continuously throughout the collection of data and updated during each new trial. Averaged spike rates and various trial-by-trial statistics were also available on-line.

The data were subsequently subjected to a more extensive off-line computer analysis. For moving stimuli, the measure of response used was the average spike rate in a narrow time window centered around the peak response for each direction of motion. The size of this window was adjusted to correspond roughly to the width of the receptive field along its narrowest measured axis (to compensate for asymmetries in receptive-field width). The analysis was also performed using the peak firing rate as a measure of response. Generally, the results were very similar for the two measures but the peak response is far more sensitive to random variations. For stationary stimuli, the measure of response was the average spikes per second during the stimulus exposure.

Histology

At the end of the 4- to 8-week recording period, each animal was anesthetized with an overdose of pentobarbital sodium and perfused with saline followed by 10% buffered formalin. The brain was then photographed and allowed to sink in sucrose formalin. The MT brains were sectioned at 30° forward of the frontal plane, and V1 brains were sectioned in the frontal plane. Sections were cut at 33 μm and alternate sections were stained with cresyl violet or a Gallyas silver myelin stain (16). The position of area MT within the superior temporal sulcus was determined from the myeloarchitectonic boundaries seen in serial sections. The locations of recording sites were determined on the basis of several small electrolytic lesions (4 μA, 20 s) made on each penetration.

RESULTS

We carried out a quantitative analysis of the responses of 110 isolated MT neurons on 18 penetrations in four animals. To make quantitative comparisons with the properties of neurons in V1, we also studied 58 isolated V1 neurons recorded along 13 penetrations in four animals. The results will be presented in the following order. First, the incidence of direction and orientation tuning among MT neurons will be reported. Second, the relationship between optimal axis of motion and optimal orientation of single MT neurons will be examined. These results will be used as the basis for a distinction between two types of MT neurons. Third, we will report the direction- and orientation-tuning characteristics of MT neurons. Finally, we will compare the direction- and orientation-tuning characteristics of MT neurons with those of V1 neurons.

Incidence of direction and orientation tuning in MT

All of the 110 MT neurons studied had receptive-field centers within the central 20° of the visual field. These recording sites were located within the region of the superior temporal sulcus where dense myelination extends from the bottom of layer III to layer VI, almost totally obscuring the two prominent bands of Baillarger that characterize the cortex lateral to MT. One-hundred and nine neurons were tested with moving stimuli and all were found to give directionally selective responses (i.e., they did not respond uniformly to all directions of motion) to at least one of the three types of moving stimuli used in this experiment. Of those MT neurons tested quantitatively with a moving slit, 100% (99) were directionally selective. Of those tested with a single moving spot, 93% (77 of 83) were found to be directionally selective. The six neurons that failed to respond selectively to the moving spot were all found to

be selective for the moving slit. Of those tested with a moving random-dot pattern, 100% (38) were found to be directionally selective. Strength of response, optimal direction of motion, and optimal orientation were always very similar when tested through either eye. An example of a direction-tuning curve obtained from an MT neuron is shown in Fig. 1.

Of the 89 MT neurons that were tested for sensitivity to stimulus orientation with stationary flashed stimuli, 74 (83%) were found to be selective for orientation. About two-thirds of the orientation-tuned neurons exhibited transient responses. An example of this type of tuning is shown in Fig. 2. These neurons often responded selectively to both the onset and the offset of the stimulus with "on" and "off" responses tuned to the same orientation. The remaining orientation-tuned neurons exhibited fairly sustained responses throughout the stimulus exposure, although there was usually a decrement of response rate following an initial burst. An example of this type of tuning is shown in Fig. 3. Thirty-five percent (26) of the orientation-tuned neurons exhibited suppression of activity below the spontaneous level when the stimulus was in the "null" orientation (90° out of phase from the preferred orientation).

We began the quantitative analysis of direction selectivity by fitting smooth functions to the direction-tuning data. Tuning curves were fitted with a Gaussian function of the following type

$$r_i = a + be^{-0.5((x_i - x_0)/s)^2}$$

where a represents the minimum firing rate, b represents the difference between the maximum and minimum firing rate, x_0 represents the preferred direction of motion, s represents the standard deviation of the fitted Gaussian, and r_i represents the firing rate for a stimulus moving in direction x_i. The best-fitting Gaussian function was determined for each tuning curve by an iterative least-squared-residuals algorithm. The Gaussian provided

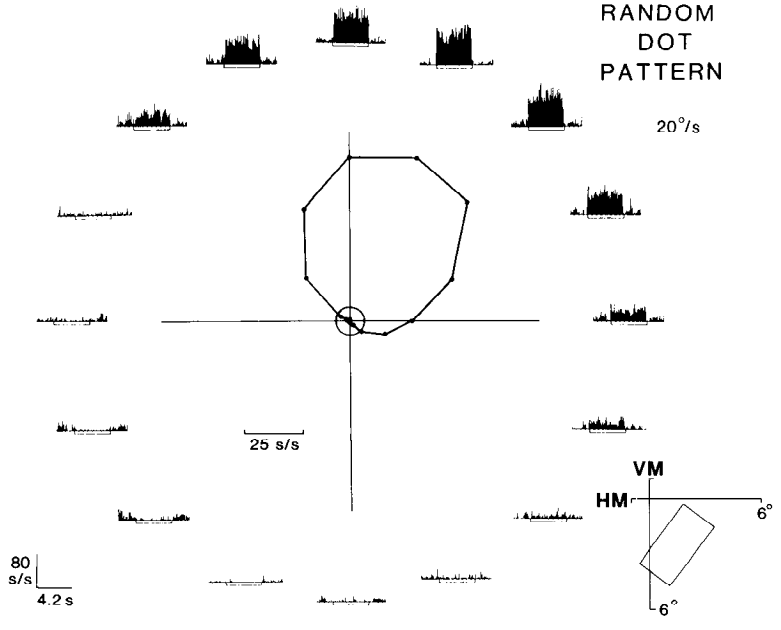


FIG. 1. Example of direction tuning of a typical MT neuron. Individual histograms represent responses summed over 5 trials to each of 16 directions of motion of a random-dot pattern moving at 20°/s. Line beneath each histogram indicates period of time during which stimulus was moving through receptive field (shown at lower right). In center, response for each direction is plotted on a polar graph. Radial axis represents response (measured as spikes per second), the polar axis represents direction of stimulus motion, and small circle represents level of spontaneous activity. Marked suppression of activity in direction 180° away from optimal is characteristic of many MT neurons. VM, vertical meridian, HM, horizontal meridian.

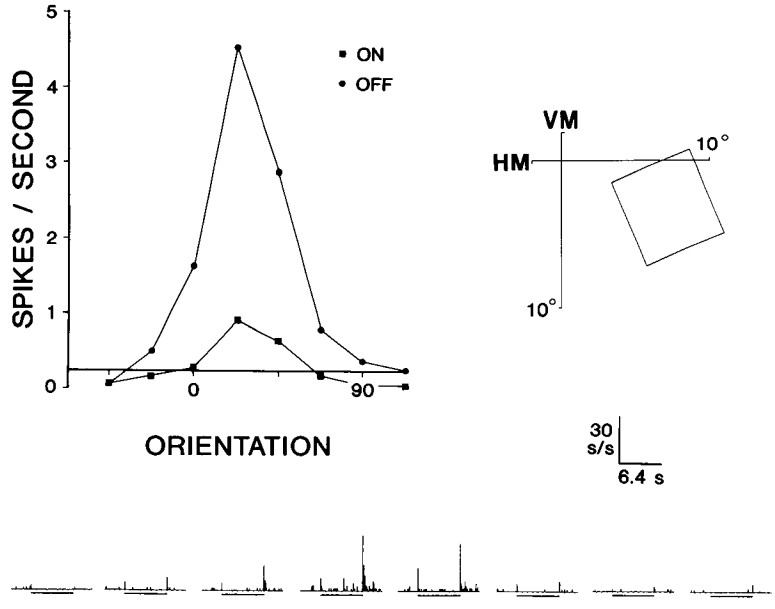


FIG. 2. Tuning of an MT neuron to orientation of a stationary flashed slit. This neuron exhibited a small transient "on" response and a larger "off" response. Histograms at bottom represent responses to 5 trials for each of 8 orientations. Both "on" and "off" responses are plotted as a function of orientation on graph at upper left. Horizontal line represents level of spontaneous activity. Receptive field is shown at upper right. See also legend to Fig. 1.

an excellent fit to nearly all tuning data. It has the further advantage of being parametric (not true of a "hand-drawn best fit") and also reduces "noise" in the curve (characteristic of methods based on linear interpolation). The Gaussian method was used pri-

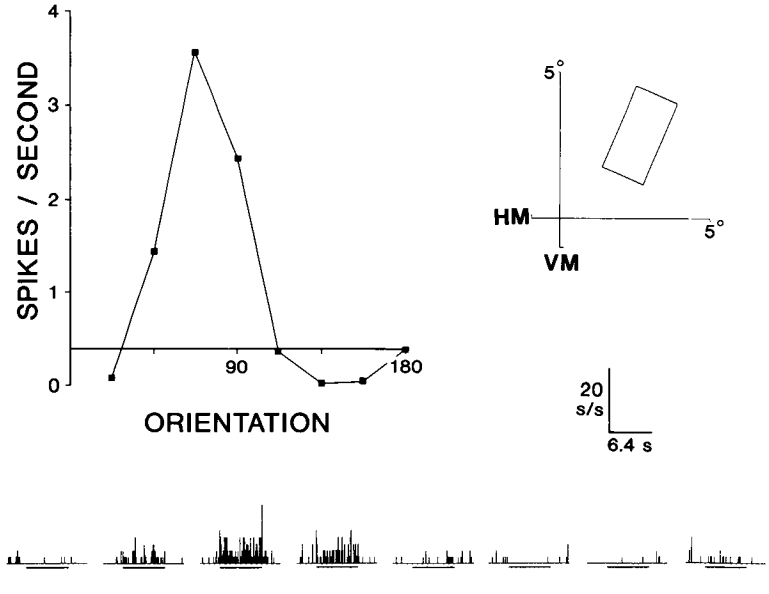


FIG. 3. Tuning of an MT neuron to orientation of a stationary flashed slit. This neuron exhibited a sustained response during stimulus exposure. See also legends to Figs. 1 and 2.

marily because it provides a relatively unbiased estimate of the optimal stimulus value, i.e., the peak of the curve (x_0).

The quantitative analysis of orientation selectivity was also begun by fitting Gaussian functions to the tuning data using the same procedure outlined above for direction-tuning data.

Relationship between optimal direction of motion and optimal orientation

We examined the angular difference between optimal direction of motion (measured with a single spot or random-dot field) and the optimal orientation (measured with a stationary-flashed slit) for each of the 61 MT neurons that exhibited selectivity to both and for which we could make precise assessments of the optimal values. If a neuron had an orientation preference that was precisely perpendicular to the preferred direction of motion, the difference measure was assigned a value of 0°. If the orientation preference was parallel to the preferred direction of motion, the difference was assigned a value of 90°. The distribution of these difference measures, plotted in Fig. 4, is clearly bimodal. Using χ^2 tests, we found that both of the peaks in Fig. 4 differ significantly from a uniform distribution (peak 1: $\chi^2 = 22.3$, df = 1, $P < 0.001$; peak 2: $\chi^2 = 6.0$, df = 1, $P < 0.025$). Neurons for which the difference measure was less than 30° (near perpendicular) were classified as type I. Neurons for which the difference measure was greater than 60° (near parallel) were classified as type II. Sixty-one percent (37) of the neurons were classified as type I and 29% (18) as type II, as shown in Fig. 4. Direction- and orientation-tuning data from a type I neuron are shown in Fig. 5 and data from a type II neuron are shown in Fig. 6.

Sixty-one percent (11) of the type II neurons exhibited a direction preference for the moving slit that was quite similar to the direction preference for the moving-spot or random-dot field. The results shown in Fig. 6 exemplify this type of relationship. For the remaining type II neurons, however, the direction tuning for the moving slit was bimodal with preferred directions roughly symmetrical about the single preferred direction for the moving spot and intermediate between the preferred direction for the moving spot and the preferred orientation for the stationary slit. An example of this relationship is shown in Fig. 7. A few neurons (6), which were tested with a moving slit but not with a stationary slit, also exhibited this type of bimodal tuning to the moving slit. Because they behaved in a manner that was characteristic only of cells that were selective for orientation parallel to the preferred direction of motion, these neurons were also classified as type II.

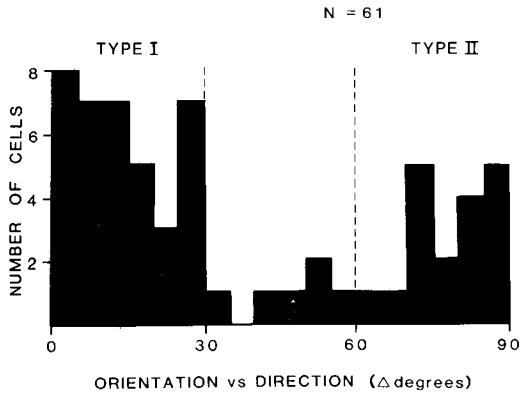


FIG. 4. Distribution of angular difference between optimal direction of motion and optimal orientation. Differences of 0° reflect an orientation preference that is perpendicular to preferred direction of motion. Differences of 90° reflect an orientation preference that is parallel to preferred direction of motion. Type I MT neurons (61%) are defined as those that have an optimal orientation roughly perpendicular to preferred direction of motion, i.e., a difference measure of less than 30°. Type II neurons (29%) are defined as having an optimal orientation roughly parallel to preferred direction of motion, i.e., a difference measure greater than 60°. Proportion of cells in these 2 groups differs significantly from a uniform distribution. Cells with difference measures between 30 and 60° (10%) were not classified as type I or II.

Because the properties of type I and II neurons may reflect a significant functional specialization, we will examine them separately in the analysis that follows.

Quantitative analysis of direction and orientation tuning in MT

We used three measures to quantify the direction-tuning characteristics of MT neurons. The first measure, tuning bandwidth, is the full width of the tuning curve at one-half of its maximum height. The second measure, differential response magnitude, is the difference between the observed maxi-

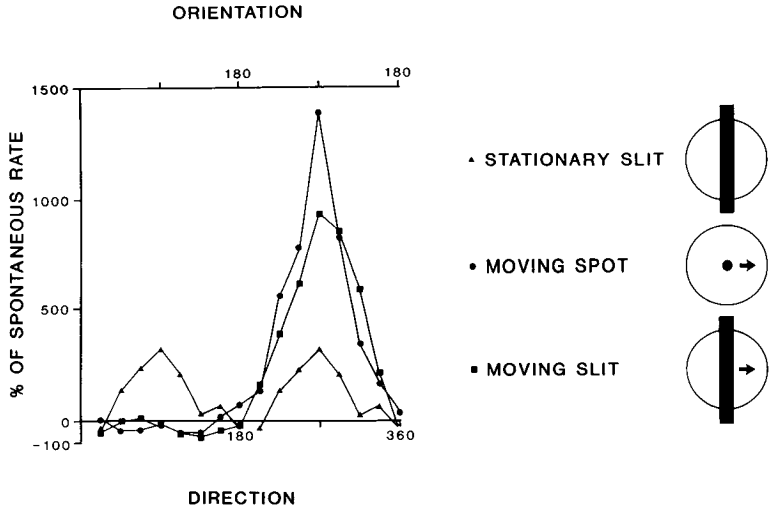


FIG. 5. Relationship between direction and orientation tuning that is characteristic of type I MT neurons. Responses (percent of spontaneous rate) are plotted on graph at left as a function of direction (lower axis) for moving stimuli and as a function of orientation (upper axis) for stationary stimuli. Direction tuning for moving spot is indicated by circles and that for moving slit is indicated by squares. Orientation tuning for stationary slit is indicated by triangles and 2 cycles are plotted to facilitate comparison with direction tuning. Alignment of peaks for moving and stationary stimuli reflects an orientation preference that is perpendicular to preferred direction for both types of moving stimuli. This relationship is illustrated schematically at right.

mum and minimum responses. The final measure, index of directionality (DI), reflects the ratio of response strength in the preferred direction relative to that in the opposite direction. This index is computed by the formula (6)

$$DI = 1 - \left(\frac{\text{opposite response}}{\text{preferred response}}\right)$$

High values indicate a tendency toward unidirectionality, and low values indicate a tendency toward bidirectionality. Derivation of the three measures is illustrated in Fig. 8.

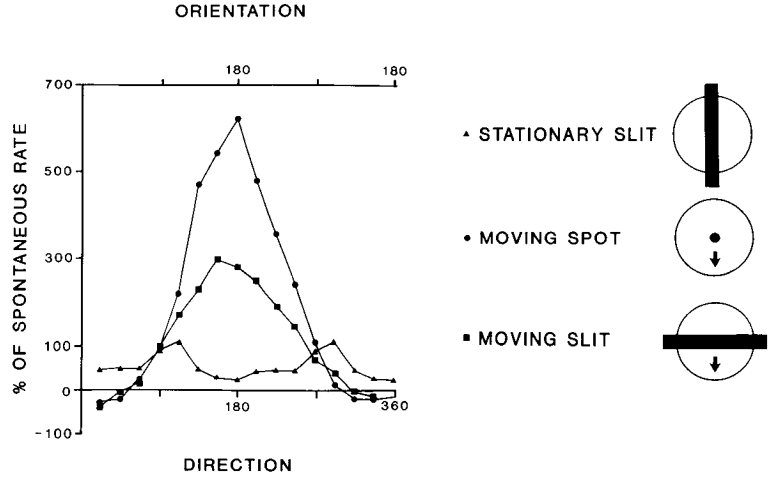


FIG. 6. Relationship between direction and orientation tuning that is characteristic of some type II MT neurons. Direction tuning for moving spot is similar to that for moving slit. Optimal orientation for stationary slit is shifted ~90° away from optimal direction of motion. This relationship, reflecting an orientation preference that is parallel to direction preference, is illustrated schematically at right. See also legend to Fig. 5.

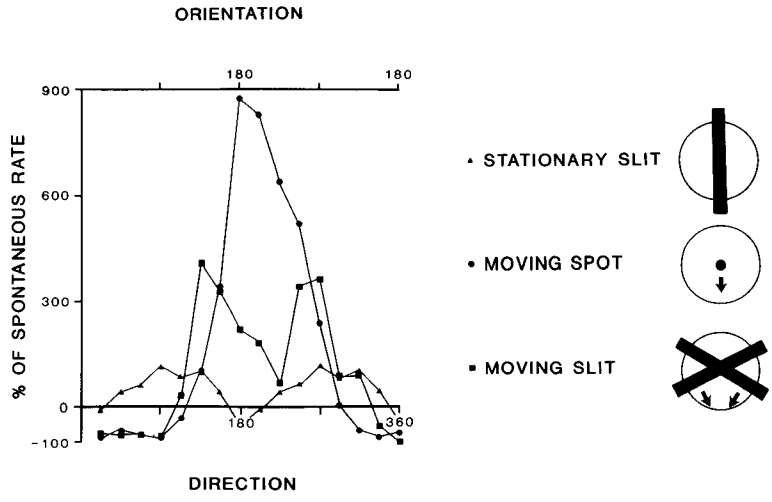


FIG. 7. Relationship between direction and orientation tuning that is characteristic of some type II MT neurons. Orientation preference for stationary slit is shifted ~90° away from optimal direction for moving spot, reflecting an orientation preference parallel to preferred direction. Direction tuning curve for moving slit indicates 2 preferences that are symmetrical about single moving-spot preference and intermediate between moving-spot and stationary-slit preferences. These unusual relationships are illustrated schematically at right. See also legend to Fig. 5.

The first two of these three measures, tuning bandwidth and differential response magnitude, were also used to quantify the orientation-tuning characteristics of MT neurons. The quantitative analysis of orientation tuning is reported for "on" responses only. For most neurons, the optimal orientation and tuning bandwidth of the "off" response were similar to those of the on response.

The tuning bandwidth and directionality index measures used here are basically dependent on ratios of responses to different stimuli and are, consequently, relatively insensitive to the manner in which response is

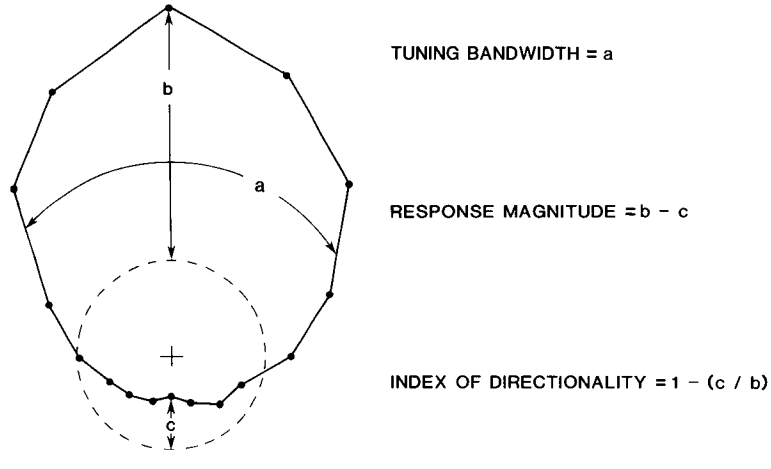


FIG. 8. Derivation of quantitative tuning measures. At left is a polar plot of a direction tuning curve. Broken line represents spontaneous activity level. Tuning bandwidth, a, is defined as full width of curve at a height one-half of distance between maximum and minimum responses. Differential response magnitude is difference between maximum (b) and minimum (c) response. Index of directionality is equal to 1 − (c/b). See also legend to Fig. 1.

measured. The response magnitude, an absolute measure, is more susceptible to variability resulting from the manner in which it is obtained from different neurons. Specifically, variations in the size of the time window over which the response is averaged will introduce some variability. This is particularly a problem when comparing stimuli presented differently, such as stationary vs. moving stimuli, or when comparing different populations of neurons with different receptive-field sizes. Nonetheless, most of the response magnitude differences reported below were robust and large enough to suggest general trends.

In the remainder of this section, we will describe results obtained by applying the three quantitative measures. First, we will compare the responses of MT neurons to the three types of moving stimuli. Second, we will report the analysis of orientation-tuning characteristics and make comparisons to direction tuning.

Statistical analyses of the three quantitative measures were performed by analysis of variance and Fisher's Z for significance of correlation. The results of this analysis for both direction and orientation tuning are summarized in Table 1.

DIRECTION TUNING.

Bandwidth. Figure 9 shows three examples of direction-tuning curves illustrating the range of variation for tuning bandwidth. The sample distributions for the three types of moving stimuli (slits, single spots, and random-dot fields) are shown in Fig. 10. Tuning for the single moving spot was significantly broader than that for the slit (MSP: mean = 105°, MSL: mean = 91°, $P < 0.01$) or for the random-dot field (MRD: mean = 83°, $P < 0.01$). The moving slit and random-dot

TABLE 1. *Mean tuning bandwidths, response magnitudes and directionality indices for areas MT and V1*

	Moving Slit (MSL)				Moving Spot (MSP)		Moving Random Dot (MRD)		Stationary Slit (SSL)			
	MT		V1		MT		MT		MT		V1	
Bandwidth, deg	I	83	Sim	70	I	105	I	78	I	65	Sim	54
	II	112	Cpx	68	II	121	II	96	II	69	Cpx	50
	Tot	91	Tot	68	Tot	105	Tot	83	Tot	64	Tot	52
	MT: MSP > MSL = MRD > SSL											
	V1: MSL > SSL											
Response Magnitude, s/s	I	21.6	Sim	7.0	I	16.4	I	17.3	I	4.5	Sim	9.5
	II	26.4	Cpx	6.7	II	32.4	II	22.9	II	8.8	Cpx	6.3
	Tot	19.9	Tot	7.1	Tot	19.0	Tot	18.1	Tot	5.8	Tot	9.2
	MT: MSL = MSP = MRD > SSL											
	V1: MSL = SSL											
Directionality Index	I	0.90	Sim	0.56	I	0.96	I	1.01				
	II	1.14	Cpx	0.48	II	1.07	II	1.20				
	Tot	1.00	Tot	0.55	Tot	0.98	Tot	1.05				
	MT: MSL = MSP = MRD											

Significant differences ($P < 0.05$) between cell types and between areas are indicated by brackets. Significant differences ($P < 0.05$) between effects of different stimuli are indicated by ">." Totals (Tot) for MT include types I, II, and unclassified cells. Totals for V1 include simple (Sim), complex (Cpx), and unclassified cells. Stationary-slit measures are for "on" responses only.

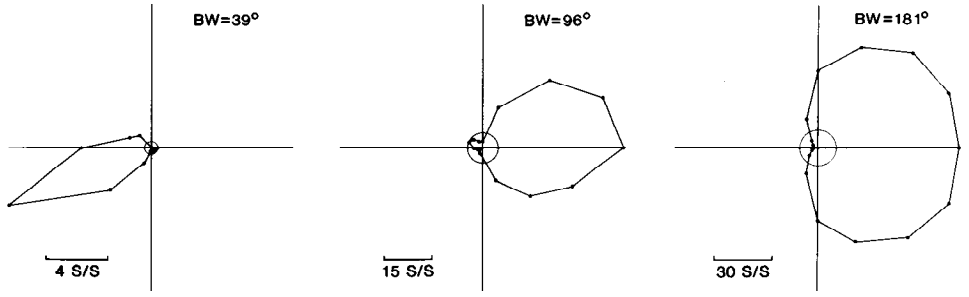


FIG. 9. Range of variation of direction-tuning bandwidth is illustrated by tuning curves obtained from 3 different MT neurons. Full-width half-maximum measures of tuning bandwidth are indicated for each curve. Direction-tuning bandwidth of center curve is representative of average for MT neurons. Stimulus for each curve shown here was a moving slit. See also legend to Fig. 1.

tuning bandwidth did not differ significantly.

The coefficient of correlation between measures obtained with these different stimuli provides an indication of whether or not there is any systematic relationship between the effects of the different stimuli on single neurons. There was a low but significant positive correlation between moving slit and moving random-dot bandwidth ($r = 0.36$, $P < 0.05$). Tuning bandwidth for the moving spot was uncorrelated with either that for the moving slit or that for the moving random-dot field. The lack of correlation between the moving spot and the other two stimuli may reflect a greater population variability in selectivity of MT neurons to very small stimuli, such as the single spot.

The moving-slit tuning bandwidths were significantly broader for type II than for type I cells (I: mean = 83°, II: mean = 112°, $P < 0.01$). Type I and II cells exhibited similar tuning bandwidths for the moving spot and the moving random-dot field.

Response magnitude. The sample distributions for response magnitude for the three types of moving stimuli are shown in Fig. 11. The responses to all three stimulus types were of similar magnitude (MSL: mean = 19.9 s/s, MSP: mean = 19.0 s/s, MRD: mean = 18.1 s/s), indicating a similar sensitivity to these different types of moving stimuli.

There were also highly significant positive correlations between the response magnitudes obtained from single neurons for all three types of moving stimuli. The magnitude of a neuron's response to a moving slit is generally very predictable from that to a moving spot ($r = 0.84$, $P < 0.01$) and less so from that to a moving random-dot field ($r = 0.48$, $P < 0.01$). Responses of single neurons to moving spots were also well correlated with those elicited by a moving random-dot field ($r = 0.62$, $P < 0.01$).

Responses of type II neurons were slightly stronger for all three stimulus types. The difference was largest for single moving spots (I: mean = 16.4 s/s, II: mean = 32.4 s/s), but none of the differences was statistically significant.

Index of directionality. Figure 12 shows three examples of MT direction-tuning curves illustrating the range of variation for the index of directionality. Neurons ranged from strongly unidirectional, with almost complete suppression of spontaneous activity in the null direction (high index values) to nearly bidirectional (low index values). The sample distributions for the three types of moving stimuli are shown in Fig. 13. All three distributions are tightly clustered around 1.0, indicating an average tendency for unidirectional excitation with no inhibition in the null direction (MSL: mean = 1.00, MSP: mean = 0.98, MRD: mean = 1.05).

The similarity among these three sample distributions is complemented by the similarity among directionality index measurements taken from single neurons. Strength of directional selectivity for moving slits was positively correlated with that for moving spots ($r = 0.38$, $P < 0.01$) and for moving random-dot fields ($r = 0.55$, $P < 0.01$). Likewise, there was a significant positive correla-

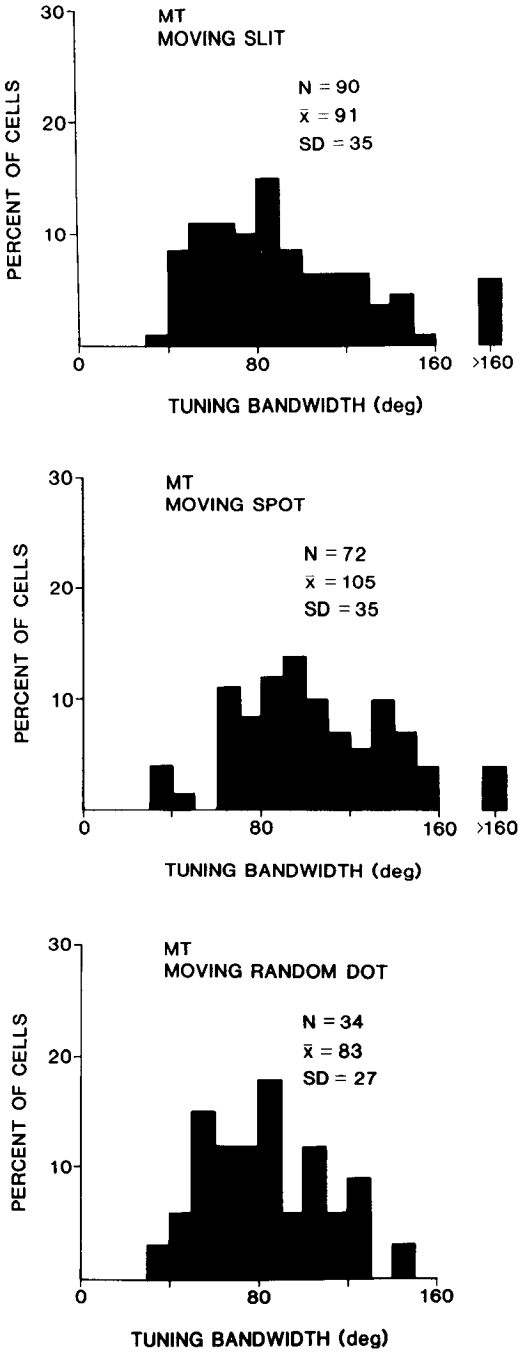


FIG. 10. Distributions of direction tuning bandwidth measure for moving slit (top), moving spot (center), and moving random-dot field (bottom) for neurons in area MT.

tion between directionality index measures for moving spots and random-dot fields ($r = 0.57$, $P < 0.01$).

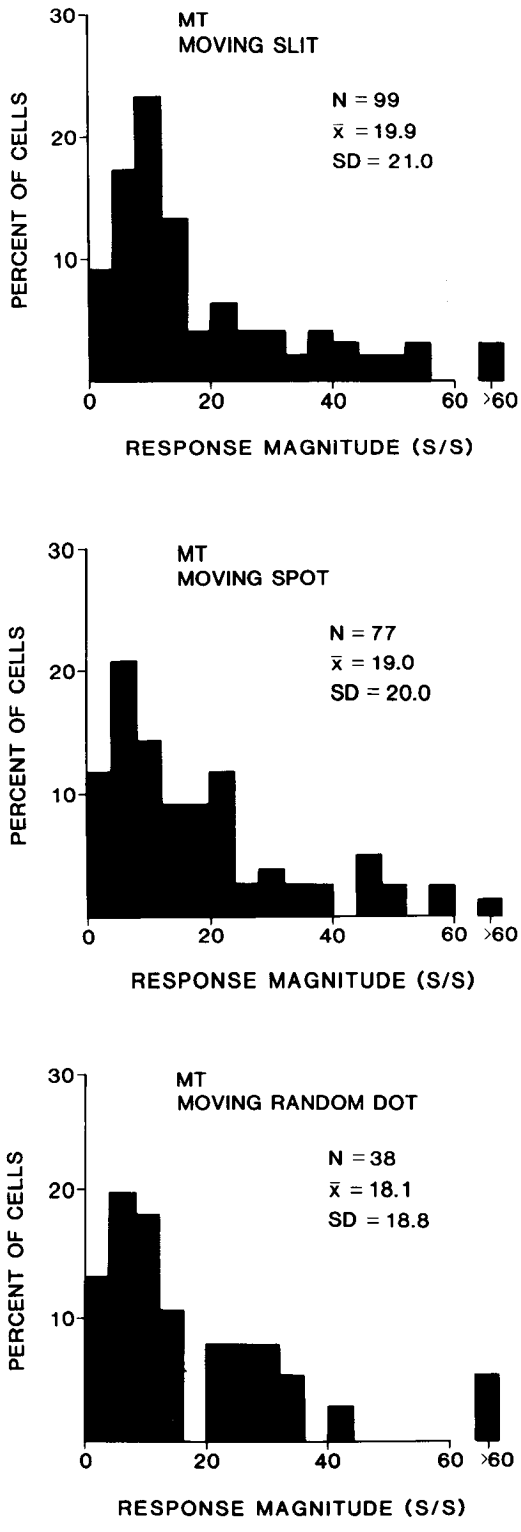


FIG. 11. Distributions of response magnitude measure for moving slit (top), moving spot (center), and moving random-dot field (bottom) for neurons in area MT.

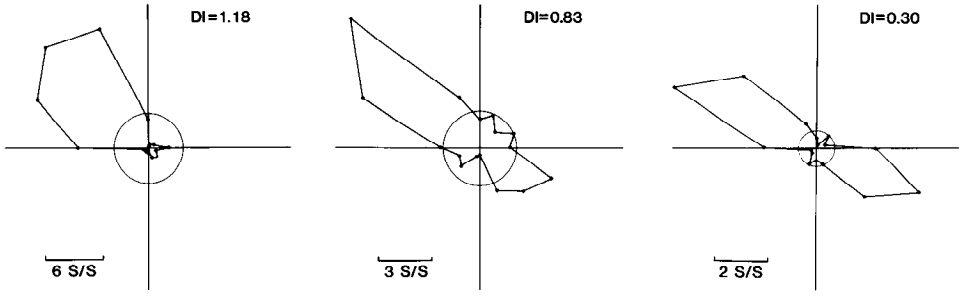


FIG. 12. Range of variation of direction selectivity along preferred axis of motion is illustrated by tuning curves obtained from 3 different MT neurons. Index of directionality, a measure of direction selectivity, is indicated for each curve. Average index of directionality for MT neurons (1.00) falls between strongly unidirectional curve at left and directionally biased curve at center. Stimulus for each curve shown here was a moving slit. See also legend to Fig. 1.

On the average, type II cells were slightly more directionally selective for all three moving stimuli than were type I cells. Moving spot directionality index values for type II cells were significantly larger than those for type I cells (I: mean = 0.96, II: mean = 1.07, $P < 0.05$). A similar difference was seen for moving slits (I: mean = 0.90, II: mean = 1.14, $P < 0.05$).

Summary. In summary, MT neurons exhibited a broad range of direction-tuning bandwidths to all stimuli, with slightly broader tuning to single moving spots. MT neurons gave strong unidirectional excitatory responses of similar magnitude to all three stimuli. Type II neurons were more broadly tuned to moving slits and yet more directionally selective for both moving slits and single spots than were type I neurons.

COMPARISON OF ORIENTATION AND DIRECTION TUNING IN MT. The tuning characteristics of MT neurons to moving and stationary oriented stimuli were compared using the tuning bandwidth and response magnitude measures.

Bandwidth. The distribution of orientation-tuning bandwidths ("on" responses only) is shown in the top of Fig. 14. The mean bandwidth, 64°, is nearly 30° narrower than the mean direction-tuning bandwidth for the moving slit (MSL: mean = 91°, $P < 0.001$). Moreover, orientation- and direction-tuning bandwidths (moving slits) for single MT neurons were not significantly correlated ($r = -0.02$).

The orientation-tuning bandwidths of type I and II MT neurons did not differ significantly.

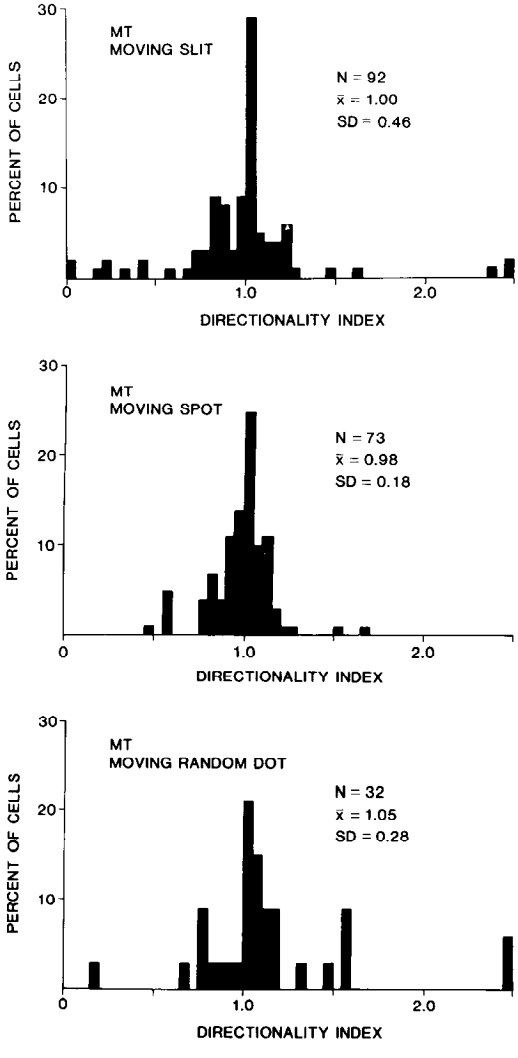


FIG. 13. Distributions of directionality index measure for moving slit (top), moving spot (center), and moving random-dot field (bottom) for neurons in area MT.

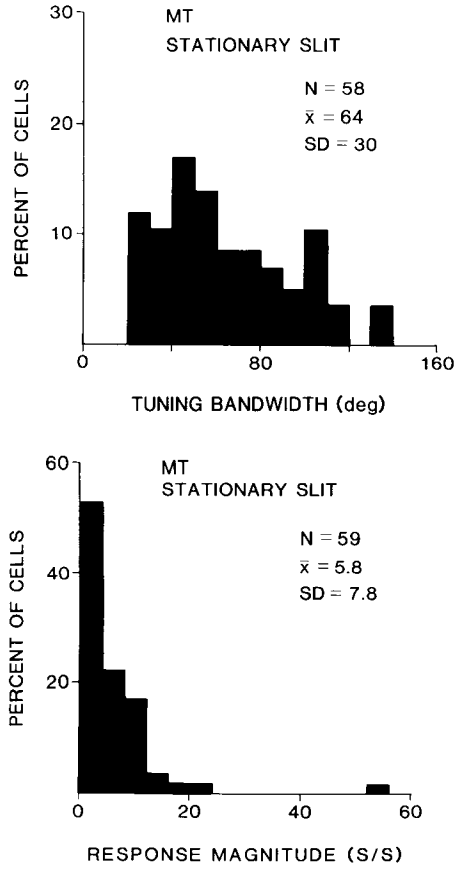


FIG. 14. Distributions of orientation-tuning bandwidth (top) and response magnitude (bottom) for stationary flashed slit ("on" response only) for neurons in area MT.

Response magnitude. The distribution of response magnitudes for stationary oriented stimuli is shown in the bottom of Fig. 14. The mean response magnitude, 5.8 s/s, is less than one-third of the mean response magnitude for the moving slit (MSL: mean = 19.9 s/s, $P < 0.001$). Although the magnitude of this difference partially reflects the fact that many MT responses to stationary stimuli were transient, the peak responses to flashed stimuli were usually also smaller than those to moving stimuli.

There was a positive correlation between response magnitude for the moving slit and response magnitude for the stationary slit (MSL: $r = 0.66$, $P < 0.01$). The moving spot response magnitude was also highly correlated with that for the stationary slit (MSP: $r = 0.73$, $P < 0.01$).

The response magnitudes of type I and II MT neurons did not differ significantly.

Summary. In summary, stationary orientation-tuning bandwidth among MT neurons was much narrower than that for moving stimuli. Responses to stationary-oriented stimuli were smaller than those to moving stimuli.

Comparison of direction and orientation tuning in areas V1 and MT

Eighty-nine percent (49 of 55) of the sampled V1 neurons were selective for the axis of motion of a moving slit. All of these neurons had at least a small bias toward one direction of motion along the perferred axis. All but one (51 of 52) of the sampled neurons were selective for the orientation of a stationary slit. This single neuron was selective for the axis of motion of a moving slit.

V1 neurons were classified as either simple or complex type using conventional criteria (13, 27, 48). These criteria are *1*) spatial arrangement of light excitatory and light inhibitory zones, *2*) sensitivity to stimulus speed, *3*) receptive-field size, and *4*) spontaneous activity level. Sixty-two percent of the sampled neurons were classified as simple and 33% as complex on the basis of these criteria. The remaining 5% were not classified.

We will first compare direction tuning in V1 with that in MT. Second, we will compare orientation tuning in V1 and MT. Third, we will compare the differences between the responses elicited by moving- and stationary-oriented stimuli in V1 with those in MT. Direction- and orientation-tuning characteristics of V1 neurons were quantified by means of the tuning bandwidth, response magnitude, and index of directionality (direction tuning only) measures described above. The quantitative results of these analyses are summarized in Table 1.

V1 AND MT: DIRECTION TUNING. The distribution of direction-tuning bandwidths for single V1 neurons is plotted in the top of Fig. 15. This distribution overlaps that for MT (see Fig. 10); however, the mean direction-tuning bandwidth for a moving slit is significantly narrower than that in MT (V1: mean = 68°, MT: mean = 91°, $P < 0.001$).

The distribution of V1 response magnitude

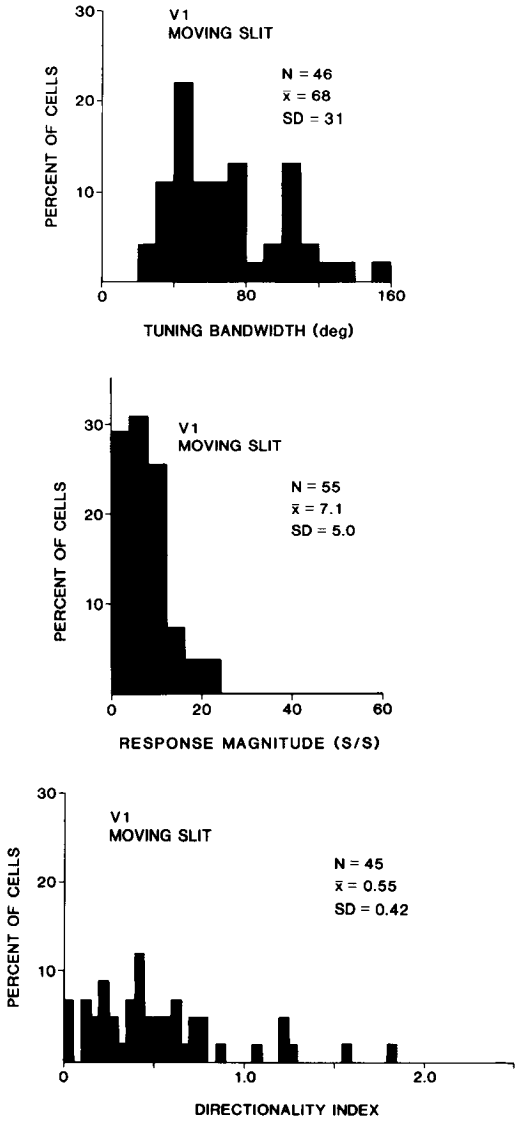


FIG. 15. Distributions of the moving-slit direction-tuning bandwidth (top), response magnitude (center) and directionality index (bottom) for neurons in area V1.

to moving stimuli is plotted in the middle of Fig. 15. Once again, this distribution has considerable overlap with that for MT neurons (see Fig. 11). On the average, however, responses to moving stimuli were significantly weaker in V1 (V1: mean = 7.1 s/s, MT: mean = 19.9 s/s, $P < 0.001$). This difference does not appear to be a simple effect of receptive-field size, because responses to moving stimuli were always averaged over the time that the stimulus was within the receptive field.

Finally, the distribution of the index of directionality for V1 neurons is plotted in the bottom of Fig. 15. This measure was more variable for V1 than for MT (see Fig. 13). Moreover, the mean of the distribution is significantly lower than that for MT neurons (V1: mean = 0.55, MT: mean = 1.00, $P < 0.001$) reflecting a greater tendency toward bidirectionality among the population of V1 neurons.

In summary, a quantitative comparison of the direction-tuning characteristics of V1 and MT neurons revealed that *1*) MT neurons are more broadly tuned for direction of motion than are V1 neurons; *2*) responses of MT neurons to moving slit stimuli are stronger than the responses of V1 neurons to the same stimuli; and *3*) MT neurons are more directionally selective along a preferred axis of motion, whereas V1 neurons tend more toward bidirectionality.

V1 AND MT: ORIENTATION TUNING. The distribution of orientation-tuning bandwidths for V1 neurons is plotted in the top of Fig. 16. When compared to MT, we find that orientation-tuning bandwidth in V1 has a similar distribution (see Fig. 14). On the average, however, tuning bandwidth in V1 was significantly narrower than that in MT (V1: mean = 52°, MT: mean = 64°, $P < 0.05$). The orientation-tuning bandwidth distributions of V1 simple and complex type cells did not differ significantly (simple: mean = 54°, complex: mean = 50°).

The distribution of V1 response magnitudes for stationary-oriented stimuli is plotted in the bottom of Fig. 16. Although responses in V1 are often larger than those in MT (see Fig. 14) (V1: mean = 9.2 s/s, MT: mean = 5.8 s/s), these differences are not statistically significant.

In summary, a quantitative comparison of the orientation-turning characteristics of V1 and MT neurons has revealed that *1*) V1 tuning bandwidth for stationary-oriented stimuli is slightly narrower than that in MT; and *2*) V1 responses to stationary stimuli are similar in magnitude to those elicited from MT neurons.

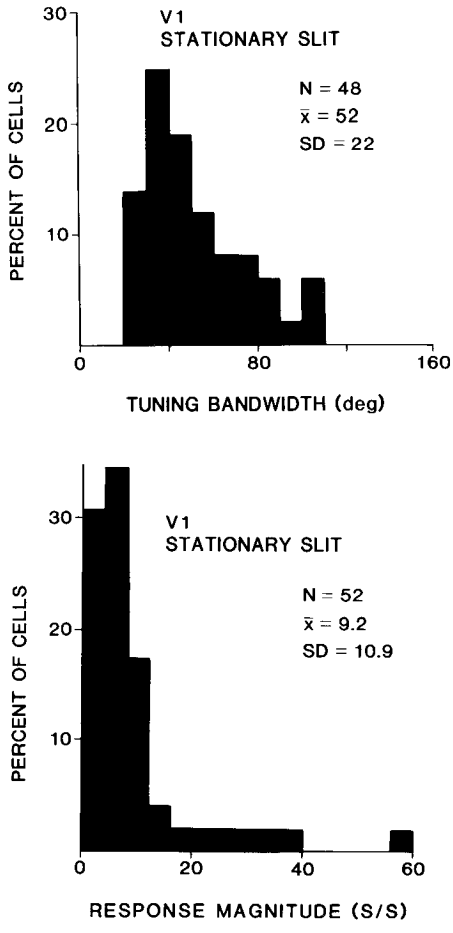


FIG. 16. Distributions of orientation-tuning bandwidth (top) and response magnitude (bottom) for stationary-flashed slit ("on" response only) for neurons in area V1.

V1 AND MT: RESPONSES TO MOVING AND STATIONARY STIMULI. The relationship between orientation- and direction-tuning bandwidth in V1 was similar to that in MT in two respects. First, as was the case for MT neurons, V1 orientation-tuning bandwidth was significantly narrower than direction-tuning bandwidth for moving stimuli (SSL: mean = 52°, MSL: mean = 68°, $P < 0.01$). Second, there was no significant correlation between direction- and orientation-tuning bandwidth for single neurons in either area, suggesting some independence of the mechanisms underlying these selectivities.

The relationship between the magnitude of responses to stationary and moving stimuli in V1 differed from that in MT. In area MT, responses to moving stimuli were significantly stronger than those to stationary-oriented stimuli. In contrast, the V1 neurons responded slightly but not significantly more to stationary-oriented stimuli than to moving stimuli (SSL: mean = 9.2 s/s, MSL: mean = 7.1 s/s). As in MT, the response magnitudes of single neurons in V1 to stationary-oriented stimuli were correlated with those to moving stimuli ($r = 0.55$, $P < 0.01$).

Finally, the preferred axis of motion of V1 neurons was always found to be roughly perpendicular to the preferred orientation for stationary stimuli. They were, in this respect, similar only to the type I MT neurons and different from the type II MT neurons.

DISCUSSION

In this experiment, we examined direction and orientation tuning of single neurons in area MT of macaques. The results confirm previous reports that the large majority of MT neurons are selective for the direction of stimulus motion (3, 15, 34, 66, 71, 75). However, in contrast to the results of earlier studies of macaque MT (71, 75), we have demonstrated that most neurons (83%) are also selective for the orientation of stationary-flashed stimuli. This finding agrees with recent reports (6, 77) of a high incidence of orientation selectivity in owl monkey MT. The combined testing of orientation selectivity and direction selectivity with multiple stimulus types in the present study has revealed the existence of at least two types of MT neurons. Type I neurons exhibit an orientation preference for stationary-flashed slits that is roughly perpendicular to the optimal direction of motion for moving stimuli. Type II neurons, on the other hand, exhibit an orientation preference that is roughly parallel to the optimal direction of motion. The analysis with different stimulus types has also demonstrated that some aspects of the direction tuning of MT neurons are insensitive to changes in stimulus form. Finally, we have demonstrated a number of ways in which MT neurons differ from those in V1 with regard to direction and orientation tuning.

The remainder of this discussion will consider *1*) the results of previous studies of macaque MT, *2*) evidence for homology be-

tween macaque MT and MT in other primate species, *3*) the significance of the two types of directionally selective MT neurons, *4*) the effect of stimulus form in determining the direction tuning of MT neurons, and *5*) the transformation of direction and orientation selectivity from V1 to MT.

Comparison with other studies of area MT

Maunsell and Van Essen (34, 35) have recently completed a detailed study of the response properties of neurons in macaque MT. These experiments differed from our own in that they were performed primarily with binocular stimulation and did not include an extensive study of the effects of two-dimensional patterned stimuli, such as single small spots or random-dot fields. The results of their study, however, are similar to our own in a number of respects.

Maunsell and Van Essen (34) present an average direction-tuning curve for their sample of MT neurons. Applying our criteria to this curve results in a direction-tuning bandwidth for a moving slit of ~65–70°. The difference between this measure and our own (91°) may be due to different methods of calculating the mean as well as their use of binocular stimulation. Their reported mean index of directionality (0.932) is quite similar to our own (1.00, Student's t test, $P > 0.1$).

In contrast to early studies (71, 75), both our own experiments and those of Maunsell and Van Essen found a high incidence of orientation selectivity among macaque MT neurons (83 and 77%, respectively). Maunsell and Van Essen, like ourselves, noted that responses to stationary flashed slits were often transient, and off responses were often seen. Again, applying our tuning-bandwidth measure to their mean orientation-tuning curve yields a figure somewhat narrower than ours (~30–40° vs. 64°), again possibly reflecting an effect of binocular stimulation or different methods of measurement and calculation.

Maunsell and Van Essen (34) report the existence of neurons with an orientation preference parallel to the direction preference. They attribute these observations to "the effect of combining random fluctuations in the separate measurements of preferred direction and orientation" and suggest that the incidence of parallel selectivity does not differ significantly from chance. However, we found that the relationship between optimal orientation and direction for MT neurons was stable during retesting. Furthermore, the frequency of neurons with an orientation preference roughly parallel to the preferred direction of motion was found to be significantly greater than that expected on the basis of random probability ($\chi^2 = 6.0$, df = 1, $P < 0.025$).

Relation to MT in other species

There are several lines of evidence for homology between MT in the macaque and MT in new world primates, particularly the owl monkey. These include similarity of anatomic connections (11, 20, 21, 29, 31–33, 37, 46, 52–59, 62–64, 66, 68–70), visual topography (5, 17, 66), architectonics (5, 17, 64, 66), and physiological response properties (3, 6, 15, 34, 35, 66, 71, 72, 75). However, Zeki (77) has argued that the differences between MT in the macaque and that in the owl monkey are as striking as the similarities. The "differences," according to Zeki, are a higher incidence of orientation selectivity, a broader range of binocular interactions, and greater stricture of the stimulus requirements necessary to evoke a response from owl monkey MT neurons when compared to those in macaques. The present study and that of Maunsell and Van Essen (34) provide further support for a homology with owl monkeys by demonstrating an equally high incidence of orientation selectivity in macaque MT. In a recent study of disparity tuning, Maunsell and Van Essen (35) have also observed a high incidence of binocular interactions in macaque MT, reducing the purported species differences even further. Furthermore, in response to Zeki's claim, Baker et al. (6) report that "a wide variety of nonoptimal stimuli evoked vigorous responses" from owl monkey MT neurons.

Additional evidence in support of a homology now arises from the finding of similarities among the quantitative response properties of macaque and owl monkey MT. Baker et al. (6) recently surveyed the properties of neurons in several extrastriate visual areas of the owl monkey. The stimulus types were identical to those used in the present study. The reported incidence of direction and orientation selectivity for owl monkey

MT is very similar to that in the macaque monkey. Furthermore, many owl monkey MT neurons, like those in macaques, respond strongly to moving random-dot fields and single small spots.

Although Baker et al. (6) used a somewhat different measure of tuning bandwidth, their results for moving stimuli are similar to our own. They report direction-tuning bandwidth for a single moving spot to be significantly broader than that for a moving slit. We have also found this to be the case in macaques. Mean responses to the three moving stimuli are, like those in macaque MT, of similar magnitude (~15 s/s) and are similar to our own (~19 s/s). The final measure for moving stimuli, index of directionality, is significantly smaller, on the average, for owl monkeys (mean = 0.806) than for macaques (mean = 1.00, Student's t test, $P < 0.05$) indicating a weaker tendency toward unidirectionality in the owl monkey.

The reported incidence and strength of selectivity for orientation in owl monkey MT is also similar to that which we have observed in macaques. Baker et al. report transient but tuned on and off responses. As in macaques, orientation-tuning bandwidth is often narrower for stationary flashed slits than for moving slits. Mean response magnitude is also much weaker for stationary stimuli (9.35 s/s) and similar to that in macaques (5.8 s/s).

There are several possible explanations for the discrepancy between recent quantitative studies of macaque and owl monkey and the earlier studies of Zeki. These include *1*) differences between the criteria used to define area MT (Zeki used patterns of callosal degeneration and visual topography, whereas more recent studies have used myeloarchitectonic criteria); *2*) differences in anesthesia (Zeki used barbiturate anesthesia; most other studies have used nitrous oxide or ketamine); and *3*) differences between the procedures used to collect and analyze data (Zeki's observations were basically qualitative). It is also difficult to compare Zeki's observations with our own because details of stimulus presentation are rarely reported (e.g., 71, 77).

In summary, recent experiments provide further support for a homology between owl monkey and macaque MT by demonstrating a high degree of similarity, both with regard to the incidence of neurons with qualitatively similar response properties and with regard to the quantitative aspects of these properties. Although there are some physiological differences between MT in these species, such as the larger receptive fields and greater local scatter in the visuotopic representation characteristic of macaque MT (5, 17, 66), it appears that the similarities far outweigh these differences.

Type II MT neurons and pattern-motion detection

In area V1 and elsewhere, visually responsive neurons are selective for orientations that are roughly perpendicular to their optimal direction of motion. Type II MT neurons, in contrast, are selective for orientations roughly parallel to their optimal direction of motion. They are, in this respect, unlike motion-sensitive neurons at any earlier stage in the primate visual system. Are these neurons merely anomalous or do they play some special role in the analysis of visual motion? Movshon et al. (39) have recently demonstrated that a small proportion of MT neurons are sensitive to the motion of patterns independent of the motion of oriented components within those patterns. Is it possible that these pattern-motion detectors and our type II MT neurons represent a single class of neurons within area MT? In the following section, we will present two different models of local neural circuitry that can account for sensitivity to pattern motion and we will demonstrate how the unusual properties of type II MT neurons can be explained as emergent properties of these mechanisms. The difference between the two models lies in whether or not they rely on prefiltering for orientation, i.e., whether or not it is essential to extract information about the motion of oriented components in a pattern in order to derive pattern-motion information.

ORIENTATION-DEPENDENT MODEL. The determination of pattern motion from many oriented component-motion detectors may be approached with the "velocity-space combination rule" proposed by Adelson and Movshon (1). This is illustrated by the example in Fig. 17. Each contour in a moving pattern has an apparent motion, as seen through an aperture, consistent with a set of

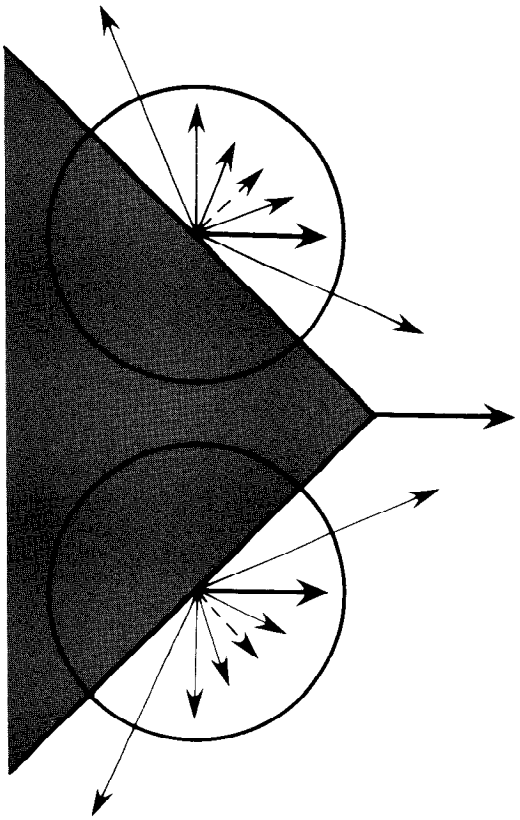


FIG. 17. "Velocity-space rule" solution to problem of extracting pattern motion (1). A simple two-dimensional pattern is formed from 2 oriented contours. Pattern has a direction and speed of motion indicated by velocity vector drawn at apex. When viewed through apertures (circles), each oriented contour appears to move along axis perpendicular to its orientation (dashed-line vector). Motion of each contour is consistent with a family of motions (a "velocity space" represented by set of velocity vectors associated with each contour) of pattern in which they are embedded. Direction and speed of motion of pattern can be determined by "intersection" of velocity-space vectors for each of 2 contours, i.e., single speed and direction of motion that is simultaneously consistent with motion of both oriented contours (indicated by bold vector for each contour).

possible speeds and directions of the entire pattern. This set is a "velocity-space" and is unique for each contour. The velocity of the pattern is uniquely determined by the velocity-space "intersection," i.e., the single direction and speed of motion that is simultaneously consistent with the motion of all of the oriented components.

The neural circuitry required to solve the pattern-motion problem after prefiltering for orientation is likely to be complex. Adelson and Movshon (1) have suggested that an implementation might involve computation of "the weighted combination of signals arising from a collection of one-dimensional motion analyzers having different velocity preferences." Ideally, the input to a pattern-motion detector that is velocity sensitive would arise from detectors for all possible component orientations. Each of these orientation detectors must also be speed selective. The speed selectivity of each orientation detector in the input population must equal the apparent speed of motion of a component of the same orientation when it is embedded in a pattern moving at the optimal velocity for the pattern-motion detector.

How does this model of neural circuitry behave under the stimulus conditions we have used to study MT neurons? Both the single moving spot and the random-dot field contain some energy in many orientations, which is sufficient to activate oriented component-motion detectors. Thus these stimuli will activate many of the set of component-motion detectors that specifies uniquely, and therefore activates a single pattern-motion detector.

If an oriented contour appears to be stationary when it is embedded within a moving pattern, then the pattern must be moving along the axis of orientation of the stationary contour. Thus the only stationary orientation detectors that can provide input to a pattern-motion detector are those selective for orientations that are parallel to the preferred direction of motion for the pattern-motion detector. The predicted optimal orientation for a stationary slit is therefore parallel to the predicted optimal direction of motion for a two-dimensional pattern. This relationship is one of the defining characteristics of type II MT neurons.

Similarly, if the speed of motion of a moving slit is identical to the optimal speed for a moving pattern, then the optimal direction of motion for the slit will also be identical to that for the pattern. At lower speeds, however, there will be two optimal directions of motion. These two directions correspond to the two directions of motion for contours moving at this lower speed that are uniquely compatible with the velocity preference of the pattern-motion detector. They will be

symmetrical about the optimal direction of motion for a pattern, and their separation will be proportional to

$$\cos^{-1}\left(\frac{\text{stimulus speed}}{\text{optimal speed}}\right)$$

This property, namely that direction selectivity for a moving slit is bimodal and symmetrical about the preferred direction for a moving spot, is also characteristic of some type II MT neurons.

NONORIENTATION-DEPENDENT MODEL. An alternative model for derivation of pattern motion does not require prefiltering for orientation. This solution amounts to tracking the motion of small unoriented subunits of the pattern. The motion of any subunit alone will be equivalent to the motion of the pattern.

The local circuitry required for the neural implementation of this alternative solution is based on what is known of the neural circuitry underlying "purely directional" neurons in the retina, which were first studied by Barlow and his colleagues (7), although the mechanisms were formalized much earlier by Hassenstein and Reichardt (25). In general terms, these directionally selective mechanisms incorporate lateral connections between subunits, which have spatially adjacent receptive fields (7, 25, 45, 60). Direction selectivity is generated through lateral inhibitory interneurons that are time delayed and asymmetric. Motion from the receptive field of one subunit to another along the direction of the lateral inhibitory operators will result in net suppression of the postsynaptic neuron, whereas motion in the opposite direction will result in excitation. Similar properties can be generated by complementary excitatory lateral interneurons.

The extension of this type of neural circuitry to a large two-dimensional array will yield directionally selective output with some properties that are not intuitively obvious. We have, therefore, formalized a model based on this type of local circuitry and performed a computer simulation of its output behavior under the various stimulus conditions used in our study of MT neurons (2).

The model is composed of a rectangular array of subunit neurons with circular unoriented receptive fields (Fig. 18). The output

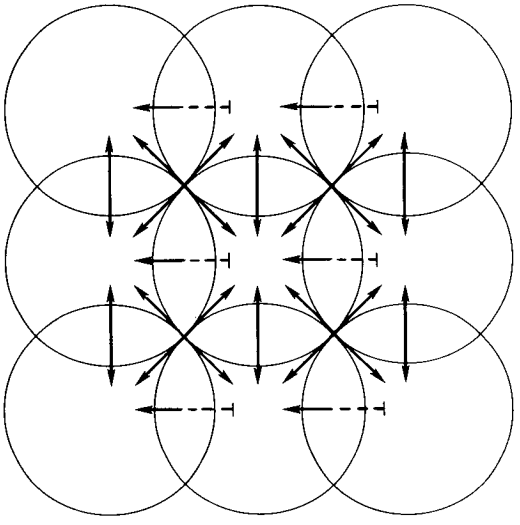
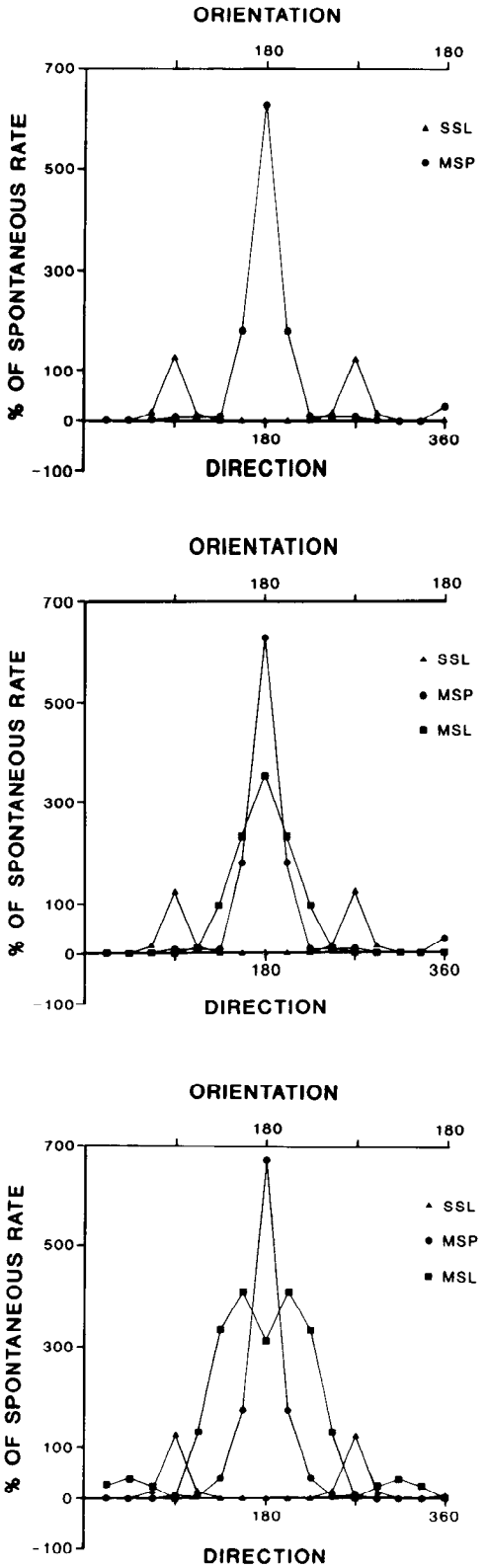


FIG. 18. Schematic representation of a neural mechanism for implementation of a pattern-motion detector relying on unoriented input. This mechanism requires lateral inhibitory neurons that are asymmetric and time delayed. It is formed by extension of a model of Barlow and Levick (7) type to 2 dimensions. Circles represent receptive fields of subunit neurons and aggregation of these fields represents receptive field of postsynaptic directionally selective neuron. There are time-delayed inhibitory interneurons (bold arrows) from each subunit neuron to all but 1 of adjacent subunits (dashed lines). Like simpler one-dimensional case, this model is normally most sensitive to motion in single direction where there are no lateral inhibitory interneurons, i.e., to right in this arrangement.

of each subunit neuron acts on the postsynaptic directionally selective neuron, and the output magnitude is proportional to the area of the receptive field that is stimulated by light. Each subunit neuron has eight neighboring neurons with directly adjacent receptive fields. Time-delayed inhibitory interneurons extend in the direction of seven of the eight neighboring neurons, i.e., there are lateral inhibitory connections in all directions except one. The inhibitory connections are made onto the postsynaptic neuron (the directionally selective neuron) near the output of the adjacent neurons. Thus they have the potential to nullify the excitatory effect of the adjacent neurons (presynaptic inhibition would also be functionally equivalent to this scheme). This potential decays with time and with the distance over which the lateral interaction takes place. The consequences of this arrangement are similar to those described above for two neurons. Movement



in the direction of any inhibitory lateral connection will not result in a net excitation of the postsynaptic neuron. Movement in the single direction with no inhibitory connection does result in excitation, i.e., a directionally selective response.

The effects of simulated stimulation with a moving spot are straightforward. The output is maximal when the stimulus is moving in the direction in which there are no lateral inhibitory connections (Fig. 19, top).

The effects of simulated stimulation with a stationary slit are initially less obvious. The magnitude of the response is clearly orientation-dependent; the optimal orientation, however, is precisely parallel to the preferred axis of motion for the moving spot. Intuitively, this reflects the fact that mutual inhibition of subunits is minimized when the array is stimulated by a stationary slit along the preferred axis of motion. The tuning plot in Fig. 19, top, illustrates the selectivity for both the stationary slit and the moving spot. The relationship between the orientation and direction selectivity is similar to that obtained from many type II MT neurons. (The orientation-tuning curve is plotted twice to facilitate comparisons with direction tuning.)

Finally, the effects of simulated stimulation with a moving slit are the most complex.

FIG. 19. Direction and orientation tuning from a computer simulation of a pattern-motion sensitive neuron. This simulation is based on a model that requires asymmetric lateral interconnections between nonorientation-selective inputs (see text and Fig. 18). Simulated output is plotted for 8 different orientations and 16 different directions. Both response scaling and "spontaneous activity" level (horizontal line) are arbitrarily chosen. Similarities to type II MT neurons are striking (cf. Figs. 6 and 7). Top: stationary slit (SSL) orientation tuning, indicated by triangles, is plotted twice to facilitate comparison with moving spot (MSP) direction tuning, indicated by circles. Like type II MT neurons, optimal orientation for a stationary slit deviates 90° from optimal direction of motion, indicating an orientation preference parallel to direction preference. Center: like most type II MT neurons, direction tuning for a moving slit (MSL), indicated by squares, is similar to that for a moving spot and parallel to stationary-slit orientation preference. Bottom: like some type II MT neurons, moving-slit direction-tuning curve is bimodal, indicating 2 preferred directions that are symmetrical about that for moving spot and intermediate between moving spot direction preference and orientation preference. This simulation differs from that shown at center only by a one-third reduction in speed for moving stimuli.

The response magnitude is direction dependent, but there is also an interaction between direction selectivity and stimulus speed. When the stimulus is moving at relatively fast speeds, the direction preference is identical to that for the moving spot. Simulated tuning curves for the three types of stimuli are plotted together in Fig. 19, center. Similar tuning curves obtained from a type II MT neuron can be seen in Fig. 6 for comparison.

When the speed of motion is reduced, the moving slit tuning becomes distinctly bimodal with symmetrical peaks to either side of the single peak for the moving spot. The three tuning curves obtained from simulation with a lower speed are plotted together in Fig. 19, bottom. Another set of similar tuning curves obtained from a type II MT neuron can be seen in Fig. 7 for comparison. In general, the lower the speed of motion, the greater the separation of the two moving slit peaks; at very low speeds they are nearly identical to the peaks for the stationary-slit tuning.

COMPARISONS OF PROPERTIES AND LIMITATIONS OF MODELS. An unexpected result of this modeling exercise was the high degree of similarity between the theoretically predicted tuning functions arising from both of the models and the empirically obtained tuning curves for type II MT neurons. The primary criterion for our classification as a type II neuron is the observation of orientation tuning that is parallel to the preferred axis of motion. Both of the models considered show this property. Moreover, although we have not systematically examined the interaction between speed and direction tuning, we have found some type II neurons to have bimodal tuning to a moving slit. In fact, both models predict that bimodal direction tuning is a function of the speed of the moving slit.

The fact that two entirely different approaches to the solution of the problem of pattern-motion selectivity both yield results that mimic the most salient properties of our type II MT neurons, argues that these neurons are indeed coding information about the true motion of two-dimensional patterns. Moreover, it seems possible that type II neurons represent the same class of neurons that have been shown in other experiments (39) to respond selectively to pattern motion.

Each model relies on the existence of a specialized input population. The model incorporating prefiltering for orientation naturally requires an input population of orientation- and speed-sensitive motion detectors. In contrast, the subunits of the array in the alternative model are assumed to be unoriented nondirectional neurons at some earlier stage of processing.

The striate output to MT consists primarily of (Brodmann's) layer IVb stellate and pyramidal neurons and layer V/VI pyramidal neurons (31). The available data from monkeys and cats show that these output laminae of V1 contain populations of both orientation selective (simple and complex) as well as unoriented neurons (14, 18, 19, 23, 24, 30, 44, 48), i.e., they contain some neurons with properties required by each model. Area MT also receives inputs from areas V2, V3, and Van Essen's VP (33). Fragmentary evidence suggests that these areas contain populations of both orientation-selective and nonorientation-selective neurons (9, 75).

A second feature of the model relying on unoriented inputs is that it assumes the existence of a specialized neural substrate underlying lateral interactions. These interactions could take various forms, the most conventional of which involves inhibitory and excitatory interneurons. In cat area 17, it has been possible to demonstrate the role of lateral inhibitory connections in determining the properties of postsynaptic neurons by modulation with chemical antagonists (50, 51, 61) and through intracellular recording of postsynaptic inhibitory potentials (12). It may therefore be possible to distinguish between the two models by measuring postsynaptic potentials or by modulation of neurotransmitter effects in MT, using an approach similar to that taken in the study of inhibitory synaptic interactions in cat area 17.

SUMMARY. The properties of two models of pattern-motion sensitivity have been examined using the same stimulus conditions that we have used to examine the properties of MT neurons. We discovered, quite surprisingly, that some unusual behaviors of type II MT neurons (e.g., a stationary orientation preference parallel to the optimal axis of motion) can be explained as emergent properties of the local neural circuitry responsible for sensitivity to the true direction of motion of two-dimensional patterns. Furthermore, this finding argues that our type II cells

represent the same population of neurons that have been shown in other experiments (39) to be sensitive to the motion of patterns.

Comparison of effects of stimulus form

The three stimuli used in this experiment differed considerably in a number of respects, including size, shape, luminance, density, and orientation. The use of these different types of moving stimuli constitutes a test of the claim that MT neurons are relatively insensitive to stimulus form (3, 34, 66, 71).

Form invariance of MT neurons is supported by our observation that the average response magnitude measure was very similar for the three different stimuli and was highly correlated for single neurons. Direction selectivity was also similar for the three types of moving stimuli as measured by the index of directionality. There were, however, some differences in the effects produced by the different stimuli. The most affected direction-tuning measure was bandwidth. Tuning for the moving spot was, on the average, significantly broader than that for either the moving-slit or random-dot field. Furthermore, we observed very little correlation between tuning for the moving spot and that for either of the other two stimulus types. Examination of the tuning curves suggests an explanation for some cases: it was common to see suppression below the spontaneous firing rate when stimuli move along the axis 90° away from the preferred axis. Suppression of this sort causes responses to drop off more rapidly as direction of motion deviates from optimal, resulting in narrower tuning. For some neurons, moving-spot stimuli appeared to be less effective in eliciting this suppression than either the slit or the random-dot field. This may be an effect of spatial summation because the single spot was the smallest stimulus used.

Direction and orientation tuning in V1

COMPARISON WITH PREVIOUS REPORTS. The results of our analysis of the direction and orientation tuning of macaque V1 neurons are similar to previous reports (13, 14, 27, 44, 48, 49). We found a direction-tuning bandwidth of 68° for a moving slit; DeValois et al. (13) report a value of 65° for moving-slit stimuli; and Poggio et al. (44, 45) report 50°. Although Schiller et al. (48, 49) do not measure bandwidth by the same method, their results appear to be similar. Like us, DeValois has reported tuning to be similar for simple and complex cells. Our distribution of the directionality index is also similar to that of DeValois in that it tends toward bidirectionality. Furthermore, like DeValois, we did not detect any significant differences between the directionality indices for simple and complex cells.

COMPARISON OF V1 WITH MT. Earlier studies of macaque MT have suggested that it is specialized for the processing of motion, as demonstrated by the high incidence of directionally selective neurons relative to V1 and other extrastriate visual areas (15, 71, 75). It is unclear from these studies, however, whether there exists a significant transformation of the response properties of single neurons from area V1 to area MT. Area MT receives a strong input from primary visual cortex (33, 37, 64, 66) and many V1 neurons are known to be very sensitive to motion (13, 14, 27, 44, 48). Does the relatively high incidence of motion selectivity in MT reflect a selective input from these directionally selective V1 neurons? Is there a significant transformation occurring from V1 to area MT?

Our quantitative comparison of areas V1 and MT has demonstrated several differences between their direction- and orientation-tuning characteristics. Most significantly, MT neurons tend to be more responsive to moving stimuli than are V1 neurons. MT neurons are also more selective for motion in a single direction along a preferred axis and yet more broadly tuned to moving stimuli. The tuning of MT neurons to stationary-oriented stimuli is slightly broader than that of V1 neurons.

These findings indicate that MT and V1 neurons differ on the average, supporting the hypothesis that MT is specialized for motion analysis. They do not, however, rule out the possibility that the subset of V1 neurons projecting to MT possesses functional properties similar to those of neurons in MT. That is, the characteristics of MT neurons might simply reflect the properties of their V1 afferents. However, we have demonstrated an unusual relationship between direction and orientation tuning in some MT neurons, the type II neurons, which has not been observed in V1. This relationship may reflect a funtional cell class specialized for higher-

level motion processing (39), which is nonexistent at the level of primary visual cortex (40).

In summary, there are significant quantitative and qualitative changes in the direction- and orientation-tuning characteristics of MT neurons when compared with V1 neurons. These results provide support for the claim that in MT there is an enhancement of sensitivity to stimulus motion and a reduction of sensitivity to stimulus form (34, 66, 71). This presumably reflects a special role for MT in the analysis of motion. More generally, the present study is consistent with the hypothesis that the extrastriate visual areas are task-specific modules, each specialized to extract information about some basic stimulus feature.

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