

CODING OF VISUAL STIMULUS VELOCITY IN AREA MT OF THE MACAQUE

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Abstract—We have studied the interaction of the direction and speed selectivities of neurons in cortical visual area MT of the macaque monkey. For a given cell, preferred direction and the shape of the direction tuning curve for moving edges were similar at different stimulus speeds, and deviations from the optimal speed did not systematically alter direction tuning bandwidth. Similar speed tuning was obtained for responses to motion in the preferred and anti-preferred directions even when the response to anti-preferred motion was an inhibitory one. The results are discussed in terms of the unique contributions of area MT to visual motion analysis.

Motion perception MT Velocity Monkey Extrastriate cortex Visual cortex

INTRODUCTION

The cerebral cortex of mammals is known to contain a large number of distinctive visual areas in addition to the primary visual or striate cortex. It has been hypothesized that each of these areas may be responsible for the analysis of one or a few stimulus parameters (Zeki, 1978; Van Essen, 1979; Allman *et al.*, 1981). Among the extrastriate visual areas, the evidence for stimulus specificity is particularly good for the middle temporal visual area (MT). MT neurons are strikingly sensitive to the direction of stimulus motion, but relatively insensitive to stimulus form or color (Zeki, 1974; Maunsell and Van Essen, 1983a; Albright, 1984). In the macaque monkey, MT is a small, topographically organized, myeloarchitectonically distinctive region buried along the dorsal third of the posterior bank of the superior temporal sulcus (Zeki, 1974; Gattass and Gross, 1981; Van Essen *et al.*, 1981). It receives projections from striate cortex as well as from a number of extrastriate visual areas and, by way of the pulvinar, from the superior colliculus (Cragg and Ainsworth, 1969; Ungerleider and Mishkin, 1979; Maunsell and Van Essen, 1983c). Directionally selective cells in MT are organized into a columnar system reminiscent of the orientation system in striate cortex (Albright *et al.*, 1984). MT neurons are also sensitive to stimulus orientation, speed and binocular disparity (Maunsell and Van Essen, 1983a, b; Albright, 1984).

The term speed properly refers to the rate of motion, a scalar quantity, whereas velocity, a vector measure, encompasses both rate and direction of stimulus motion. The importance of both speed and direction of a visual stimulus as parameters for MT neurons strongly suggests that the area plays a role in the perception of stimulus velocity. However, other visual structures also contain cells sensitive to the direction or speed of stimulus motion; in particular, striate cortex, which provides a major input to MT, contains at least some neurons sensitive to both parameters (Hubel and Wiesel, 1968; Schiller *et al.*, 1976; DeValois *et al.*, 1982; Orban *et al.*, 1983). It has been unclear whether the velocity-coding capabilities of MT neurons represent an elaboration of processing over that accomplished by the primary visual cortex. In order to investigate the role of MT neurons in velocity coding, we studied the interaction of their direction and speed selectivities using moving bars of light. We were interested in determining if direction preference remains constant over changes in speed and if MT neurons have single preferred velocities. Many MT neurons demonstrate inhibitory responses to non optimal directions of motion; it was also of interest to determine the dependence, if any, of these inhibitory responses on stimulus speed. We reported here that the direction preference of MT neurons remains strikingly similar over large changes in stimulus speed. Moreover, MT neurons may be subdivided on the basis of their

speed selectivities for nonoptimal directions of stimulus motion.

METHODS

Animal preparation

Repeated recordings were made in five chronically implanted male *Macaca fascicularis* weighing between 3.1 and 4.4 kg. Approximately one week before the initial recording session, a 3.5 cm diameter stainless steel well and cap and a stereotactically positioned headbolt were mounted on the animal's skull with dental acrylic. Small stainless steel screws inserted into the skull helped the dental acrylic to secure the hardware. The well was mounted over parietotemporal cortex (center at approximately AP-0) on the left hemisphere to allow an angled, anterior-to-posterior approach to MT. The implant was performed under ketamine hydrochloride anesthesia (Ketaset, 30 mg/kg; supplemented with 50 mg as needed) in aseptic conditions. Valium (2 mg) was given towards the end of surgery.

Each animal was recorded from once or twice weekly for up to a maximum of 13 sessions in the course of these and other experiments. On the morning of a recording session, the animal was given an injection of atropine (0.15 mg/kg) to reduce mucous secretions, followed by an initial restraining dose of ketamine (10 mg/kg). Next, the monkey was anesthetized with a mixture of halothane, nitrous oxide and oxygen, and intubated with a tracheal tube. The monkey was then positioned in a stereotaxic apparatus by means of the headbolt and a special holder attached to the apparatus. The cap was removed from the recording well to expose a small hole that had been drilled through the exposed bone on the first day of recording. At this point, halothane anesthesia was discontinued and the animal subsequently anesthetized by a 2:1 mixture of nitrous oxide and oxygen. Paralysis was then induced with an intravenous injection of pancuronium bromide (Pavulon) in saline or dextrose-lactated Ringer's solution. Pavulon was infused continuously at a rate of 0.03 mg/kg/hr. Body temperature, heart rate and end-tidal CO₂ were monitored throughout the recording session. Respiration rate was adjusted to give an end-tidal CO₂ level of about 4%. The pupils were dilated with cyclopentolate HCl (Cyclogyl, 1%) and the corneas covered with contact lenses selected by retinoscopy to focus the animal's eyes on a rear-projection tangent screen approximately 57 cm away.

Recording sessions lasted 12–17 hr and were separated by a minimum of 2 days. One hour before the end of each session, Pavulon infusion was discontinued. When the animal had recovered sufficiently to breathe normally on its own, it was returned to its home cage.

Recording

Extracellular potentials were recorded from single isolated neurons using varnish-coated tungsten microelectrodes (Frederick Haer) with exposed tips of approximately 10 μ m and impedance of approximately 2–10 M Ω . In order to make penetrations roughly normal to the cortical surface of MT, electrodes were angled 40° from vertical in the parasagittal plane, passing dorsoanteriorly to ventroposteriorly (Fig. 1). Small electrolytic lesions (4 μ A, 20–30 sec) were made at strategic positions along some penetrations to facilitate subsequent histological reconstruction.

All recordings were made from the cortex in MT representing the central 20° of the visual field. Background activity was amplified and displayed on an oscilloscope. Spikes were judged to be arising from isolated neurons if they could reliably trigger an adjustable spike amplitude and rise-time filter and appeared constant in waveform and amplitude. Spikes thus recorded were converted into digital pulses and sent to a computer for storage and display (see below).

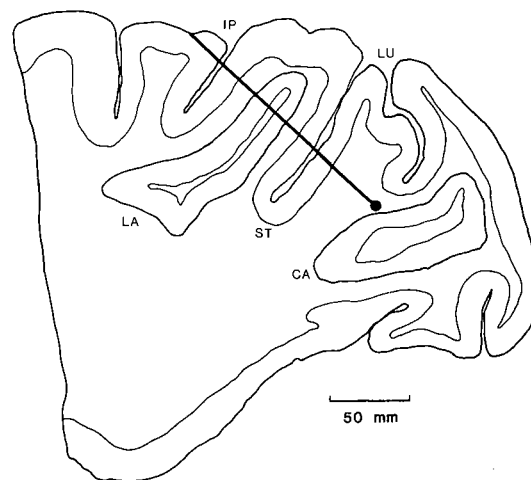


Fig. 1. Parasagittal reconstruction of an electrode penetration passing through area MT (shaded). Anterior portion of the section has been cut off. CA, calcarine sulcus; IP, intraparietal sulcus; LA, lateral sulcus; LU, lunate sulcus; ST, superior temporal sulcus.

Stimulation

Visual stimuli were presented on a $60^\circ \times 60^\circ$ rear-projection tangent screen with a background intensity of about 2 cd/m^2 . Prior to stimulation, the locations of the fovea and the center of the optic disk of both eyes were projected onto screen with an ophthalmoscope and cornercube prism. The horizontal meridian was defined as the line passing through both of these points and the vertical meridian as an orthogonal line passing through the fovea. Stimulus intensity was approximately 1.5 log units above background intensity.

Once a unit was isolated, preliminary testing was performed with a hand-held projector to ascertain that the unit was at least moderately responsive to each of the types of stimuli used for quantitative testing. [A few units ($<10\%$ of those isolated) did not respond convincingly to one or more of the stimulus types and were excluded from further testing.] A rough assessment of speed selectivity was also made. Then, a stimulus evoking a good response was used to determine ocular dominance, if any, and the receptive field was plotted for the eye giving the best response. If equally good responses could be evoked from the two eyes, the contralateral eye was used for further testing.

Quantitative testing was performed with the aid of a PDP-11/34A computer which automatically controlled the presentation of stimuli by an optical bench equipped with X- and Y-axis mirrors, a stepping-motor controlled rotation device and an electronic shutter. Deflection of the mirrors to produce a moving beam of light was accomplished by a highly accurate servo-controlled optical scanner with a flyback time of less than 5 msec (General Scanning, model No. G-300PD with corresponding A-600 control amplifiers). Deflection of the mirrors was calibrated to reach precisely to the end-points of the tangent screen. Timing of stimulus motion was controlled by an internal computer clock with an accuracy of 1 msec. From these parameters, actual stimulus speed on the tangent screen could be calculated. Rate of rotation of the galvanometer shaft was held constant, producing a slight increase in stimulus speed from the vantage point of the animal as the stimulus moved away from the fovea. However, the increase in stimulus speed from 0 to 20° eccentricity is only about 11%. Since all receptive fields were within the central 20° of the visual field, and since the receptive field width was actually 10° or less for the majority of

neurons studied, and since the changes were equally relevant to all stimulus speeds, we did not attempt to compensate for these minor changes in speed as the stimulus traversed the screen.

Moving stimuli consisted of slits and spots of light swept approximately 25° across the tangent screen along a path centered on the neuron's receptive field. Each of the types of moving stimuli was presented in 16 directions of motion with a constant angular deviation (22.5°) separating one direction from the next. For the moving slit, orientation was always perpendicular to the direction of movement. Stationary flashed slits, positioned in the receptive field so that they evoked the maximal response from a given orientation, were presented for 2.5 sec in each of 8 orientations with a constant angular deviation of 22.5° separating neighboring orientations. Slit stimuli extended beyond the borders of the receptive field for all cells.

For each of the above kinds of stimuli, a test consisted of a series of 5–10 pseudorandomly interleaved presentations of each direction or orientation. Quantitative testing of an isolated cell usually began with a moving spot series at the speed estimated to be optimal with hand testing, followed by a stationary slit series. Velocity testing, using sets of moving slit series consisting of randomized directions and speeds, was then undertaken. Speeds used included the optimal speed and values in approximately octave steps above and below the optimal; in all, the range of speeds tested in the study extended from about $1^\circ/\text{s}$ to about $240^\circ/\text{s}$. The entire set of tests for a single neuron could require 3 hr or more, especially when very low speeds were used. Many neurons were studied successfully for several hours; some, however, became injured or poorly isolated during testing and had to be abandoned before many different speeds could be tested.

Data collection and analysis

Action potentials were collected and displayed on-line as individual peristimulus histograms enabling comparison of firing rate during stimulus presentation with that obtained immediately preceding onset and following offset. Histograms were displayed continuously during collection of data and updated during each trial. Averaged spike rates and cumulative statistics for each direction or orientation used in a given series could also be viewed.

Additional off-line computer analysis was subsequently performed on the resulting cumulative spike histograms. To account for asymmetries in receptive field dimensions, responses to the moving slit were compensated by considering only the spike rate within a time window determined by the response to the stimulus swept through the receptive field along its narrowest axis. For cells with symmetrical receptive fields, this window was adjusted to correspond to the width of the greatest response elicited for that stimulus at that particular speed. Further, the time window could be adjusted to include responses to very fast stimuli which did not appear on the histograms until after stimulus offset.

For all analyses, responses to moving stimuli were measured as the average rate of firing during the time window minus the spontaneous rate. Since stimuli moving at different speeds are present in the receptive field for differing amounts of time, it is inappropriate to use a measure that is biased towards stimuli of long duration, such as total number of spikes (Movshon, 1975). Both the peak rate of firing and average rate of firing have been used in analyses of cortical direction and speed selectivity, typically giving similar results when directly compared (Movshon, 1975; Maunsell and Van Essen, 1983a; Albright, 1984). However, peak rate of firing is more sensitive to random fluctuations and necessitates more stimulus repetitions. Accordingly, we have chosen to use average rate of firing as the response measure. Because responses are averaged over longer times for slow stimuli, measured responses to slow stimuli tend to be more accurate than those to fast stimuli for a given number of stimulus presentations. Standard errors of the mean (see Figs 2 and 6–8) indicate, however, that greater variability of response to fast stimuli was not a problem.

Responses to stationary slits were calculated as the average rate of firing during the entire stimulus exposure minus the spontaneous rate.

Histological verification of recording sites

At the conclusion of experimentation, the monkeys were anesthetized with an overdose of intravenous sodium pentobarbital and perfused through the heart with saline followed by 10% buffered formalin. To facilitate cutting, the brains were then infiltrated with sucrose by storing them in a solution of 30% sucrose in

10% formal-saline until they sank. Sections were cut in the parasagittal plane at 33 μ m and alternate sections stained with cresylecht violet or the Gallyas silver myelin stain (Gallyas, 1969).

Electrode penetrations were reconstructed from the serial sections stained with cresylecht violet. Electrode tracks were tentatively drawn in on a representative section at each medial-lateral recording level at $\times 10$ by comparing portions of tracks from adjacent sections. These tracks were then confirmed and the locations of recording sites along each determined under higher power on the basis of the electrolytic lesions made on some penetrations. Neighboring sections stained for myelin were used to determine the boundaries of MT. At most levels, these boundaries were clearly indicated by a transition from a heavy staining in the infragranular layers in MT to a lighter and more distinctly banded staining outside MT, and were sharp enough to draw a firm border between MT and the surrounding cortex. At other levels, however, the transition was less well-defined, and at these levels upper and/or lower "tentative" zones were then judged on the basis of the response properties of the cells recorded along them. Specifically, cells with small fields, sharp direction selectivity and strong responses in these zones were judged to be within area MT.

RESULTS

We analyzed the responses of total of 48 MT neurons recorded along 29 penetrations in the 5 animals. All of these neurons were tested with 8 or 16 directions of motion of the moving slit with each direction presented at between three and eleven speeds. Most of these neurons were also tested with a stationary oriented contour and a spot moving at the optimal speed. First, we will describe the incidence and characteristics of direction and speed selectivity in the sample. Second, the interaction of direction and speed selectivity will be considered. In particular, the effects of speed manipulation on direction preference and on the bandwidth of the direction tuning curve will be presented. Next, we will compare speed tuning for preferred and anti-preferred directions of stimulus motion. Finally, some observations bearing on the issue of "pattern-motion selectivity" (see, for example, Albright, 1984, and Movshon *et al.*, 1985) will be described.

Direction and speed selectivity

Analysis of velocity selectivity for 47 MT neurons began with separate assessments of direction and speed selectivity. One cell, which showed an unusual type of direction tuning, will be discussed separately in the section on pattern-motion selectivity.

Direction selectivity. At the optimal speed, the moving slit produced direction selective responses from all cells, in the sense that they did not respond similarly to all directions of motion. Direction selectivity was quantified for each cell using two measures. First, a direction tuning index was computed for each moving slit speed (Baker *et al.*, 1981).

Direction Index (DI)

$$= 1 - \frac{\text{Response in anti-preferred direction}}{\text{Response in preferred direction}}.$$

Many MT neurons, like those in striate cortex, respond optimally to motion in the two directions along some single preferred axis; the DI compares responsiveness for these two directions. Low index values indicate a tendency towards bidirectionality and high values, a tendency towards unidirectionality. Values greater than 1.0 indicate inhibition below spontaneous rate in the anti-preferred direction. DI values ranged from 0.25 to 1.63 with a mean of 1.01. Almost half of the neurons (23/47) were unidirectional for stimulation at the preferred speed (DI greater than 0.90). Several units (4/47) were bidirectional (DI less than or equal to 0.70 with a tuning curve showing preference for both directions along some given axis). The remaining units (20/47) were considered directionally biased (DI between 0.50 and 0.90).

Second, for each speed, response was plotted as a function of direction of stimulus motion. Tuning bandwidth (full width of the resultant direction tuning curve at half of its maximum height) was calculated. Direction tuning bandwidth at the preferred speed ranged from 25 to 151° (mean: 88°). No correlation was obtained between sharpness of direction tuning and responsiveness measured at the preferred direction and speed.

The overall picture of direction tuning in this sample was highly consistent with that emerging from previous studies. Using identical methods, Albright (1984) found a mean DI for MT neurons of 1.00 and a mean direction tuning bandwidth of 90° for a slit of light moving at the preferred speed. Using similar methods, Maun-

sell and Van Essen (1983a) found a mean DI of 0.93, and a mean bandwidth of about 70° (as inferred from the data they present).

Speed selectivity. For each cell, a plot of response magnitude (for stimulation in the best direction) versus speed was constructed. An example is shown in Fig. 2. At top, responses in average spikes per second above baseline are shown as a function of stimulus speed. In this and subsequent plots, the significance level [mean plus (or minus) two standard errors of the spontaneous firing rate] is shown as a dotted line. Mean responses to a given speed were considered statistically significant if they fell outside of this significance level. Vertical bars indicate standard errors of the mean for five repetitions of each speed. At bottom are shown actual cumulative peristimulus time histograms collected for each speed. The horizontal line below each histogram indicates the time that the stimulus was on. (Because higher speeds correspond to shorter bins for data collection over a fixed distance of stimulus movement, this time was shorter for progressively higher speeds.) Inspection of the speed tuning plots revealed a clear preference among the speeds tested for all but one neuron. Some cells were not tested with enough speeds to establish an absolute preference but rather a preference within a restricted range. For cells tested with six or more speeds, sharp tuning like that shown in Fig. 2 was common; 8 of 14 neurons tested with six or more speeds were thus designated as "speed tuned". Several other cells in this group would probably also have been speed tuned if additional speeds had been tested. For each speed tuned neuron, the full-width, half-height tuning bandwidth was measured. Speed tuning bandwidth averaged 2.49 octaves (range: 1.35–4.60) a figure highly consistent with previous results (Maunsell and Van Essen, 1983a; Felleman and Kaas, 1984). There was no correlation between sharpness of speed tuning and responsiveness of the cell measured at the preferred speed and direction. Optimal speeds (among those tested for each neuron) ranged from about 5 to about 150°/sec; presumably the small size of the sample and the fact that very few cells received testing with the moving slit at extreme speeds explains the absence of units with lower and higher preferred speeds such as those reported by the above authors. The most common preferred speed within the range tested was about 40°/sec, consistent with earlier findings in the macaque. Since preferred speed is weakly cor-

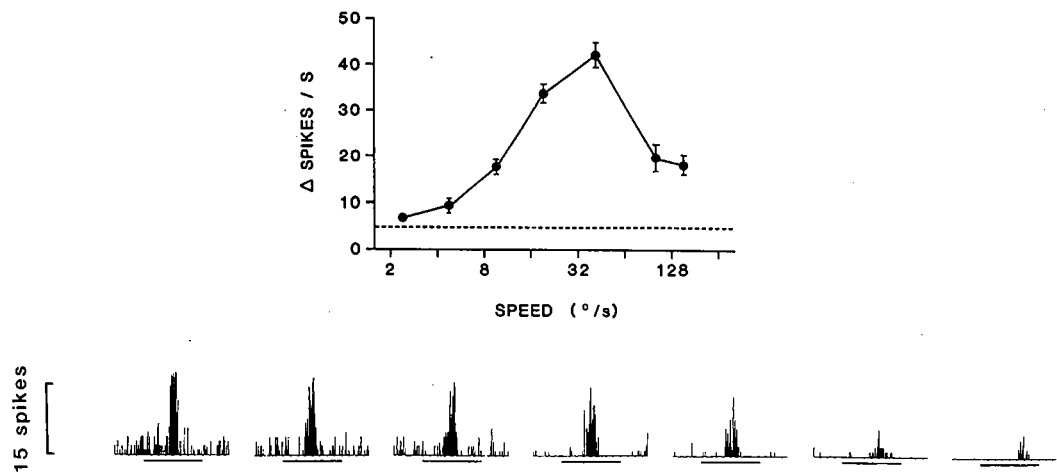


Fig. 2. Speed selectivity of an MT neuron for a slit moving in the preferred direction. (Speeds slightly offset from octave steps were used as a result of a small miscalibration of the speed of stimulus motion during a portion of the experiment.) Top: response is plotted in total spikes per second above baseline. Here, while excitatory responses were obtained at all speeds tested, there is a strong peak at about 43 $^{\circ}$ /sec. Bottom: cumulative histograms illustrating responses to each speed of stimulus motion plotted at top. The line below each histogram indicates the time that the stimulus was on. (Since faster speeds correspond to smaller bins for data collection, this time was progressively shorter at higher speeds; the progressive rightward shift of the response center in the histograms reflects the cell's fixed visual response latency.)

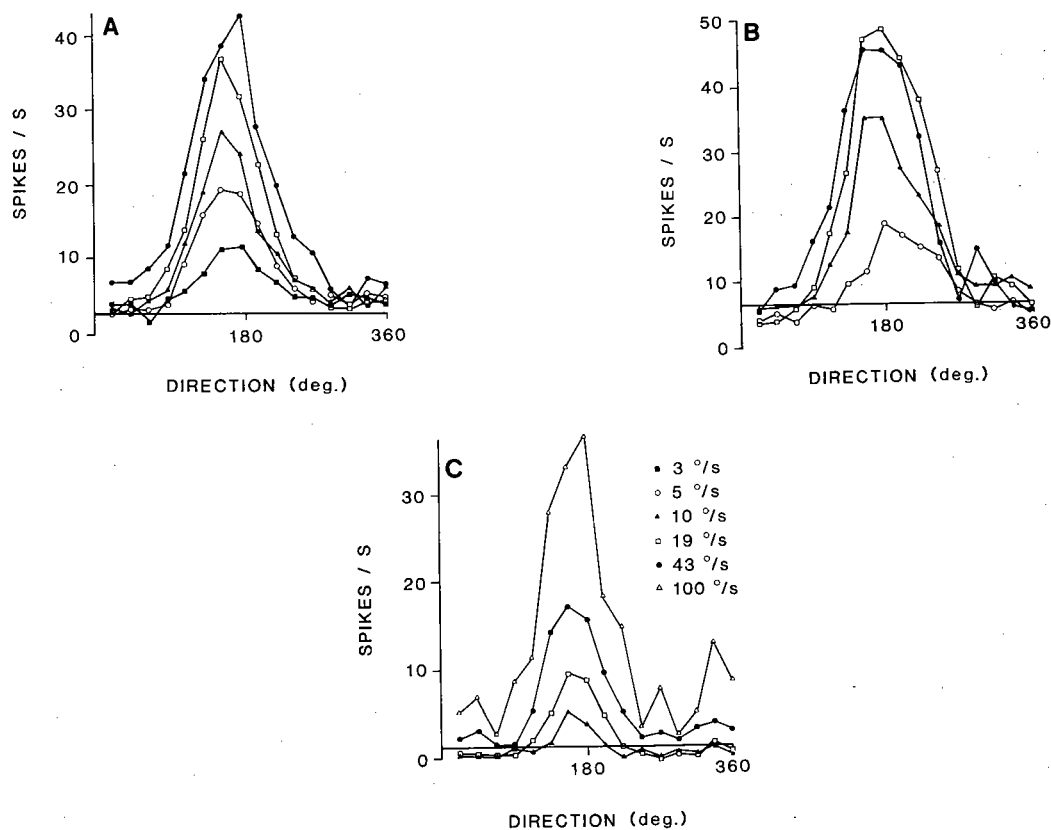


Fig. 3. Direction tuning curves for three representative MT neurons tested with the moving slit at different speeds. Position of the X-axis indicated level of spontaneous activity. The labelling conventions given in plot C apply to all three cells. For purposes of comparison the set of curves for each cell has been shifted so that the cell's best response corresponds to a stimulus moving at 180 $^{\circ}$ relative to an upward motion.

The overall shape and sharpness of the tuning curves are similar at different speeds.

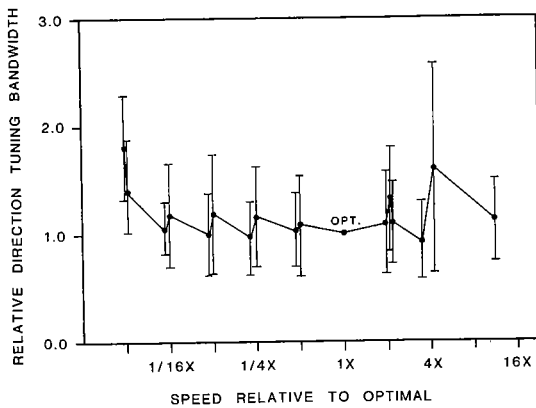


Fig. 4. Relationship of direction tuning bandwidth and stimulus speed relative to the optimal speed. Tuning bandwidths for each neuron were normalized to the bandwidth obtained with stimulation at the preferred speed defined as 1.0. Vertical bars indicate the standard deviations of relative bandwidths at each speed.

related with receptive field eccentricity (Maunsell and Van Essen, 1983a) the fact that cells in the present sample had fields within the central 20° may also have contributed to the absence of higher preferred speeds.

Interaction of direction and speed selectivity

After having established that virtually all cells in the present sample were both direction and speed selective, the next step was to determine whether direction selectivity was influenced by stimulus speed. First, the general characteristics of the direction tuning curve (overall shape, preferred direction) were examined at the various speeds tested for each cell (Fig. 3). For all cells, these remained remarkably consistent under speed manipulation. One exception to this

generalization was the observation that some (but not all) cells did tend to have more ragged direction tuning curves at the most extreme speeds tested ($1-2^\circ/\text{s}$ and particularly above $150^\circ/\text{s}$). The variability of response at high speeds of stimulus motion is probably due at least in part to low overall spike counts for fast stimuli.

Next, the data were examined to determine whether direction tuning became sharper (i.e. whether tuning bandwidth became smaller) at the preferred speed. Figure 4 shows mean tuning bandwidth for the sample as a function of stimulus speed relative to optimal. If tuning sharpens as the preferred speed is approached, this curve should resemble a V, indicating broader tuning at speeds farther from the optimal. On the other hand, if direction tuning bandwidth is completely uncorrelated with the efficacy of the speed used for testing, the curve will be flat. It is clear from the curve shown in Fig. 4 that speed relative to optimal does not influence the sharpness of direction tuning for the sample as a whole.

In order to quantify changes in bandwidth with deviations from the optimal stimulus speed for individual neurons, we calculated a bandwidth change index in the following manner. For each cell, direction tuning bandwidth in degrees was plotted against deviation of stimulus speed from optimal in octaves. Lines were then fitted separately for the portions of the plot corresponding to increases and decreases in speed above the optimal. Thus, there were two such lines for each cell which responded to motion at speeds both and below the optimal.

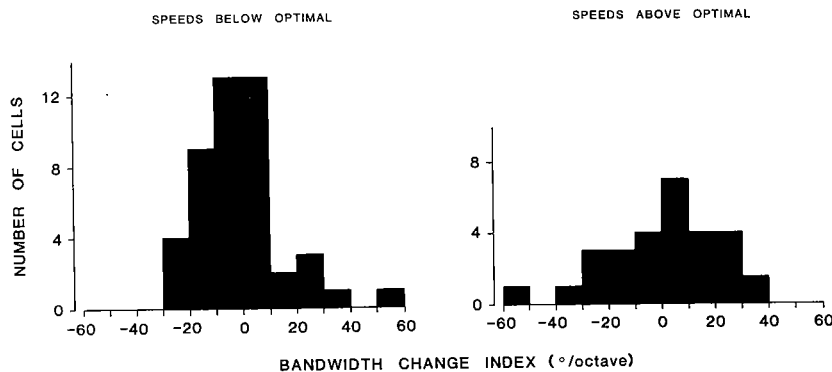


Fig. 5. Left: distribution of bandwidth change indices calculated on the basis of responses to speeds lower than the optimal. The bandwidth change index for each cell was computed as the slope of the line relating direction tuning bandwidth to stimulus speed relative to the optimal. Negative values indicate that tuning bandwidth tends to become smaller (i.e. direction tuning becomes sharper) as speed decreases from the optimal. Positive values indicate that direction tuning bandwidth tends to become larger (i.e. tuning becomes less sharp) as speed decreases. Right: distribution of bandwidth change indices calculated on the basis of responses to speeds higher than the optimal.

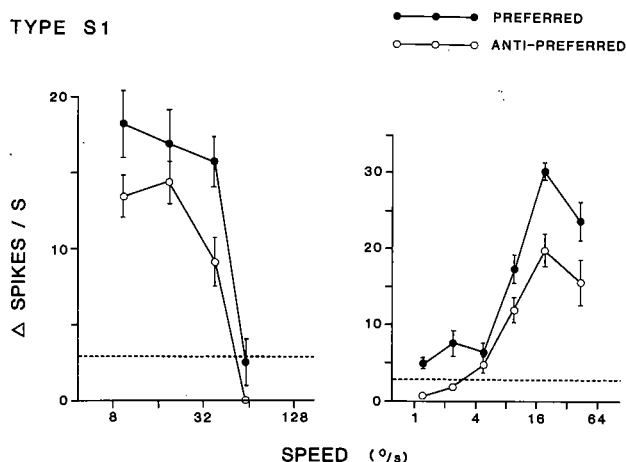


Fig. 6. Speed tuning curves characteristic of S1 neurons. The shapes of the speed tuning curves for the preferred and anti-preferred directions are strikingly similar. Both cells had strong excitatory responses in each direction along the preferred axis. DI at the optimal speed: left, 0.25; right, 0.34. See also legend to Fig. 2.

The bandwidth change index was defined as the slope of the fitted line and expressed in degrees per octave. The value of the index thus is a measure of how much direction tuning bandwidth tends to change as speed deviates from the optimal. Figure 5 illustrates the distribution of the indices for all neurons for speeds lower than the optimal (top) and speeds higher than optimal (bottom). The distribution of bandwidth change indices is flatter for stimulus speeds greater than optimal; this is presumably due to the fact that bandwidth measurements for stimulation at high speeds, based as they are on smaller numbers of spikes, tend to be inher-

ently more variable than bandwidth measurements for stimulation with low speeds. However, for both higher and lower speeds, the distribution of the indices is clustered around plus or minus $20^\circ/\text{octave}$; large changes in direction tuning bandwidth (greater than $20^\circ/\text{octave}$) with deviations from optimal speed are relatively unusual. This indicates that for most MT neurons, direction tuning bandwidth is either similar at different speeds, or varies in an unsystematic fashion.

Next, we examined the relationship between strength of direction selectivity (as measured by the direction index) and stimulus speed relative

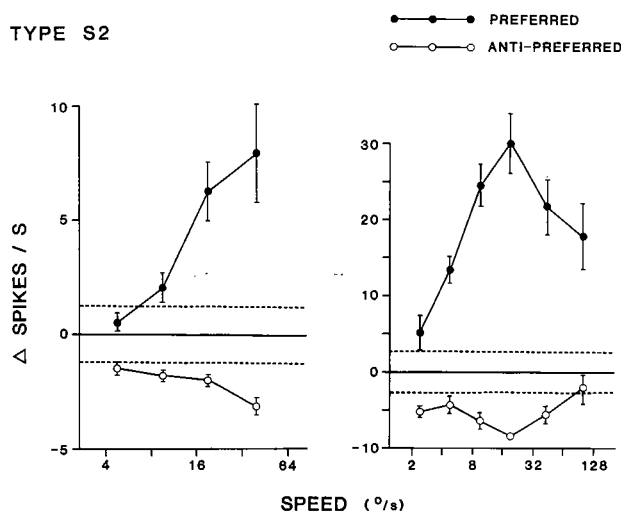


Fig. 7. Speed tuning curves characteristic of S2 neurons. Solid line corresponding to 0 spikes/sec above baseline indicates spontaneous activity; points below this line indicate inhibition. Speed tuning curves for the preferred and anti-preferred directions are approximate mirror images. DI at the optimal speed: left, 1.46; right, 1.63. See also legend to Fig. 2.

to optimal. No systematic *overall* relationship was found; for some cells, direction index tended to increase as speed approached the optimal; for others, direction index decreased as the optimal speed was approached, and for a few no relationship at all was evident. To further investigate this pattern of results, we constructed speed tuning curves for each cell for responses to the slit moving in the anti-preferred direction and compared them to the curves obtained for stimulation in the preferred direction. For 37 of the 47 neurons tested, the response to motion in the anti-preferred direction was sensitive to speed. About half of these neurons (19/37), referred to as Speed Class 1 (S1), showed approximately the same optimal speed and very similar speed tuning curves for preferred and anti-preferred directions of motion. Figure 6 shows two examples of neurons from this group. As in Fig. 2, mean responses to each speed are shown along with standard errors from five repetitions of each speed, and dashed lines indicate significance levels. Several points falling below significance levels (i.e. indicating a lack of response) have been included as they are relevant to the shape of the curve. All members of this class had DIs of less than 1.00 at the optimal speed (indicating some responsiveness in the anti-preferred direction), and all of the bidirectional cells in the sample were included in this class.

Another 18 neurons, referred to as Speed Class 2 (S2), showed speed tuning curves for the preferred and anti-preferred directions that were approximate mirror images. In other words, the preferred-direction peak corresponded to a trough of the anti-preferred-direction speed tuning curve, and so forth (Fig. 7). It follows that

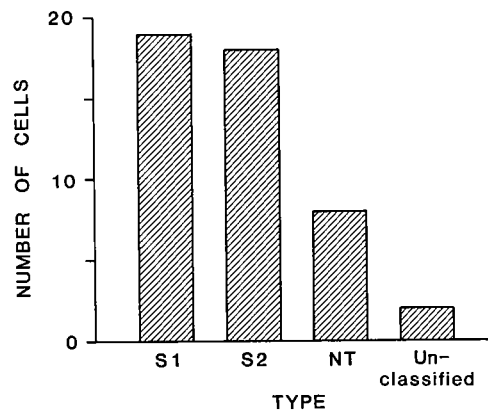


Fig. 9. Proportions of MT cells falling into the four speed classes described in the text. S1: cells with similar speed tuning for excitatory responses in both preferred and anti-preferred directions. S2: cells with similar speed tuning for excitatory responses to anti-preferred motion. NT: cells whose responses to anti-preferred motion were not speed sensitive. "Unclassified" cells had ambiguous speed tuning or no response for anti-preferred motion.

for these cells, strength of direction selectivity was maximal at the preferred speed. All cells but one in this group had direction indices greater than 1.00 at the optimal speed (indicating the presence of inhibition in the anti-preferred direction).

For seven cells, the response to motion in the anti-preferred direction was not speed selective ("not tuned," class NT). Such cells showed neither a clear preferred speed nor a systematic change in mean response with changes in speed for motion in the anti-preferred direction. (See Fig. 8, left.) Cells in this category *were* selective for speed of motion in the preferred direction despite their lack of tuning in the anti-preferred direction. Three cells displayed either ambiguous speed tuning or no response to motion in

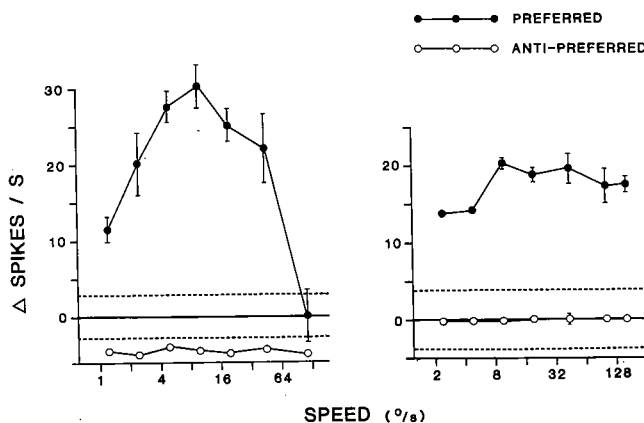


Fig. 8. Left: cell is inhibited similarly by all speeds tested (class NT). DI at optimal speed = 1.32. Right: cell not classified as S1, S2 or NT. No excitatory or inhibitory response is produced by stimulation in the anti-preferred direction. DI at optimal speed = 1.00. See also legends to Figs. 2 and 7.

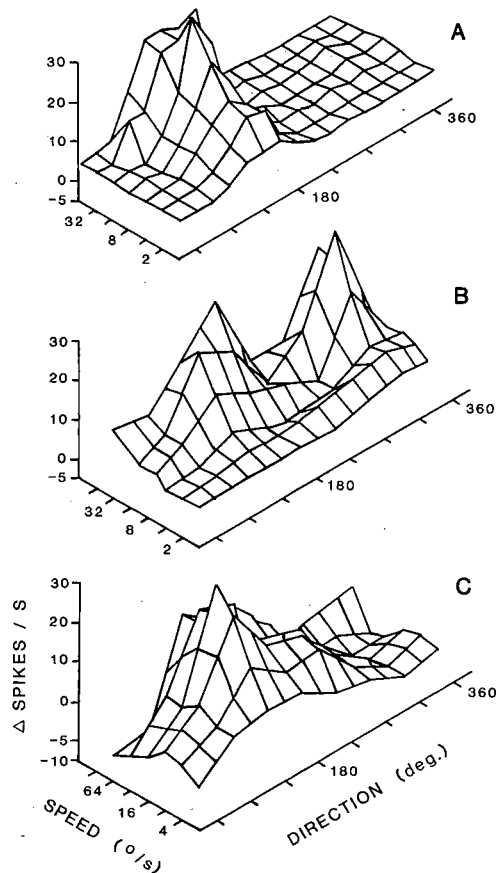


Fig. 10. Interaction of direction and speed selectivities for three MT neurons. Responsiveness in spikes/sec. above baseline is plotted as a function of both direction and speed. (A) S1 cell. Excitatory response to motion in the anti-preferred direction is very slight. (B) S1 cell. Response to motion in the anti-preferred direction is strongly excitatory and forms a sharp secondary peak. (C) S2 cell. Inhibitory response to the anti-preferred direction of motion appears as a trough.

the anti-preferred direction and thus were not classified as S1, S2 or NT (Fig. 8, right).

The proportions of cells falling into each of the classes described are summarized in Fig. 9.

Finally, we obtained, for speed tuned neurons, a correlation coefficient of 0.70 between speed tuning bandwidth and the bandwidth of the direction tuning curve obtained with the optimal speed. Although the sample was small ($n = 8$), this correlation was statistically significant ($t = 2.40$, d.f. = 6, $P < 0.05$), suggesting that cells with sharp speed tuning also tend to have sharp direction tuning. There was no correlation between speed tuning bandwidth and strength of direction selectivity (direction index).

Figure 10 shows examples of the interaction of the direction and speed selectivities of three

neurons. Responsiveness is plotted as a function of both speed and direction. These plots illustrate the different types of velocity selectivity found in MT. The cell whose data are shown in A has a single strong excitatory peak, corresponding to the single preferred velocity. The cell in B has two strong excitatory peaks, corresponding to the optimal speed for each of the two directions along the preferred axis of motion. The cell in C has a single strong excitatory peak and also a small inhibitory trough corresponding to motion in the direction opposite to that producing the excitatory peak.

Pattern-motion selectivity

Recently, we have found that "Type II" MT neurons—neurons with an orientation preference parallel to their preferred direction of motion—are the same population shown by Movshon *et al.* (1985) to code the motion of whole patterns independent of contours making up the patterns (Rodman and Albright, 1987). Attempts at modelling the neural circuitry underlying Type II responses (Albright, 1984; Albright *et al.*, 1986) have suggested that Type II MT neurons should exhibit *bimodal* direction tuning for a slit moving at suboptimal speeds, the twin peaks separating farther as the stimulus speed is progressively lowered. Some Type II neurons exhibiting bimodal tuning at a single speed tested have been observed previously (Albright, 1984).

Twenty-eight neurons in the present sample were tested with the stimuli relevant to the Type II classification (moving spots and stationary slits) (Albright, 1984); 13 of these were determined to be Type II. Only one of the Type II neurons (and none of the others) exhibited bimodal direction tuning for the moving slit at any speed. Moreover, the twin peaks in the tuning curve for the single cell (excluded from the previous analysis) with bimodal tuning seemed to separate less, rather than more, with decreasing stimulus speed, contrary to the predicted behavior.

DISCUSSION

The results of this study confirm that most MT neurons are selective for both direction and speed of a moving oriented edge and show that direction tuning remains similar over changes in speed. No consistent relationship was found between direction tuning bandwidth and stimulus speed relative to optimal. For cells giving an

excitatory response to both directions of motion along the preferred axis ($DI < 1.00$, S1 cells), movement in the preferred and anti-preferred directions produced maximal responses at the same stimulus speed. For cells tending to show inhibition in the anti-preferred direction ($DI > 1.00$, S2 cells), the speed producing the maximal excitatory response in the preferred direction also produced maximal inhibition in the anti-preferred. S2 cells, thus, showed maximal direction selectivity (as measured by the DI) at the preferred speed. For some cells (NT) the response in the anti-preferred direction was insensitive to speed. Speed tuned neurons with sharp speed tuning also tended to have sharp direction tuning.

Comparison with previous studies in MT

The incidence and types of direction and speed selectivity seen in this sample are consistent with the results of previous studies of MT in both macaque (Van Essen *et al.*, 1981; Maunsell and Van Essen, 1983a; Albright, 1984) and owl monkey (Baker *et al.*, 1981; Felleman and Kaas, 1984). Moreover, although none of these authors extensively examined the interaction between direction and speed selectivity, some relevant observations were made. For example, Felleman and Kaas examined the dependence of the direction index on speed for a few neurons. They reported that most of these cells showed the highest index of directional selectivity when stimulated at the preferred speed; these might correspond to the S2 class described here. However, the direction index measure computed by Felleman and Kaas differs from ours in that it does not consider inhibitory responses; the authors do not state whether the neurons whose DI values were the highest at the optimal speed tended to show more suppression of spontaneous activity than other cells. They further report that other neurons did not show maximal direction selectivity at the optimal speed. From the data shown for one such neuron (cumulative response histograms at the different speeds tested for both preferred and anti-preferred directions) it is clear that this cell would have fallen into the S1 class; it had an excitatory response in the anti-preferred direction which demonstrated sensitivity to speed strikingly similar to that shown by the preferred direction response.

Maunsell and Van Essen (1983a) noted that in macaque MT, responses in the anti-preferred direction, whether excitatory or inhibitory, were

generally greatest at the speed producing maximal responsiveness in the preferred direction. This statement is consistent with the findings of the present study.

Role of MT neurons in velocity coding

The present data show that individual MT neurons are selective for both direction and speed of a moving visual stimulus. Cells which demonstrate inhibition in the anti-preferred direction become maximally direction-selective at the optimal speed for the preferred direction of motion (S2 neurons). For stimulation at the optimal speed, some S2 neurons are capable of delivering two pieces of information: the maximal rate of firing codes a particular speed and direction, while the strongest decrease in firing rate can, potentially, code the opposite velocity. The maximal firing of an S1 cell also codes a particular velocity, but the lower firing levels are ambiguous. (See Fig. 9.) In particular, movement in the anti-preferred direction at the optimal speed cannot be distinguished from movement in a more favored direction at a nonoptimal speed.

Comparison of the properties of MT neurons with findings from psychophysical experiments supports the notion that cells in this area provide important information about both the speed and direction of a visual stimulus. Human sensitivity to speed of visual motion, as measured by differential speed detection thresholds, is best at values of 4–32°/sec, a range over which MT neurons respond well (Orban *et al.*, 1984). Moreover, masking experiments show direction-of-motion adaptation effects consistent with the width of an average MT direction tuning curve (Ball and Sekuler, 1979; Maunsell and Van Essen, 1983a).

Finally, a role for MT in velocity coding is supported by reports of a functional organization of both speed and direction selectivity in MT. Preferred axis and preferred direction of motion are organized in a columnar fashion (Albright *et al.*, 1984). Furthermore, nearby units show a strong tendency to have similar preferred speeds (Maunsell and Van Essen, 1983a). These observations suggest that there may be some overall organization of the representation of stimulus velocity as well.

Comparison with striate cortex

What elaboration, if any, do the velocity coding abilities of MT neurons represent over the velocity coding potentially performed by

cells in striate cortex? Some neurons in both cat and monkey striate cortex are direction selective (Goodwin *et al.*, 1975; Hammond, 1978; Bishop *et al.*, 1980; Movshon *et al.*, 1980; DeValois *et al.*, 1982); cells in cat striate are also speed sensitive (Movshon, 1975; Goodwin and Henry, 1978) as are cells in monkey striate (Orban *et al.*, 1983). Moreover, Hammond and Reck (1980) reported that preferred direction and broadness of tuning for moving bars was invariant with changes in speed, as we have found for MT. Finally, orientation (and therefore direction) selectivity is represented in a columnar fashion (Hubel and Wiesel, 1974). However, there are some differences between the two areas with regard to direction and speed selectivities. First, striate cortex neurons, at least in the macaque, tend to be less selective for direction along the preferred axis than are MT neurons [average direction index 0.55 and 1.00 for striate cortex cells and MT neurons respectively (Albright, 1984)]. There is evidence that most direction-selective striate neurons would fall into the class S1 described in this study (Movshon, 1975; Goodwin and Henry, 1978). Thus, one likely transformation that takes place between striate cortex and MT may be the genesis of a substantial population of neurons that can code stimulus velocity by means of inhibitory as well as excitatory responses.

Secondly, the range of speeds to which neurons in MT are optimally responsive is much greater than that for striate neurons (Van Essen, 1985). Preferred speeds in MT range from about 2 to 256°/sec, whereas striate neurons prefer speeds only in the range of 1–32°/sec, with the great majority of preferred speeds falling between 2 and 16°/sec. Thus, the velocity coding function of MT may be largely to provide information about stimulus velocities not represented in striate cortex. There is some clinical data in the human to support this possibility. Zihl *et al.* (1983) have reported a striking case of a patient who experienced bilateral posterior brain damage and whose only subsequent complaint was a disturbance of motion perception. A CAT scan revealed rather symmetrical lesions of lateral temporo-occipital cortex and underlying white matter. No damage to primary visual cortex was reported; moreover, the patient's visual fields were intact, with no impairment of form or color vision. On the basis of the anatomical and behavioral data, the authors suggested that the damaged regions included tissue homologous to MT. Inter-

estingly, under some conditions, the patient did report some impression of stimulus movement with targets moving at up to 18°/sec; no impression of motion was ever reported when higher speeds were used. Although it is of course premature to conclude that this patient had an "MT lesion", it is tempting to speculate that her lack of motion perception at higher speeds resulted from damage to homologous tissue, with residual motion perception at low speeds subserved by intact striate cortex. It is relevant, moreover, that experiments utilizing small chemical lesions of MT in the macaque produce eye movement deficits consistent with a systematic underestimate of stimulus speed (Newsome *et al.*, 1985).

Finally, recent experiments by Movshon *et al.* and Albright *et al.* (Albright, 1984; Gizzi *et al.*, 1983; Movshon, Adelson *et al.*, 1985; Rodman and Albright, 1987) have suggested that some cells in MT, unlike other visual neurons, code the motion of whole patterns independently of the motions of contours making up the patterns. Simulations of the neural machinery underlying the responses of these MT neurons suggest that precise speed preferences may be crucial to their function (Albright *et al.*, 1986). Velocity tuning in MT may, therefore, contribute to a specific *type* of motion analysis not performed by the striate cortex.

Neural basis of velocity coding

The results presented here raise several points about the neural basis of the representation of visual stimulus velocity. First, the matching of speed selectivity for preferred and anti-preferred directions of slit motion in S1 and S2 cells suggests that the underlying neural wiring must be quite precise. It is not known for certain whether the direction and speed selectivities of MT neurons can be generated or sharpened within MT or are passed along from structures providing inputs to the area. However, selective ablation of inputs to MT suggests that MT is capable of generating direction selectivity, at least, from non direction-selective input (Rodman *et al.*, 1985, and in preparation). Secondly, the behavior of S2 cells suggests that analysis of slit motion in MT makes use of a type of coding ubiquitous in the visual system, namely that of opponent processing of stimulus contrasts. As is the case for brightness contrast and color selectivity, there is an antagonistic organization to the representation of the relevant stimulus dimension at the single-cell level, such that excitation

encodes one value of the stimulus dimension, and inhibition, the opposite value (here, the anti-preferred direction of motion).

The present study, as well as previous reports, has provided evidence that cortical direction selectivity characteristics remain invariant over changes in speed when the stimulus is a moving oriented slit of light. However, it is relevant to point out that speed-dependent alterations in direction tuning have been obtained in some cat striate cortex cells with moving textured stimuli (static noise fields) (e.g. Hammond and Reck, 1980). These alterations have been interpreted as evidence for separate underlying mechanisms of velocity coding for different types of visual stimuli. Movshon *et al.* (1980) have suggested that the progressively more bilobed direction tuning observed at optimal and higher speeds of texture motion is the result of sensitivity to the slower motion of oblique oriented components. Although we have not systematically studied the interaction of direction and speed selectivities for texture motion in MT, we have failed to observe strongly bimodal texture tuning curves in a sample of 34 MT neurons tested with texture motion at speeds estimated near optimal by hand (Albright, 1984). It remains unclear thus, whether texture and bar velocity tuning mechanisms are separable in area MT.

SUMMARY

The data presented here show that individual MT neurons are selective for both direction and speed of a moving stimulus and have preferred velocities. Moreover, both excitatory and inhibitory responses are velocity selective. The velocity coding properties of MT neurons differ from those of striate cortex cells in the role potentially played by inhibitory responses, in that MT cells may code a wider range of velocities, particularly high velocities, and in their contributions to pattern-motion processing. These observations help to further specify the contribution made by area MT to the analysis of visual motion.

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