Sensitivity of MST Neurons to Optic Flow Stimuli. I. A Continuum of Response Selectivity to Large-Field Stimuli

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SUMMARY AND CONCLUSIONS

1. Neurons in the dorsomedial region of the medial superior temporal area (MSTd) have large receptive fields that include the fovea, are directionally selective for moving visual stimuli, prefer the motion of large fields to small spots, and respond to rotating and expanding patterns of motion as well as frontal parallel planar motion. These characteristics suggested that these neurons might contribute to the analysis of the large-field optic flow stimulation generated as an observer moves through the visual environment.

2. We tested the response of MSTd neurons in two awake monkeys by systematically presenting a set of translational and rotational stimuli to each neuron. These $100 \times 100^\circ$ stimuli were the motion components from which all optic flow fields are derived.

3. In 220 single neurons we found 23% that responded primarily to one component of motion (planar, circular, or radial), 34% that responded to two components (planocircular or planoradial, but never circuloradial), and 29% that responded to all three components.

4. The number of stimulus components to which a neuron responded was unrelated to the size or eccentricity of its receptive field.

5. Triple-, double-, and single-component neurons varied widely in the strength of their responses to the preferred components. Grouping these neurons together revealed that they did not form discrete classes but rather a continuum of response selectivity.

6. This continuum was apparent in other response characteristics. Direction selectivity was weakest in triple-component neurons, strongest in single-component neurons. Significant inhibitory responses were less frequent in triple-component neurons than in single-component neurons.

7. There was some indication that the neurons of similar component classes occupied adjacent regions within MSTd, but all combinations of component and direction selectivity were occasionally found in immediate juxtaposition.

8. Experiments on a subset of neurons showed that the speed of motion, the dot density, and the number of different speed planes in the display had little influence on these responses.

9. We conclude that the selective responses of many MSTd neurons to the rotational and translational components of optic flow make these neurons reasonable candidates for contributing to the analysis of optic flow fields.

INTRODUCTION

Optic flow fields are the patterns of visual motion that an observer encounters while moving through the environment. Embedded in these patterns is information regarding self-motion and the structure of the environment (Gibson 1950; Koenderink 1986). Self-motion can be considered as translation along (Fig. 1A) and/or rotation around (Fig. 1B) head-centered axes in three-dimensional space. All optic flow fields are the result of some combination of these translational and rotational movements. Thus any complete model of self-motion must account for the influence of all of these movements on vision.

Some areas of extrastriate visual cortex are well suited to the analysis of visual motion. Among these is the medial superior temporal area (MST) identified in the superior temporal sulcus (STS) of the macaque monkey (Maunsell and Van Essen 1983; Ungerleider and Desimone 1986; Van Essen et al. 1981). MST has a preponderance of directionally selective neurons (Desimone and Ungerleider 1986; Tanaka et al. 1986; Van Essen et al. 1981) probably organized into two functionally distinct subregions (Komatsu and Wurtz 1988). The lateroventral region of MST (MSTi) is characterized by neurons that respond best to the motion of small spots of light. Chemical lesions and electrical stimulation of this region modify the maintenance of pursuit cyc movements, suggesting that MSTi might contribute to the generation of these motion-dependent movements (Dürsteler and Wurtz 1988; Komatsu and Wurtz 1989).

The dorsomedial region of MST (MSTD) is characterized by neurons that respond best to large-field motion, such as moving patterns of dots (Komatsu and Wurtz 1988). MSTd neurons have the largest receptive fields seen in MST, frequently covering more than a full quadrant of the contralateral visual field and extending into the ipsilateral visual field. Observations in anesthetized monkeys indicate that some MST neurons are sensitive to visual motion other than that in the frontoparallel plane (planar motion); they selectively respond to rotating or expanding visual stimuli (Saito et al. 1986; Tanaka et al. 1986, 1989; Tanaka and Saito 1989). These neurons were limited to a region in MST that almost certainly overlaps MSTd (Komatsu and Wurtz 1988). The preference of MSTd neurons for large-field visual stimulation and their sensitivity to rotating and expanding patterns of motion make them ideally suited to the analysis of optic flow fields.

We have examined the responses of MSTd neurons to stimuli designed to simulate the components of optic flow fields. In this paper our goal has been to study each of these neurons with the same set of $100 \times 100^\circ$ stimuli positioned to provide the best coverage of the estimated receptive field. In contrast to the approach used in previous studies (Saito et al. 1986; Tanaka et al. 1986, 1989; Tanaka and Saito 1989), our systematic presentation of planar, circular, and radial stimuli to all neurons isolated allowed us to quantify the relative strength of the response to each pattern of stimulus motion. This allowed us to determine the extent to
SELF MOVEMENT IN THREE DIMENSIONS

A Translation along axes

Up

\( Y \text{ axis} \)

In

\( Z \text{ axis} \)

Out

\( X \text{ axis} \)

Left

Counterclockwise

\( Z \text{ axis} \)

Clockwise

\( X \text{ axis} \)

Down

Right

B Rotation around axes

\( Y \text{ axis} \)

\( X \text{ axis} \)

\( Z \text{ axis} \)

\( \text{Up} \)

\( \text{In} \)

\( \text{Out} \)

\( \text{Left} \)

\( \text{Right} \)

\( \text{Down} \)

FIG. 1. Basis set of motion components. All motions in 3-dimensional space (represented by the 3 axes \( X, Y, \) and \( Z \)) consist of combinations of translation (A) and/or rotation (B) along or around these axes. In 2 cases rotation is very similar to translation; translation along the \( x \)-axis is similar to that for rotation around the \( y \)-axis; translation along the \( y \)-axis is similar to rotation around the \( x \)-axis. In these cases we routinely tested only translation.

which neurons that prefer circular or radial motion form subpopulations that are distinct from neurons that prefer planar motion. We found that, although some MSTd neurons are sensitive only to planar, circular, or radial stimuli, most are sensitive to two or three components of optic flow field motion. We also found that several response characteristics of these neurons vary systematically along a continuum that extends from those responding to a single optic flow component to those responding to all three components.

In the following paper (Duffy and Wurtz 1991) we consider the extent to which all of these responses to complex motion stimuli might result from sensitivity to simple planar motion. By varying the size and position of the optic flow stimulus, we stimulated different subregions of the receptive field. We found that the contribution of planar motion is least evident in single-component neurons and most evident in triple-component neurons. We then developed a hypothesis about possible mechanisms that would produce such a variety of responses to optic flow stimuli.

A brief report of this work has appeared previously (Duffy and Wurtz 1989).

METHODS

Behavioral and physiological procedures

Two monkeys (Macaca mulatta, No. 53XL and No. 79NR) were trained to sit in a plastic primate chair and perform a visual fixation task to obtain a liquid reward. The monkeys sat in the chair for several hours per day and were then returned to their home cages. High-protein monkey chow (Purina) was available ad libitum in their home cage and was supplemented daily by fresh fruit. All experimental protocols were approved by the Institute Animal Care and Use Committee and complied with National Institutes of Health policy on the humane care and use of laboratory animals.

After preliminary training, in which the monkey learned to look at a spot of light (Wurtz 1969), the monkey was prepared for recording experiments. With the animal under general anesthesia [pentobarbital sodium (Somnife), initially 20 mg/kg iv], scleral search coils were implanted in each eye according to the method of Judge et al. (1980). The search coil leads were passed subcutaneously to the top of the skull and attached to a plug. A stainless steel cylinder for single-neuron recording was positioned over a trephine hole in the skull over parietal cortex (AP 2, ML 115). Between 15 and 20 stainless steel screws were threaded into tapped holes in the skull; and, after the screws and the exposed skull were coated with a cyanoacrylate cement (Verbond), the cylinder, eye coil plugs, and a stainless steel socket for head restraint were embedded in an acrylic cap that covered the top of the skull. In the immediate postoperative period the monkey was given analgesics as judged appropriate by the attending veterinarian.

After surgery the monkeys were trained on the behavioral task used in these experiments, with the positions of both eyes monitored by the use of the magnetic search coil technique (Robinson 1963). At the start of each trial, the projected image of a red light-emitting diode (LED, 0.25° in diameter, 2.7 cd/m²) appeared on a tangent screen 50 cm in front of the monkey. If the monkey fixated the LED image within 0.5-1.5 s after the patterned light stimulus was projected onto the screen. The fixation point remained illuminated for 0.5-1.5 s after the patterned light stimulus was turned off. Task parameters were adjusted to maintain a high success rate, and the monkeys acquired the final version of the task to the 95% correct level in a few weeks.

The behavioral tasks were controlled by the Real-Time Experimental system (REX) (Hays et al. 1982) running on a dedicated PDP 11/33 computer. Single-neuron discharges were recorded, amplified, digitized at 1 kHz, and stored along with indications of stimulus and behavioral events on a disk and then archived on magnetic tape. Eye position was monitored during all experiments for behavioral control but was not stored. On-line displays indicated the relation of single-neuron discharge to stimulus and behavioral events and showed eye position continuously, but all data analysis was performed off-line.

Recordings were made in one hemisphere of each monkey. A guide tube and grid system (Crist et al. 1988) allowed recordings to be made through stainless steel guide tubes extending vertically in the stereotaxic plane through the dura to a depth \( \sim 5 \text{ mm} \) above the STS. At the beginning of the recording session a guide tube stylet was removed and an epoxy-coated tungsten electrode.
(Frederick Haer) was inserted. Electrode impedance ranged between 1.5 and 2.0 MΩ. The electrode was then advanced using a hydraulic microdrive (Narishige). Neuronal activity and electrode depth were noted to establish the relative position of landmarks. These landmarks included the successive gray and white matter layers and neuronal response properties. Multicell records were used only to guide electrode positioning relative to light-sensitive groups of neurons. Studies were initiated only on well-isolated neurons to increase the probability that recording would remain stable for the several hours required to conduct these experiments.

MSTd was identified by physiological criteria previously established in this laboratory (Komatsu and Wurtz 1988): direction selectivity, large receptive fields that came close to the fovea, and preference for large random-dot stimuli. Identification of MST was verified by the sequence of recordings and their depth in the STS, with the electrode moving through MST on the anterior bank and then frequently through the middle temporal area (MT) on the posterior bank.

Histological verification of recording sites was done in one of the two monkeys (No. 53X); histology from the other monkey is not yet available. When the experiments were completed, electrolytic marks were made along a penetration in each of three guide tubes at sites on both the anterior and posterior banks of the STS. Two days later the monkey was deeply anesthetized with pentobarbital sodium followed by intracardiac perfusion, first with saline and then with 10% Formalin. The posterior one-half of one hemisphere was frozen and cut into 50-µm serial sections in the sagittal plane. Every fourth section was stained for cell bodies with thionin, and every fifth section was stained for myelinated fibers with a modified silver stain (Gallyas 1979). Camera lucida drawings were made of the relevant sections to establish the locations of marks on the three penetrations relative to anatomic landmarks in the STS. The approximate location of other recording sites was estimated from the relative position of the guide tubes and the distribution of electrode tracks emanating from them.

Visual stimulation procedures

The translucent tangent screen onto which stimuli were back projected subtended the central 100° × 100° of the monkey’s visual field when the fixation point was in the center of the screen. Manually controlled light stimuli were first used while the monkey fixated to test the neuron for light sensitivity, to estimate the approximate borders of the receptive field, and to determine motion sensitivity and direction preferences. We used both a handheld projector that produced a random dot pattern, which could be varied from 10° × 10° to 100° × 100°, and an ophthalmoscope, which projected an image of a bar that varied between 2° × 5° and 10° × 25°.

In examining the responses of MST neurons, we found that the estimate of receptive field size was dependent on the stimulus used to determine those dimensions. When using a 3° × 12° bar stimulus, we obtained smaller receptive fields, typically 10° × 20°, that included the fovea. When using a 30° × 30° random-dot pattern stimulus, we obtained larger receptive fields, typically 50° × 50°, that also included the fovea. We regarded even the larger stimulus areas as a conservative estimate of receptive field size because we could only produce limited motions with our handheld stimuli. All estimates of receptive field size and position in text and figure captions are derived from the larger estimate on the basis of the sustained response of neurons to these handheld stimuli. We have used these estimates of field size because they are the best we could generate, but we emphasize that in many cases they are only rough estimates of the size of the receptive field.

After the approximate receptive field dimensions and response properties were established, computer-generated stimulus patterns were rear projected onto the tangent screen by a TV projector (Sony 900). REX controlled the pseudorandom sequence of stimulus presentation as well as the time when the stimulus and the fixation point were turned on and off. Stimulus duration was either 1,000 or 1,500 ms. The random-dot stimulus patterns were generated off-line, stored, and displayed by the use of an 80286-based personal computer. The programs controlling these displays accepted user specifications for the type of motion being simulated. The dots subtended 0.75° and were 1.8 cd/m² against a background of 0.2 cd/m². All data analyzed in these experiments were derived from the experiments using computer-generated displays.

The projected stimulus filled the 100° × 100° tangent screen in front of the monkey. We endeavored to provide the best coverage of the receptive field area estimated by hand by the use of a strategy very much like that used by Tanaka and co-workers (Saito et al. 1986; Tanaka and Saito 1989; Tanaka et al. 1989). We began by centering the stimulus on the fixation point because the receptive fields included the fovea and frequently extended well into the ipsilateral visual field. For these neurons, centering the stimulus on the fixation point placed a large fraction of the stimulus on the receptive field. For neurons with receptive fields that extended more peripherally, we shifted the stimulus to cover the receptive field better. In some cases best coverage of the receptive field required a shift in stimulus position of 30°–50°. Such a shift was accomplished by moving the fixation point toward the right or left edge of the screen to bring a larger fraction of the contralateral visual field onto the screen. We rotated the monkey chair so that the eye remained in the same position in the orbit to avoid any potential orbital position effects such as those observed in posterior parietal cortex (Andersen and Mountcastle 1983; Andersen et al. 1985).

The display was capable of generating all components of translation along or rotation around the horizontal, vertical, or depth axes. These 12 basic types of motion along the three axes of three-dimensional space are depicted in Fig. 1. Figure 1A shows translation of the observer in head centered coordinates along the X-, Y-, and Z-axes, whereas Fig. 1B shows rotation of the observer around the X-, Y-, and Z-axes. The algorithms used to simulate each type of motion are described in the APPENDIX.

Figure 2 illustrates the more restricted set of motion stimuli used. Translations along the horizontal (X) and vertical (Y) axes (Fig. 1A) are represented by the frontoparallel planar motion stimuli (labeled planar). In most cases, four stimuli were sufficient to describe the planar directionality of these neurons. This was verified in 57 neurons tested with eight planar directions (at 45° intervals), which, in general, yielded broad unimodal directional tuning that was adequately indicated by the four directions of planar stimulus motion shown in Fig. 2.

Rotational stimuli consisted of clockwise and counterclockwise circular motion around the depth (Z) axis of Fig. 1A. Experiments on 36 neurons showed that rotation around the X- and Y-axes produced responses much like those evoked by translation along the Y- and X-axes, respectively. Therefore subsequent experiments did not include the X- and Y-rotations.

Translation along the depth (Z) axis of Fig. 1A produced a radial expansion of the stimulus, as shown for inward and outward radial motion in Fig. 2.

The stimuli contained 300 dots randomly distributed across the screen. All dots were moving as soon as they appeared on the screen. For all stimuli, the appearance of new dots was controlled to maintain constant and uniform dot density. For planar stimuli, as a dot disappeared on one edge of the screen, another appeared at the opposite edge. For circular stimuli, dots disappearing at the edge of the square screen (Fig. 2) reappeared at an appropriate point and time to simulate continued circular motion. For radial stimuli, as a dot disappeared in the periphery, one appeared near the center (or vice versa) along that trajectory and at a point selected to maintain uniform dot density throughout the stimulus.
That is, each dot appeared at the point closest to the center (or periphery) that accommodated it without changing the dot density between itself and the center (or periphery) of the stimulus.

The average dot speed was 40°/s in all stimuli, a speed at which MST neurons consistently respond (Tanaka and Saito 1989). In planar stimuli this was the speed of all dots. However, to simulate optic flow fields accurately, the circular and radial stimuli had to have increasing dot speed from the center to the periphery (as indicated by the length of the arrows in Fig. 2). In these stimuli, the average speed across the stimulus was maintained at 40°/s.

In the first 126 neurons studied (53XL1-53XL126), all dots conformed to these speed specifications. In the remaining 94 neurons, the dots in each stimulus were randomly divided among three groups moving at average speeds of 20, 40, and 60°/s, respectively. Incorporating this range of speeds in the stimuli achieved two goals. First, it minimized the differences between planar stimuli and circular or radial stimuli. Whereas planar stimuli have a uniform speed, circular and radial stimuli have speed gradients that incorporate speeds above and below the average. Superimposing several groups of dots moving at different average speeds resulted in all stimuli having a broad range of individual dot speeds. Second, the three overlapping groups of dots moving at different average speeds enhanced the realism of our optic flow field simulations by adding motion parallax cues. The three groups of dots were seen by human observers as being on three superimposed transparent planes moving at various distances in depth (the slowest dots appearing to be furthest from the observer). The effects of variations in dot density, speed, and number of planes are presented in RESULTS.

The set of eight stimuli (4 planar, 2 circular, 2 radial) were randomly interleaved along with a no-stimulus control trial to produce blocks of 6–10 responses per stimulus. We displayed the discharge of cells on a series of trials on a raster display and the average response over a series of trials on a spike density display. We produced this spike density display by replacing the 1-ms-wide square pulse that represented each spike by a Gaussian pulse with a width corresponding to a standard deviation of 20 ms. These spike density displays were produced with the use of algorithms of Richmond et al. (1987).

RESULTS

We studied 220 single neurons in MSTd with both manual and computer-controlled visual stimuli. The MSTd neurons we studied had large receptive fields: 86% of the neurons had receptive fields that included a substantial part of the upper contralateral quadrant. In addition, 50% of the neurons included part of the lower contralateral quadrant, 23% included part of the upper ipsilateral quadrant, and 21% included part of the lower ipsilateral quadrant. Although the size of the field was difficult to determine exactly, our estimate of the mean size corresponded to a square 63° on each side. The largest receptive fields were usually ~100×100°, with one field being 100×185°. The smallest receptive fields were ~5×10°.

Selectivity for components of optic flow stimuli

Neurons yielded two types of responses to the components of optic flow stimuli (Fig. 2). As shown in Fig. 3, the
FIG. 3. Significance of the tonic component of the visual response compared with the early phasic component. A: spike density displays of the responses of a neuron (see METHODS) to the standard set of 8 stimuli. This neuron gave a clear tonic response to the leftward, downward, and inward components of motion but a phasic response regardless of the type of motion stimulus. The receptive field was primarily in the upper left visual quadrant contralateral to the side of the brain in which the neuron was studied. B: control stimuli. In the no-dots condition the monkey fixated but no stimulus came on; these trials were used as a baseline with which stimulus-evoked activity was compared. In the static condition dots came on but there was no movement. In the random condition, dots came on but the trajectory of each dot was randomly assigned to that of a dot in 1 of the 8 stimuli in A. In this and subsequent figures (unless otherwise indicated), spike density histograms represent the average of 6–8 trials, with the location of the vertical bar indicating time of stimulus onset and its height indicating a discharge rate of 150 spikes/s. Tick marks on the horizontal baseline indicate 200 ms. Dark horizontal bar indicates the duration of the stimulus period, here 1 s.

The first response was usually a phasic increase in discharge rate that occurred in the interval between 70 and 400 ms after stimulus onset and lasted between 100 and 300 ms (for example, the response to outward radial motion in Fig. 3A). The second response was a tonic increase in discharge rate that could be clearly identified no later than 400 ms after stimulus onset and lasted 100–400 ms after the stimulus was turned off. We found both an increase in tonic discharge rate (Fig. 3A, inward radial motion) and a decrease in tonic discharge rate (Fig. 3B, static stimulus), to which we will refer as excitatory and inhibitory responses, respectively.

We have found neurons that selectively respond to the three types of stimulus motion described previously (Saito et al. 1986): planar (frontoparallel), circular, and radial. Figure 4 illustrates the responses of a planar-selective neuron, which preferred leftward stimulus motion (Fig. 4A); a circular-selective neuron, which preferred counterclockwise stimulus motion (Fig. 4B); and a radial-selective neuron, which preferred inward stimulus motion (Fig. 4C). In each of these neurons many stimuli evoked a phasic response, but only one stimulus evoked a tonic response. The continuation of the discharge after the end of the stimulus (Fig. 4A, leftward, for example) was frequently observed.

Three other types of neurons combine these response selectivities. We refer to neurons that combine two response selectivities as double-component neurons (Fig. 5A and B) and neurons that combine all three response selectivities as triple-component neurons (Fig. 5C). Figure 5A shows a planocircular double-component neuron that responded to
rightward planar and clockwise circular motion stimuli. There is no response to either of the radial motion stimuli. Figure 5B shows a planoradial double-component neuron that responded to rightward planar and outward radial motion. There is no response to either of the circular motion stimuli. Figure 5C shows a planocirculoradial triple-component neuron that responded to rightward and upward planar motion stimuli, counterclockwise circular motion stimuli, and outward radial motion stimuli.

Although a given neuron may respond to more than one type of stimulus motion, the response to each type of motion remains direction selective. For example, the planocircular neuron (Fig. 5A) yields a direction-selective response to planar and circular stimuli; only rightward planar motion and only clockwise circular motion evoked a substantial response. Similarly, the planoradial neuron (Fig. 5B) responds to rightward planar motion and outward radial motion, but not to all planar or all radial motion stimuli.

We quantified the responses of each neuron to the stimuli shown in Fig. 2. To do so we compared the mean activity during the tonic response in the period from 400 ms after stimulus onset to the end of the stimulus with the activity during the same period in the no-dots control trial. We excluded the first 400 ms to remove even the most prolonged initial phasic response. Figure 6 shows the responses illustrated in Figs. 4 and 5 quantified in this manner. The diamonds show the discharge rate for each stimulus condition; the filled diamonds indicate excitatory responses that were significantly different from the control period. We found that this statistical determination of the significance of a response closely matched our recognition of responses by inspection. A separate analysis that compared the average response to each stimulus with the average response to all stimuli (rather than with the control period) generally yielded the same results.

Table 1 shows the results of the statistical classification of the 220 neurons studied. We found that 86% of MSTd neurons responded to planar, circular, and/or radial components of optic flow. Triple-, double-, and single-component neurons were all substantially represented in this sample. Fifteen percent of the responsive neurons yielded exclusively circular or exclusively radial responses. The remainder responded to planar stimuli, usually in combination with responsiveness to circular and/or radial stimuli. These observations differ from those of Saito et al. (1986), who found that 30% of their neurons yielded responses exclusively to rotation or expansion of the stimulus. The double-component neurons included equal numbers of plano-
A PLANOCIRCULAR

B PLANORADIAL

C PLANOCIRCULARRADIAL

FIG. 5. Examples of neurons that responded to multiple components of stimulus motion. Three mixed types of responses were observed combining responses to planar, circular, and/or radial stimuli. A: a planocircular neuron responded both to rightward planar motion and to counterclockwise circular motion and had a receptive field in the upper visual field extending 20–25° on each side of the vertical meridian and 15° below the horizontal meridian. B: a planoradial neuron responded both to rightward planar motion and to outward radial motion and had a large receptive field in the right (contralateral) field with unascertainable borders. C: a planocirculoradial neuron responded to rightward and upward planar motion, to counterclockwise circular motion, and to outward radial motion and had a receptive field centered in the lower right (contralateral) quadrant. Whereas each of these neurons responds to > 1 type of stimulus motion, they all remain direction selective within each type of stimulus motion. For example, the planocircular neuron responds to only 1 direction of planar motion and only 1 direction of circular motion. Vertical bar indicates 100 spikes/s. Horizontal bar indicates a stimulus period of 1.5 s.

circular and planoradial responses but no circuloradial neurons. Inspection of the spike densities also identified no case of substantial circular and radial responses in the absence of a planar response.

We considered the possibility that triple- and double-component responses might be the result of having stimulated one edge of the receptive field of single-component neurons, in spite of our attempt to effectively position the stimulus on the receptive field of the cell (see METHODS). This partial stimulation would be most likely if the receptive fields that gave triple- and double-component responses were smaller and/or more eccentrically positioned than those that gave single-component responses. Table 2 shows that the mean area of the receptive fields and the variation in these fields were similar for triple-, double-, and single-component neurons. The mean receptive field eccentricity and its variation were also similar. In addition, if partial stimulation of the receptive field accounted for the different levels of component selectivity, smaller response amplitudes might be expected from triple- and double-component neurons. Table 2 also shows no substantial difference in response amplitude between groups of neurons. Thus we conclude that partial stimulation does not account for triple- and double-component neurons. More definitive confirmation of these findings comes from the stimulation of small subfields within the receptive field, considered in detail in the following paper (Duffy and Wurtz 1991).

Continuum of response selectivity

Triple-, double-, and single-component neurons show substantial variation in the strength of their responses. This is illustrated by three-dimensional plots in which the responses of each neuron are represented as a single dot (Fig.
FIG. 6. Quantification of single and multiple component responses. Plots are of the mean response in the 400- to 1,000-ms period after stimulus onset for responses shown in the previous 2 figures. Dashed lines show activity level in the no-dots control trial (+1 SE around the mean). Response to each stimulus that was significantly different (P < 0.01 in a Student’s t test) from control trials is represented by filled diamonds. In A, B, and C the only significant excitatory responses are to planar, circular, or radial stimulus motion, respectively (single component responses). In D and E significant excitatory responses are to planar and circular or to planar and radial stimulus motion, respectively (double-component responses). In F significant excitatory responses are to planar, circular, and radial stimulus motion (triple-component responses).

The location of each dot along the planar, circular, and radial axes represents the response amplitude to that motion component. The responses of single-component neurons vary mainly along the axis of the preferred component (Fig. 7, A–C), the responses of double-component neurons vary mainly across the surface defined by the two axes of the preferred components (Fig. 7, D and E), and the responses of triple-component neurons vary in the space defined by all three component axes (Fig. 7F).

Combining triple-, double-, and single-component neurons reveals that the variation in component strength is continuous throughout the sample (Fig. 8). There is no indication of clustering into separate response groups, but rather the neurons lie along a continuum of responsiveness to each type of stimulus (even when viewed by the authors from different angles). This emphasizes that these classes are recognized by virtue of the thresholding function imposed by our statistical method for identifying significant
FIG. 7. Response of the population of single-component (A–C), double-component (D and E), and triple-component (F) neurons. Response of each neuron studied is represented as a dot, and the position of a dot along the planar, circular, and radial axes indicates the highest mean activity level of the neuron (over control levels) evoked by the stimuli having that type of motion. To simplify the display, the minimal response is set to zero (eliminating inhibition) and the maximum response is set to 75 spikes/s (only 3 neurons had responses >75 spikes/s). A neuron was placed in one category or another using the statistical tests described for Fig. 6, but once placed in that category its responses to planar, circular, and radial stimuli are all displayed. Thus several cells that had a significant response only to planar stimuli also had an easily visualized but not significant response to circular stimuli as well. Single component neurons have variation confined mainly to 1 axis; double component neurons have variation confined largely to a plane defined by 2 axes (planar and circular or planar and radial); triple-component neurons show responses distributed throughout the space defined by the 3 axes.

Responses. Clearly, the differences among triple-, double-, and single-component neurons represent quantitative variations, not qualitative distinctions. This continuum of response selectivity implies that continuous variation in some quantitative parameters might underlie differences between these neurons.

Other response parameters also vary along this continuum from triple- to double- to single-component neurons. These include the direction selectivity within each response component and the number of significant inhibitory responses.

DIRECTION SELECTIVITY. We examined the strength of the direction selectivity for each component of stimulus motion to which a neuron responded. We found that triple-component neurons have the weakest direction selectivity, with frequent significant responses to opposite directions of motion for a particular stimulus component, and that single-component neurons have the strongest direction selectivity. The neurons shown in Fig. 9 illustrate these differences. The triple-component neuron (Fig. 9A) gives significant responses to both directions of circular and radial motion. The double-component neuron (Fig. 9B) shows greater direction selectivity, responding to only one direction of radial motion but to two directions of planar motion. The single-component neuron (Fig. 9C) shows the greatest direction selectivity, with responses to only one direction of motion.

We quantified the direction selectivity for the 220 neu-
Neurons were classified according to which stimuli evoked significant excitatory responses. Stimulus trials were compared with unstimulated control trials with the use of a Student's t test (P < 0.01). Values in parentheses are percentages. *No component or direction selectivity. About 1/3 of these nonselective cells showed no significant excitatory or inhibitory responses to optic flow stimuli, in spite of having displayed apparent responsiveness to light stimuli when tested by hand; about 1/3 showed significant inhibitory responses.

TABLE 1. Classification of neurons by response components

<table>
<thead>
<tr>
<th>No. of neurons</th>
<th>Single component</th>
<th>Planar</th>
<th>Circular</th>
<th>Radial</th>
<th>Double component</th>
<th>Planocircular</th>
<th>Planoradial</th>
<th>Circuloradial</th>
<th>Triple component</th>
<th>Planocirculoradial</th>
<th>Nonselective*</th>
<th>Total</th>
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<tr>
<td></td>
<td>51 (23)</td>
<td>23 (10)</td>
<td>08 (4)</td>
<td>20 (9)</td>
<td>74 (34)</td>
<td>37 (17)</td>
<td>37 (17)</td>
<td>0 (0)</td>
<td>63 (29)</td>
<td>32 (14)</td>
<td>220 (100)</td>
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We also determined the number of directions of planar motion for which each neuron gave a significant response to obtain some idea of the directional tuning of these cells. Nearly one-half of the neurons (49%) showed specific responses to a single direction of planar stimulus motion with no significant response to any other direction of planar stimulus motion (unidirectionality, Fig. 9A). Within the triple-, double-, and single-component groups, we found a substantial difference in the number of unidirectional neurons: 19% of triple-component neurons, 62% of double-component neurons, and 87% of single-component neurons.

TABLE 2. Receptive field characteristics

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<th>Single Component Neurons</th>
<th>Double-Component Neurons</th>
<th>Triple-Component Neurons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size, deg ± SD*</td>
<td>62 ± 54</td>
<td>64 ± 53</td>
<td>63 ± 60</td>
</tr>
<tr>
<td>Eccentricity, deg ± SD†</td>
<td>24 ± 17</td>
<td>28 ± 18</td>
<td>26 ± 17</td>
</tr>
<tr>
<td>Best response, spikes/s‡</td>
<td>22</td>
<td>24</td>
<td>28</td>
</tr>
</tbody>
</table>

* Receptive field dimensions were obtained by delineating the area on the screen that evoked neuronal responses when stimulated by a random dot pattern moved manually. †Eccentricity is the distance between the fixation point and the center of the receptive field. ‡Best response to each stimulus minus activity in the control period. Mean response or best response without control level removal gave similar results.

Neurons were classified according to which stimuli evoked significant excitatory responses. Stimulus trials were compared with unstimulated control trials with the use of a Student's t test (P < 0.01). Values in parentheses are percentages. *No component or direction selectivity. About 1/3 of these nonselective cells showed no significant excitatory or inhibitory responses to optic flow stimuli, in spite of having displayed apparent responsiveness to light stimuli when tested by hand; about 1/3 showed significant inhibitory responses.

We also determined the number of directions of planar motion for which each neuron gave a significant response to obtain some idea of the directional tuning of these cells. Nearly one-half of the neurons (49%) showed specific responses to a single direction of planar stimulus motion with no significant response to any other direction of planar stimulus motion (unidirectionality, Fig. 9A). Within the triple-, double-, and single-component groups, we found a substantial difference in the number of unidirectional neurons: 19% of triple-component neurons, 62% of double-component neurons, and 87% of single-component neurons.

Neurons were classified according to which stimuli evoked significant excitatory responses. Stimulus trials were compared with unstimulated control trials with the use of a Student's t test (P < 0.01). Values in parentheses are percentages. *No component or direction selectivity. About 1/3 of these nonselective cells showed no significant excitatory or inhibitory responses to optic flow stimuli, in spite of having displayed apparent responsiveness to light stimuli when tested by hand; about 1/3 showed significant inhibitory responses.
showed unidirectional planar responses. Thus this limited measure shows a trend of increasing planar directional tuning as one passes from triple- to double- to single-component neurons.1

Inhibitory Responses. Many neurons gave tonic inhibitory responses to optic flow stimuli. Although these inhibitory responses were not used in the classification of these neurons, they did reflect the continuum from triple- to double- to single-component neurons. In our sample, 96% of the neurons yielded at least one inhibitory response, defined as activity significantly below the control rate. We looked at differences in inhibition among the triple-, double-, and single-component neurons in three ways. First, the percentage of the neurons showing any significant inhibition varied between response classes: 25% of the triple-component neurons, 41% of the double-component neurons, and 59% of the single-component neurons showed at least one significant inhibitory response. This trend is evident in the sample neurons illustrated in Fig. 9. This change in the frequency of inhibition was not due to differences in background activity, which might impair recognition of inhibition. The background discharge rate was about the same across component groups: 9.8 ± 7.7, 9.6 ± 7.3, and 9.4 ± 5.9 (SE) (spikes/s) for triple-, double-, and single-component neurons, respectively.

Triple-, double-, and single-component neurons also differed in the relative percentages of excitatory and inhibitory responses evoked from each neuron. Table 3 shows that the number of significant excitatory responses per neuron decreased from triple- to double- to single-component responses, as it must given our definition of these classes. However, there was also a substantial increase in the number of significant inhibitory responses: 7% for triple-, 26% for double-, and 64% for single-component neurons. Because tonic excitatory and inhibitory responses are mutually exclusive, the decreasing number of excitatory responses from triple- to double- to single-component neurons affords increasing opportunities for inhibitory responses. This could account for the increasing inhibition in the continuum from triple- to double- to single-component neurons. However, when we corrected for this, as described in Table 3, the inhibitory responses still increased in this continuum by 12% for triple-, 19% for double-, and 27% for single-component neurons.

The third way in which inhibition differed among triple-, double-, and single-component neurons was in the relation of inhibitory responses to excitatory responses. In some cases, inhibitory and excitatory responses were evoked by opposite directions of stimulus motion; in other cases they occurred while the opposite direction evoked no response. Eighty-six percent of triple-component inhibitory re-

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1 Fifty-seven neurons were studied with 8 directions of planar motion at 45° intervals. Forty-one of these neurons responded to planar motion: 27% responded to only 1 direction, 24% responded to 2 adjoining directions, 17% to 3, 7% to 4, 5% to 5, 3% to 6, 5% to 7, and 7% to all 8. An additional 5% responded to 2 opposite directions of planar motion. We also found some relationship between the degree of planar direction selectivity and the frequency of circular and radial unidirectionality: the greater the number of planar directions that evoked a significant response, the greater the probability that the circular and/or radial responses would be significant for both directions of circular and/or radial stimulus motion. Only 10% of the planar unidirectional neurons showed circular or radial bidirectionality. In contrast, 26% of the planar neurons that responded to the 2 adjoining directions showed circular or radial bidirectionality, 50% of the 3 direction planar neurons showed circular or radial bidirectionality, and 78% of the 4 direction planar neurons showed circular or radial bidirectionality. The relationship between planar directionality and circular or radial directionality is stronger for the triple-component neurons than for the double-component neurons.
responses, 43% of double-component inhibitory responses, and 19% of single-component inhibitory responses occurred in a direction opposite to one that evoked an excitatory response. The result is a decreasing link between significant inhibitory responses and significant excitatory responses from triple- to double- to single-component neurons. Thus along this continuum inhibition becomes increasingly evident and increasingly acts to sharpen component selectivity as well as direction selectivity.

Intracortical distribution of responses

Lesions made along electrode penetrations at the end of recording in one monkey verified that the neurons studied were on the anterior bank of the STS. These marks indicated that the recording sites were within or below the densely myelinated area with penetration tracks traversing cortex at a 45°-65° angle. Marks made as these penetrations continued into the posterior bank were located in either the densely myelinated area indicative of MT or immediately lateral and ventral to it.

These marks were intended to confirm the location of the recording sites within MST but were too sparse to indicate any localization of MST neurons or columnar organization with different stimulus selectivities. We therefore combined individual penetrations and examined the characteristics of neurons encountered in each guide tube for evidence of any pattern in the distribution of response properties. We found no clustering of neurons in different guide tubes that showed a preference for planar, circular, or radial selectivity or for triple-, double-, or single-component responses. However, within some guide tubes, we did find some consistency of response types. We reconstructed neuron locations from all penetrations within each guide tube by aligning each penetration to a physiological landmark for depth, most commonly a border between gray and white matter. The relative depth of each neuron was then transferred onto a cumulative representation of the recordings in that guide tube.

Figure 11A shows the reconstruction of neuron locations in a guide tube that failed to show a consistent pattern in the distribution of responses. In this guide tube we found circular selectivity intermixed with radial selectivity as well as single-, double-, and triple-component neurons all in close proximity to one another. In contrast, Fig. 11B shows the reconstruction of neuron locations in a guide tube that had neurons with more consistent response properties. All of the neurons in this guide tube showed planar and/or circular selectivity.

Table 3. Frequency of inhibitory responses

<table>
<thead>
<tr>
<th></th>
<th>Single-Component Neurons</th>
<th>Double-Component Neurons</th>
<th>Triple-Component Neurons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of neurons</td>
<td>51</td>
<td>74</td>
<td>63</td>
</tr>
<tr>
<td>Tonic excitatory responses per neuron*</td>
<td>1.0</td>
<td>2.7</td>
<td>4.9</td>
</tr>
<tr>
<td>Tonic inhibitory responses per neuron</td>
<td>1.8</td>
<td>1.0</td>
<td>0.4</td>
</tr>
<tr>
<td>Inhibitory responses as percent tonic responses</td>
<td>64</td>
<td>26</td>
<td>7</td>
</tr>
<tr>
<td>Inhibitory responses as percent opportunities†</td>
<td>27</td>
<td>19</td>
<td>12</td>
</tr>
</tbody>
</table>

*The definition of single, double, and triple component neurons requires a minimum of 1, 2, and 3 responses per neuron, respectively. The more robust increase found in these studies reflects the impact of increasing direction selectivity. †The fixed number of stimuli, and the fact that a tonic excitatory response precludes a tonic inhibitory response, results in more potential instances of tonic inhibition as one progresses from triple- to double- to single-component neurons. That is, a neuron having three tonic excitatory responses can have a maximum of five tonic inhibitory responses, whereas a neuron having one tonic excitatory response can have up to seven tonic inhibitory responses. Across this row, the observed number of tonic inhibitory responses for single, double, and triple component neurons is expressed as a tiny percentage of the maximum number they might have had – the number of opportunities for an inhibitory response.
parametric studies of responses to optic flow fields

To determine whether our stimuli were particularly dependent on the dot speeds, dot densities, and dot planes that we used, we evaluated these variables on the responses of 16 neurons. Approximately equal numbers of single-, double-, and triple-component neurons were represented in the sample. Stimulus motion was always in the direction preferred by the neuron studied.
Figure 12A shows the responses to stimuli in which the average dot speed was 10, 20, 40, 60, or 80°/s. In these neurons, there was no substantial change in response amplitude over this range of stimulus speeds. However, three neurons showed substantial relations between stimulus speed and response amplitude, one decreasing, one increasing, and one showing a bimodal relationship. Figure 12B shows the lack of substantial variation in the response of these neurons to stimuli that vary only in the total number of dots contained in the stimulus (from 25 to 350). Figure 12C shows the responses of these neurons to stimuli that had several planes of motion. In no case was there a substantial change in the response with increasing number of speed planes.

**DISCUSSION**

**Selectivity of MSTd neurons for optic flow stimuli**

We used a set of translational and rotational stimuli from which all optic flow fields can be derived to systematically investigate the responses of MSTd neurons. We have confirmed the observation that some MST neurons respond to circular or radial stimuli (Saito et al. 1986; Tanaka and Saito 1989; Tanaka et al. 1989). However, we found that the vast majority of MSTd neurons respond to some combination of stimulus components that include planar motion: triple-component neurons respond to planar, circular, and radial motion, whereas double-component neurons respond to planar and circular or planar and radial motion. Tanaka et al. (1986; 1989) did not find these combined responses, which we attribute to their experimental strategy. They first did qualitative stimulation to determine whether each neuron responded to planar stimuli; and, if it responded to these stimuli, they did not study it with circular or radial stimuli. In contrast, we quantified the response of all neurons to planar, circular, and radial motion; and this allowed us to recognize the high frequency of triple- and double-component neurons.

We found that these neurons fell along a continuum of response strength for planar, circular, and radial stimuli—they differed quantitatively along this continuum, not qualitatively as distinct subpopulations. Other characteristics of these responses also varied along the continuum from triple- to double- to single-component neurons. These included increasing direction selectivity and increasing impact of inhibitory responses.

Increasing inhibition might contribute to the increasing optic flow field selectivity along the continuum. Among triple component neurons, inhibition is largely limited to stimulus directions opposite those that evoke excitation and might therefore act primarily to sharpen direction selectivity. In contrast, among single-component neurons, inhibition is also evoked by a broader range of directions of stimulus motion (broader tuning). In this case the inhibition may be acting to sharpen the direction tuning of the cells and to reduce the response of a neuron to other components of motion. Thus inhibition may act to sharpen direction selectivity, direction tuning, and component selectivity.

These differences may indicate progressive changes in the receptive field organization that supports these responses. However, any interpretation of causal relationships between these response parameters requires an understanding of the underlying mechanisms. In the following paper we begin to explore these mechanisms (Duffy and Wurtz 1991).

**Neuronal strategies for optic flow analysis**

The optic flow field specifies the heading and path of self-motion (Gibson 1950; Koenderink 1986; Lee 1980) and can be used by human observers to judge the direction of simulated self-motion to within ~1° of arc (Warren et al. 1988; Warren and Hannon 1990). In fact, optic flow fields have such robust impact on perceived self-motion that they can induce the illusion of self-motion in a stationary observer (Berthoz et al. 1975). Optic flow fields can also stabilize posture (Berthoz et al. 1979), with illusory tilt being induced by circular stimuli (Dichgans et al. 1972; Held et al. 1975). The perception of self-motion and body position must continuously interact to guide and stabilize movement through the environment (Lee 1976; Lestienne et al. 1977).

The stimuli used in our experiments simulate the components of naturally occurring optic flow fields, but such optic flow fields often combine these components. To evaluate the potential contributions of MSTd neurons to optic flow field analysis, we must consider how they might respond to these combinations. The continuum of response selectivity from triple- to double- to single-component neurons affords two strategies for representing optic flow fields. First is a feature-matching strategy, in which individual neurons represent specific optic flow fields. A flow field combining planar, circular, and radial motion (e.g., self-motion forward to the right with clockwise rotation) would activate a specific set of triple-component neurons. Second is a population-encoding strategy, in which the optic flow field is represented in the responses of many MSTd neurons acting in concert. A flow field combining planar, circular, and radial motion would activate all neurons sensitive to that planar motion, and/or that circular motion, and/or that radial motion. These two ways of representing the optic flow field may coexist as independent strategies used by the same neuronal population. This raises the intriguing notion of redundancy in cortical information processing, not just by encoding information in the many neurons of a population or in several subpopulations, but also in more than one code.

The role of MSTd neurons in analyzing optic flow fields is also indicated by the stimulus parameters to which they do not respond (Fig. 12). Their lack of sensitivity to the density of the stimulus (over the range we have tested) is consistent with the lack of sensitivity of MST neurons to the texture of the stimulus (Tanaka and Saito 1989). The broad range of speed sensitivity we observed confirms previous findings (Tanaka and Saito 1989). This finding is consistent with the fact that circular and radial flow fields contain a range of speed sensitivities (slow in the center, fast in the periphery) so that broad speed sensitivity would be needed to interpret stimuli containing such motion. It is also consistent with the insensitivity to stimulus speed found in interpreting optic flow fields in studies of human performance (Warren et al. 1988). The number of apparent planes of moving stimuli had little influence on the re-
sponses of these neurons. Looking at the stimuli one has a clear perception of separate planes, with the fastest one being closest to the observer. Under the conditions of this experiment, MSTd neurons do not seem to make this distinction. Thus they might not account for this aspect of optic flow field analysis. However, motion at multiple depths is invariably included in natural optic flow fields, and the absence of such differential motion leads humans to inaccurate estimates of simulated direction of self-motion (Warren and Hannan 1990).

The relative insensitivity of MSTd neurons to the density, texture, speed, and relative depths of stimulus elements stands in sharp contrast to their selectivity for the pattern of stimulus motion. Stimulus density, texture, speed, and relative depth are all features of the optic flow field that provide specific information about the relative position of objects in the environment, environmental structure from motion. In contrast, the overall pattern of motion provides information that is more specifically attuned to the direction and path of self-motion. These findings might reflect greater MSTd involvement in optic flow field analysis to guide self-motion rather than to provide information about the position of objects in the environment.

This does not mean that MSTd neurons might not provide information about individual objects looming as they move closer to the observer. We have not systematically investigated responses to looming stimuli, but the size expansion stimuli used by Tanaka et al. (1986) contained looming and evoked responses from their "field" neurons. Casual observations that we have made while studying MSTd neurons suggest that some respond to object motion, showing the same component and direction selectivity as shown in the responses to optic flow stimuli. Therefore, although the neurons we have studied in MSTd frequently have properties appropriate for the analysis of optic flow, we do not know whether they perform this function during motion through the environment and whether they also respond to the motion of objects.

MSTd and dorsal motion pathway contributions to environmental vision

MSTd neurons respond to three stimulus parameters related to visual motion: optic flow fields, binocular disparity, and pursuit eye movements. Each of these response properties could be used in the processing of information related to self-motion through the environment, and the combination of properties strengthens the view that MSTd might play a significant part in that process.

MSTd neurons are suited to optic flow field analysis for guiding self-motion because they have large, direction-selective receptive fields that respond to large-field motion with selectivity for planar, circular, and radial stimuli. The next step in determining whether these neurons do play such a role is the examination of their responses to naturally occurring combinations of optic flow field components.

MSTd neurons are also sensitive to binocular disparity, providing information on stimulus depth relative to the plane of fixation (Roy and Wurtz 1990) [near or far selectivity in the terminology of Poggio and Fischer (1977)]. These near and far disparity neurons are located in the same area examined in the present study. It seems likely that the same neurons carry both optic flow and disparity signals, although we have not yet conducted experiments testing both response properties in the same neurons.

MSTd neurons are also active during pursuit eye movements made in the dark, activity that could be related to the generation of these movements or to a corollary discharge of these movements (Newsome et al. 1988). Because MSTd lesions do not disrupt the maintenance of pursuit to small spots of light (Dürsteler and Wurtz 1988), their involvement in generating eye movements might be limited to the ocular following of an object being fixated while the observer moves through the environment (Kawano and Miles 1986; Miles et al. 1986; Miles and Kawano 1986). Eye movement signals are also relevant to the analysis of optic flow fields because that analysis must account for eye movements that can distort the flow field. Again, whether MSTd neurons having optic flow and/or disparity responses are the same as those active during pursuit eye movements has not yet been determined.

MSTd is almost certainly a part of a proposed dorsal visual motion pathway extending from striate cortex through STS cortex into posterior parietal cortex (Ungerleider and Mishkin 1982). However, MSTd appears to be a unique element in that pathway, because it is the only area that has been shown to possess all of the response characteristics previously mentioned.

The visual motion area preceding MST is MT, which lies on the posterior bank of the STS and projects directly to MST (Maunsell and Van Essen 1983; Ungerleider and Desimone 1986). Several characteristics of MT neurons suggest that they are not appropriate for the analysis of optic flow fields: their receptive fields are much smaller than those in MST (Desimone and Ungerleider 1986; Komatsu and Wurtz 1988), they prefer small-field motion to large-field motion (Allman et al. 1985), and they do not respond selectively to circular or radial stimuli (Saito et al. 1986). However, visual processing in MT might serve as a precursor of the radial selectivity seen in MST, because cells with peripherally located receptive fields favor directions oriented away from the center of the visual field (Albright 1989). Such radial organization has been observed previously in the posterior medial part of the cat's lateral suprasylvian cortex (Rauschecker et al. 1987).

Area 7a of the inferior posterior parietal lobule receives a direct projection from MST (Boussaoud et al. 1990). Area 7a visual neurons have large receptive fields that are particularly responsive to large moving visual stimuli, with selectivity for stimulus motion toward or away from the fixation point in what has been termed opponent vector organization (Motter and Mountcastle 1981). This radial direction selectivity coexists with axial direction selectivity to create a population capable of precisely encoding the direction of motion relative to the fixation point (Motter et al. 1987; Steinmetz et al. 1987). In some cases, area 7a neurons are particularly responsive to a patterned stimulus rotating around the fixation point (Sakata et al. 1986). These response properties may be more suited to the analysis of object motion rather than the motion generated as the observer moves through the environment. Further experiments, which test the responses of area 7a neurons to optic flow stimuli, will be required to resolve this issue.
Another area that receives input from MST is the superior temporal polysensory area within the STS (Boussaoud et al. 1990). Some neurons in this area have preferred directions of motion that are radially symmetrical around the center of the visual field (Bruce et al. 1986) or respond to expanding or contracting stimuli (Hikosaka et al. 1988). Determining the contribution of this area to the analysis of optic flow will also require further experiments.

Although we know comparatively little about the analysis of optic flow beyond area MST, we do know that lesions that must alter the pathway degrade an observer’s ability to orient in the environment. Lesions in the dorsal pathway of the geniculostriate system produce deficits in the discrimination of spatial relations (Ungerleider and Mishkin 1982). Clinicians have long noted that visual orientation in the environment is specifically compromised after parietotemporal lesions (Critchley 1953; Holmes 1918), whereas these may be the only visual capacities preserved after extensive lesions sparing this region (Campion et al. 1983; Williams and Gassel 1962). Optic flow field analysis, performed in the dorsal motion pathway of which MSTd is a key element, might be responsible for this self-orientation.

APPENDIX: OPTIC FLOW STIMULI

Translational simulations (Fig. 1A) maintained a constant linear velocity. In the frontoparallel plane, translation of each dot along the X- and Y-axis was specified by

\[
\frac{dx}{dt} = S \cos \theta \quad \frac{dy}{dt} = S \sin \theta
\]

where \(dx\) is horizontal motion, \(dy\) is vertical motion, \(S\) is the speed, and \(\theta\) is the angle between the direction of motion and the X-axis, with 0 being rightward motion. Translation of each dot in depth was along a line connecting it to the center. The motion of each dot was specified by

\[
\frac{dz}{dt} = \frac{\sin(\phi) \cos(\phi)}{Z} \frac{d\phi}{dt}
\]

where \(\phi\) is the angle between the observer’s line of sight to the center of the motion and the observer’s line of sight to a dot. \(dz\) is the speed in depth being simulated, and \(Z\) is the distance from the observer to the dot plane being simulated (100 cm in our experiments).

Rotational simulations (Fig. 1B) maintained a constant angular velocity. For rotation around the X- and Y-axes the speed of motion was specified by

\[
\frac{dR}{dt} = \frac{d\phi}{dt} \frac{R}{Z} = \frac{d\phi}{dt} \frac{R}{Z}
\]

where \(dR\) is the simulated angular velocity of the observer, \(R\) is the distance of a dot from the axis of rotation, and \(Z\) is the distance from the observer to the dot plane being simulated. For rotation around the Z-axis, the dots of the random pattern rotated around a center point. The motion of each dot was specified by

\[
\frac{dx}{dt} = R \cos \frac{d\phi}{dt} \quad \frac{dy}{dt} = R \sin \frac{d\phi}{dt}
\]

where \(dx\) is horizontal motion, \(dy\) is vertical motion, \(R\) is the distance of the dot from the center of rotation, and \(\frac{d\phi}{dt}\) is the simulated angular velocity of the observer.

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