

# Planar Directional Contributions to Optic Flow Responses in MST Neurons

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**Duffy, Charles J. and Robert H. Wurtz.** Planar directional contributions to optic flow responses in MST neurons. *J. Neurophysiol.* 77: 782–796, 1997. Many neurons in the dorsal region of the medial superior temporal area (MSTd) of monkey cerebral cortex respond to optic flow stimuli in which the center of motion is shifted off the center of the visual field. Each shifted-center-of-motion stimulus presents both different directions of planar motion throughout the visual field and a unique pattern of global motion across the visual field. We investigated the contribution of planar motion to the responses of these neurons in two experiments. In the first, we compared the responses of 243 neurons to planar motion and to shifted-center-of-motion stimuli created by vector summation of planar motion and radial or circular motion. We found that many neurons preferred the same directions of motion in the combined stimuli as in the planar stimuli, but other neurons did not. When we divided our sample into one group with stronger directionality to both planar and vector combination stimuli and one group with weaker directionality, we found that the neurons with the stronger directionality were those that showed the greatest similarity in the preferred direction of motion for both the planar and combined stimuli. In a second set of experiments, we overlapped planar motion and radial or circular motion to create transparent stimuli with the same motion components as the vector combination stimuli, but without the shifted centers of motion. We found that the neurons that responded most strongly to the planar motion when it was combined with radial or circular motion also responded best when the planar motion was overlapped by a transparent motion stimulus. We conclude that the responses of those neurons with stronger directional responses to both the motion of planar and vector combination stimuli are most readily understood as responding to the total planar motion in the stimulus, a planar motion mechanism. Other neurons that had weaker directional responses showed no such similarity in the preferred directions of planar motion in the vector combination and the transparent overlap stimuli and fit best with a mechanism dependent on the global motion pattern. We also found that neurons having significant responses to both radial and circular motion also responded to the spiral stimuli that result from a vector combination of radial and circular motion. The preferred planar-spiral vector combination stimulus was frequently the one containing that neurons' preferred direction of planar motion, which makes them similar to other MSTd neurons.

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## INTRODUCTION

As we move through the environment, our movement generates motion of the visual field that is referred to as optic flow (Gibson 1950, 1986). Neurons in the dorsal region of the medial superior temporal area (MSTd) of monkey cerebral cortex have been shown to respond to planar, radial,

and circular motion, which are components of optic flow (Andersen et al. 1990; Duffy and Wurtz 1991a,b; Graziano et al. 1994; Lagae et al. 1994; Orban et al. 1992; Saito et al. 1986; Sakata et al. 1986; Tanaka and Saito 1989; Tanaka et al. 1989; Wurtz et al. 1990). In addition to determining that medial superior temporal area (MST) neurons respond to optic flow components, a series of studies has characterized the effect of altering the stimulus on the response of the MST neurons, including effects of stimulus position (Andersen et al. 1990; Duffy and Wurtz 1991b; Graziano et al. 1994; Lagae et al. 1994; Saito et al. 1986), speed of flow components (Orban et al. 1995; Tanaka and Saito 1989; Tanaka et al. 1989), and combinations of flow components (Graziano et al. 1994; Lagae et al. 1994; Orban et al. 1992). Although these response characteristics make MSTd neurons well suited to the task of optic flow field analysis, there is no direct evidence (such as selective lesions of MSTd) that these neurons actually participate in that process.

An additional test of the role of MSTd neurons in optic flow field analysis is the examination of responses to stimuli containing the vector combination of optic flow components. Observer movement would usually produce combinations of optic flow components, such as radial and circular motion during an observer's forward translation coupled with planar motion during forward and lateral movement of the observer. We have recently tested the sensitivity of the MSTd neurons to such stimuli by vector combination of radial motion with different directions of planar motion, which shifts the center of motion to different sites in the visual field (Fig. 1A). We found that many neurons responded better to such combinations of planar and radial stimuli (or to combinations of planar and circular stimuli) than to either component alone (Duffy and Wurtz 1995).

Each shifted-center-of-motion stimulus presents both a unique pattern of global motion across the visual field and different directions of planar motion throughout the visual field, and each of these features might contribute to the neuronal responses. In the first case, MSTd neurons might be uniquely sensitive to the global pattern of motion that has its center of motion in one region of the visual field. For example, neurons responding to the shifted-center-of-motion stimulus in Fig. 1A might do so because they match that particular global motion pattern in a manner such as that depicted in Fig. 1B. In the second case, MSTd neurons might respond to the preponderance of certain directions of planar motion that is a necessary consequence of such a

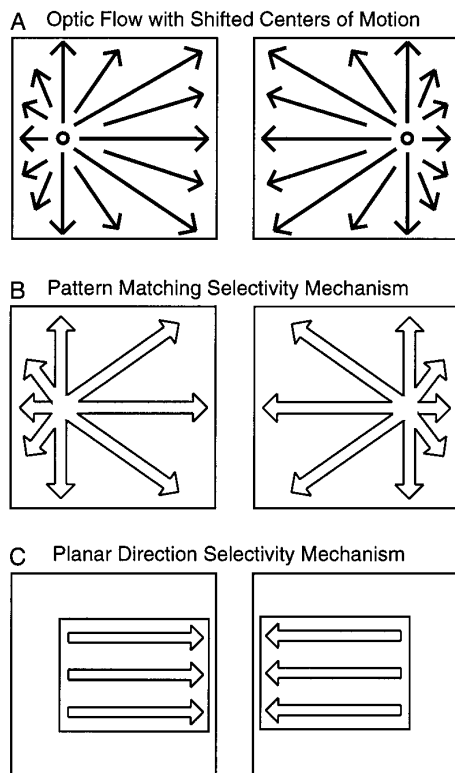


FIG. 1. Schematic diagrams of shifted-center-of-motion stimuli, and 2 alternative hypotheses about the neuronal response selectivity for such stimuli. *A*: patterns of visual motion in optic flow fields that evoke selective responses from medial superior temporal area (MST) neurons. Each frame depicts the  $100^\circ \times 100^\circ$  visual display. Arrows: direction of dot motion. Circles: center of motion in the pattern. These radial motion patterns simulate the visual scene during an observer's forward and leftward translation (*left*) or forward and rightward translation (*right*). *B*: representation of a pattern-matching mechanism, with the critical feature being the global pattern of motion. *C*: representation of a planar direction mechanism, with the critical feature being the sensitivity to the predominant planar motion in the stimulus.

shifted center of motion. For example, the neurons responding to the shifted-center-of-motion stimulus in Fig. 1A might do so because they possess directional tuning for the horizontal planar motion contained in that stimulus (Fig. 1C).

In the present experiments we compared the response of each MSTd neuron to the vector combination of planar and radial (or planar and circular) stimuli with the response to these stimuli presented separately. We first determined the response of a neuron to a set of planar, radial, and circular motion stimuli. We centered these stimuli on the monkey's fixation point, which was always in the center of the  $100^\circ \times 100^\circ$  visual display. We performed two experiments on the same sample of 243 neurons. First, we compared the response of each neuron to shifted-center-of-motion stimuli, which were generated by combining the preferred radial or circular motion of the neuron with eight directions of planar motion, with the response of the neuron to the planar motions alone. We found that the neurons that responded strongly to planar motion in a given direction responded best to the shifted-center-of-motion stimulus created by vector combination with that same direction of planar motion. The responses of these neurons are most readily understood as

responding to the total planar motion in the stimulus (Fig. 1C), whereas the responses of other neurons fit best with a mechanism dependent on the global motion pattern (Fig. 1B).

In the second experiment, we superimposed planar motion on top of radial or circular motion to produce transparently overlapping stimuli. In the transparent overlap stimuli, the center of motion always remained in the center of the stimulus but the stimuli had the same proportions of planar motion as in the shifted-center-of-motion vector combination stimuli. We found that the neurons that responded strongly to planar and vector combination stimuli also responded to transparent overlap stimuli incorporating that same preferred direction of planar motion. This confirmed the importance of planar motion to these cells, because in these experiments only the planar motion changed whereas the center of motion of the radial pattern remained the same. We find that other factors, including the number of optic flow components to which a neuron responds and the presence of inhibitory as well as excitatory responses, are critical for understanding the influence of planar motion.

In a related experiment, we tested whether neurons that responded to another vector combination stimulus, the spiral stimulus generated by combining radial and circular stimuli, also responded to planar motion. We confirmed the recent experiments by Graziano et al. (1994), who found that some MST cells respond selectively to such spiral motion. We reasoned that if these cells were specifically related to spiral stimuli, they should not have a pronounced response to planar motion. We found that even those neurons that most strongly responded to the spiral stimuli also responded to planar stimuli both alone and in vector combination with the spiral stimuli. This suggests that these neurons are like many other MST neurons in their responsiveness to planar motion.

## METHODS

### Experimental procedures

We recorded single neurons from the cortex of two adult Rhesus monkeys (*Macaca mulatta*, No. 79N and No. 26K), the same two monkeys used in previous experiments (Duffy and Wurtz 1995); the experimental procedures were described in detail in that report. Under general anesthesia, scleral search coils were implanted bilaterally (Judge et al. 1980), and recording cylinders were placed over parietal cortex (AP  $-2$ , ML  $\pm 15$ ) to allow recording from MST on both sides of the brain. A head holder was positioned on the frontal midline and was encased in a dental acrylic cap with the recording cylinders and eye coil connectors. All protocols were approved by the Institute Animal Care and Use Committee and complied with Public Health Service Policy on the humane care and use of laboratory animals.

The monkeys sat in a primate chair while performing a visual fixation task for liquid reward. They fixated on a spot of light on a  $100^\circ \times 100^\circ$  tangent screen 50 cm in front of them, and their eye position was monitored with the use of the magnetic search coil technique (Robinson 1963). Each trial began with the appearance of a red fixation spot (light-emitting diode,  $0.25^\circ$  diam,  $2.7$  cd/m<sup>2</sup>) at the center of the screen, which the monkey had to fixate within 500 ms and maintain fixation ( $\pm 2.5^\circ$ ) for 6–7.5 s. During this period of fixation, a series of two or three visual motion stimuli was projected onto the screen, each with a stimulus duration of 1 s and interstimulus intervals of 1–1.5 s.

Single-neuron activity was digitized at 1 kHz with the use of a

window discriminator and stored with stimulus and behavioral event markers with the use of the REX system (Hays et al. 1982). Recordings were made in both hemispheres of the two monkeys with the use of epoxy-coated tungsten microelectrodes that were advanced with the use of a hydraulic microdrive. Neuronal activity was monitored to establish the relative depth of landmarks, and studies were initiated only on neurons with clearly isolated discharges.

Several days before the experiments were completed, electrolytic marks were made along penetration tracks in each of three guide tubes. Drawings were made from histological sections to establish the locations of the electrolytic marks and anatomic landmarks to extrapolate the position of recording sites. About 90% of the neurons studied were in the densely myelinated zone on the anterior bank of the superior temporal sulcus that is included in the dorsal-medial region of MST (MSTd) (Komatsu and Wurtz 1988), whereas the remaining neurons were farther down the anterior bank but had the same physiological characteristics.

### *Visual stimulation procedures*

Hand-held projectors were used to define each neuron's receptive field boundaries to single spots ( $5^\circ$ ) and random dot patterns (between  $10^\circ \times 10^\circ$  and  $100^\circ \times 100^\circ$ ). The central region of the receptive field could be determined with confidence, but the edges of the field, particularly in the periphery, were less certain. Once this qualitative mapping was completed, we systematically tested each neuron with standard sets of visual stimuli. These stimuli contained 360 dots, each subtending  $0.75^\circ$  at  $1.8 \text{ cd/m}^2$  against a  $0.2\text{-cd/m}^2$  background, and were projected (Sony 900 TV projector) to fill the central  $100^\circ \times 100^\circ$  of the monkey's visual field.

Neurons were first studied with a standard set of twelve stimuli that are components of optic flow: eight planar or lamellar stimuli (directions at  $45^\circ$  intervals around  $360^\circ$ ) simulating observer translations in the frontoparallel plane; two radial stimuli (inward and outward directions relative to the fixation point) simulating forward or backward observer translation; and two circular stimuli (clockwise and counterclockwise directions around the fixation point) simulating observer roll. The algorithms for generating these stimuli were described previously (Duffy and Wurtz 1991a). For all stimuli, motion began as soon as the stimulus appeared and maintained an average dot speed of  $40^\circ/\text{s}$ , with dot wrapping and limited half-lives maintaining a uniform dot density across the screen. In planar stimuli, all dots moved at  $40^\circ/\text{s}$ . In radial and circular stimuli, dot speed varied in proportion to its distance from the center of motion in the pattern, but an average speed of  $40^\circ/\text{s}$  was maintained. All stimuli appeared as if moving in one plane, simulating motion in a rigid world without independently moving objects or other naturalistic cues (blur, brightness, disparity, occlusion, parallax, size, or texture).

After determining the response of the neurons to planar, radial, and circular stimuli, we tested those neurons that had significant responses to radial (either inward or outward) or circular (either clockwise or counterclockwise) stimuli with a set of stimuli that combined the preferred radial or circular stimulus with the eight directions of planar motion. Combination stimuli were created by the framework vector addition of planar motion to a radial or circular pattern having its center of motion at the center of the screen (fixation point) and produced the shifted-center-of-motion stimuli described in our previous paper (Duffy and Wurtz 1995). For example, combining outward radial motion and rightward planar motion produced a radial vector combination pattern with the center of motion shifted  $45^\circ$  toward the left edge of the screen (Fig. 1A).

Vector combination with planar motion transforms the basic radial or circular pattern such that the pattern remains readily recognized, but the distribution of directions of motion on the screen is

greatly changed. The vector summation of planar patterns with radial or circular patterns changes both the location of the center of motion on the screen and the global distribution of motion across the screen, although the entire  $100^\circ \times 100^\circ$  screen remains covered by the stimuli. The vector combination stimuli contained some higher-speed dots at positions far from the center of motion, distances not represented when the center of the radial or circular pattern was at the center of the screen. Such changes in the speed of motion around the edges of the stimuli are a consequence of shifting the center of motion so that these stimuli mimic naturalistic optic flow fields. We chose not to alter the stimuli for absolute uniformity of speeds between the centered-center-of-motion stimuli and the shifted-center-of-motion stimuli to avoid adding a new stimulus parameter.

The final set of stimuli was created by transparently overlapping the preferred radial or circular stimuli with the eight directions of planar motion so that the two motion stimuli were superimposed as coextensive transparent patterns. Because the transparent overlap stimuli had the same total number of dots, only half as many were in each of the two patterns; the overall brightness and dot density remained the same as it was in the planar and vector combination stimuli.

The standard set of optic flow test stimuli, the set of vector combination stimuli, and the set of transparent overlap stimuli were run in separate blocks of trials. Within these blocks the stimulus presentations were randomly interleaved. Control trials in all sets of stimuli consisted of fixation on an otherwise blank screen, and were used to establish the background discharge rate of the neurons. During all stimulation, the monkey fixated on a point at the center of the tangent screen in front of it.

We studied all neurons encountered and presented the same set of large-field optic flow stimuli to each (Duffy and Wurtz 1991a,b, 1995). We did this to better characterize the responses of the population of MSTd neurons to all of the optic flow stimuli, not just the stimuli to which they respond best. We chose this strategy so that our experiments would be more useful for modeling visual motion processing in MSTd (Hatsopoulos and Warren 1991; Lappe and Rauschecker 1993; Perrone and Stone 1994; Wang 1995; Zhang et al. 1993).

### *Neuronal response analysis*

An on-line raster display showed the occurrence of single-neuron discharges with markers added to give the temporal relation to stimulus and behavioral events. Displays used for off-line data analysis also included spike density histograms created by replacing the millisecond-wide square pulses representing spikes with Gaussian pulses with a width corresponding to an SD of 20 ms (MacPherson and Aldridge 1979). Neuronal spikes were counted in the 600-ms period beginning 400 ms after stimulus onset. We did not include the first 400 ms after stimulus onset because we have found that the activity in this early response period is less reliably related to the specific stimulus than is the response in the later period (Duffy and Wurtz 1991a). The response in this 600-ms period, averaged over six to seven stimulus presentations, was compared with the activity in a 600-ms period on six to seven control trials in which the monkey fixated but no visual motion stimulus was presented. All responses were tested for statistically significant differences from control activity with the use of Student's *t*-test at a significance level of 0.01.

We displayed these responses as polar plots (Fig. 2) in which the thin radial lines represent the responses to the eight motion stimuli, their length being proportionate to the amplitude of the response. For all plots, the amplitude of the response to the preferred radial or circular stimulus, presented without vector combination or transparent overlap, is given by the solid circle. The mean background activity, averaged across six control trials in which no

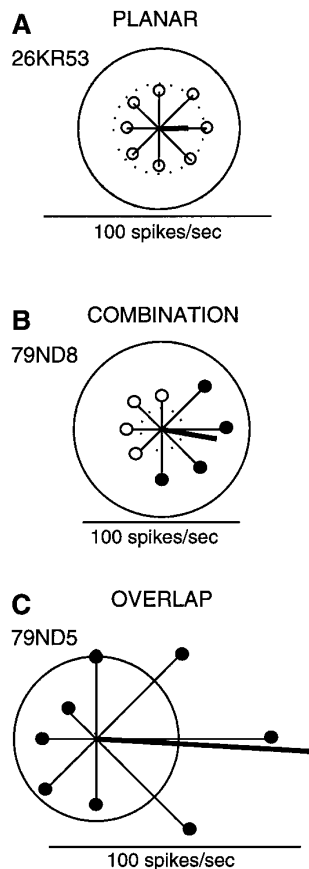


FIG. 2. Representation of the responses to planar motion (A), combined planar and radial or planar and circular motion (B), and transparently overlapped planar and radial or planar and circular motion (C). A: thin radial lines on the polar plot represent the responses to the 8 directions of planar motion. If the circle at the end of each line is filled, that response is significantly different (Student's *t*-test;  $P < 0.01$ ) from unstimulated control activity. Diameter of dotted circle: activity in unstimulated control trials. Diameter of solid circle: amplitude of the responses to the preferred radial or circular stimulus for that neuron. Thick radial line: net vector of the responses depicted by the thin radial lines; its direction is the mean direction of the plot, and its length is the resultant length of the plot. Bar below each plot: 100 spikes/s on the same scale as the polar plot components. B: thin radial lines show the responses to combination stimuli (framewise vector addition of planar and radial or planar and circular), with their direction being that of the planar motion added to create that vector combination stimulus. Other conventions as in A. C: thin radial lines show the responses to transparent overlap stimuli (planar motion overlapping radial or circular motion); the direction is that of the planar motion superimposed to create that transparent overlap stimulus. Other conventions as in A. For reference, the magnitudes of *Z* values for response profiles are  $Z = 0.9$  (A);  $Z = 5.4$  (B);  $Z = 24.9$  (C).

stimulus was presented, is indicated by the dotted circle; the apparent absence of this circle indicates very low background activity. If the response to one of the eight motion stimuli is significantly different (*t*-test,  $P < 0.01$ ) from activity in unstimulated control trials, the circle at the end of the corresponding radial line is filled. For the planar responses (Fig. 2A), each thin radial line indicates the amplitude of the response to one of the eight directions of planar motion. For the vector combination responses (Fig. 2B), each thin radial line indicates the amplitude of the response to one of the shifted-center-of-motion stimuli, its direction indicating the planar motion used to create that vector combination stimulus. For the transparent overlap responses (Fig. 2C), each thin radial line indicates the amplitude of the response to the radial or circular pattern overlapped by one of the eight directions of planar motion.

The thick radial line in each polar plot indicates the net vector for the response to the eight motion stimuli (Fig. 2). The net vector is a vector sum of the individual response vectors (Fig. 2, thin radial lines), with its angle being the mean direction and its length being the resultant length. These calculations followed the methods developed by Batschelet (1981) for the circular statistical analysis of grouped data, in this case sampled at 45° intervals around 360°. We used the Rayleigh *Z* statistic to test whether a circular profile was different from a random distribution, basing that calculation on the grouped data mean resultant length that normalizes the statistic for response amplitude (Batschelet 1981). A large *Z* value indicates that the distribution is unimodal, with a clear preferred direction. In these data we encountered only three neurons with clearly multimodal response profiles; they did not alter the overall analysis, and we left them in the sample. We will refer to the *Z* value as testing for a preferred direction, with the understanding that this measure is insensitive to multimodal distributions. Some sense of the magnitude of *Z* values for response profiles can be derived from inspecting the response profiles in Fig. 2 (Fig. 2A,  $Z = 0.9$ ; Fig. 2B,  $Z = 5.4$ ; Fig. 2C,  $Z = 24.9$ ).

RESULTS

We recorded the responses of 243 neurons located on the anterior bank of the superior temporal sulcus. The neurons were directionally selective, had large receptive fields that frequently included the fovea, and responded better to the motion of large patterned stimuli than to the motion of small spots. These characteristics are typical of neurons in MSTd (Komatsu and Wurtz 1988).

*Comparison of responses to planar and combination stimuli*

Our first question was whether neurons that responded clearly to a given direction of planar motion also responded preferentially to vector combination stimuli that were derived with the use of that direction of planar motion. Many MST neurons did so, and Fig. 3 shows an example of such a neuron. Rightward motion evoked the strongest planar responses, and outward radial motion evoked the strongest nonplanar responses (Fig. 3A). The strong directional preference for planar motion is reflected in the resultant length of the net vector (thick line in Fig. 3B; see METHODS and Fig. 2). The vector combination stimuli with shifted centers of motion, derived from outward radial motion and the eight directions of planar motion, evoke a similar response pattern (Fig. 3C). The stimulus combining rightward planar and outward radial motion evoked the strongest response, as indicated by the resultant length of the net vector (Fig. 3D), which is similar to that for the planar stimuli (Fig. 3B). The response preference for rightward planar motion is consistent with the response preference for the vector combination stimulus having its center of motion shifted to the left, which was created by combining outward and rightward motion.

A clear relationship between the responses to planar and vector combination stimuli was evident for many neurons, but others showed substantial differences between their planar and vector combination responses. Figure 4 shows the responses of a neuron having no strong planar motion responses but strong outward radial motion responses (Fig. 4A). The absence of a directional preference for planar motion is reflected in the small resultant length of the net vector.

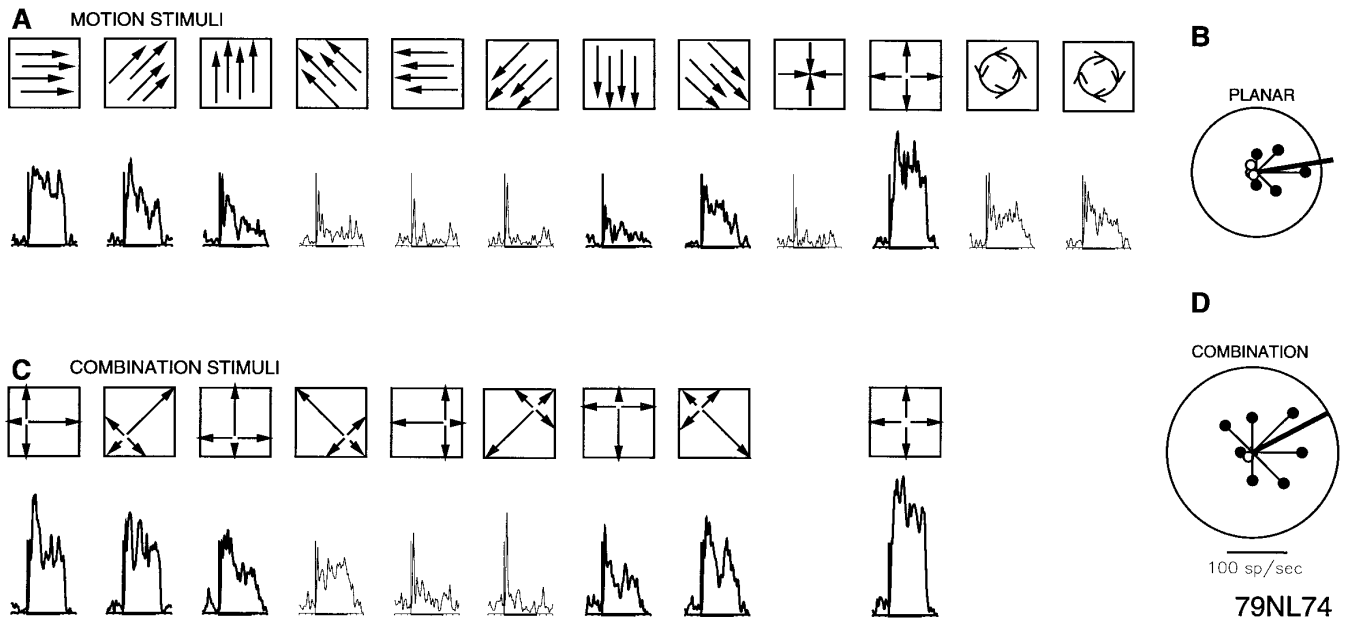


FIG. 3. Comparison between responses to the optic flow field motion stimuli and the shifted-center-of-motion combination stimuli in a neuron with similar responses to both sets of stimuli. *A*: squares along the top represent the  $100^\circ \times 100^\circ$  stimulus screen, with the arrows depicting the direction of dot motion on each part of the screen. This set of 12 basic optic flow field stimuli includes 8 directions of planar motion, 2 directions of radial motion, and 2 directions of circular motion. The spike density histograms below each stimulus show the mean responses over 6 presentations of each stimulus. Vertical lines: stimulus onset; height of lines indicates the 100-spike/s discharge rate. Thick horizontal bar: 1-s stimulus period. The spike densities in bold outline are those in which the response was significantly different from control activity (*t*-test,  $P < 0.01$ ). This neuron responded best to rightward planar and outward radial stimuli. *B*: polar plot of the planar responses shown in *A*; conventions are the same as in Fig. 2. *C*: patterns of motion in vector combination stimuli (*top*) and spike density histograms of the responses evoked by those stimuli (*bottom*), showing a preference for vector combination stimuli based on rightward planar motion. *D*: polar plot of the vector combination responses shown in *C*. This neuron shows good agreement between responses to planar and vector combination stimuli, preferring rightward planar motion and the vector combination stimulus containing rightward motion as the planar component.

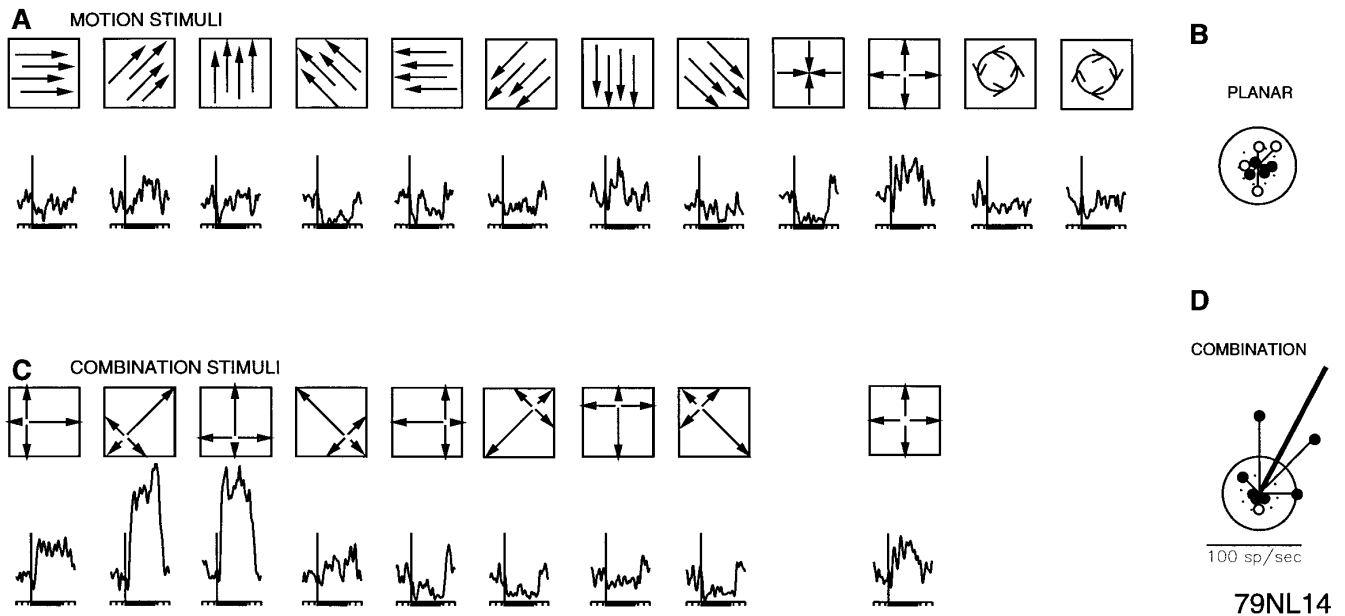


FIG. 4. Comparison between responses to the optic flow field motion stimuli and the shifted-center-of-motion vector combination stimuli in a neuron with different responses to these stimulus sets (format as in Fig. 3). *A* and *B*: this neuron responded best to outward radial stimuli, with little responsiveness to planar motion. *C* and *D*: vector combination stimuli (*top*) evoked responses (*bottom*) showing a preference for vector combination stimuli based on upward planar motion. This neuron shows a clear difference between responses to planar and vector combination stimuli, with no clear preference to planar motion but a clear preference for the vector combination stimulus containing upward motion as the planar component.

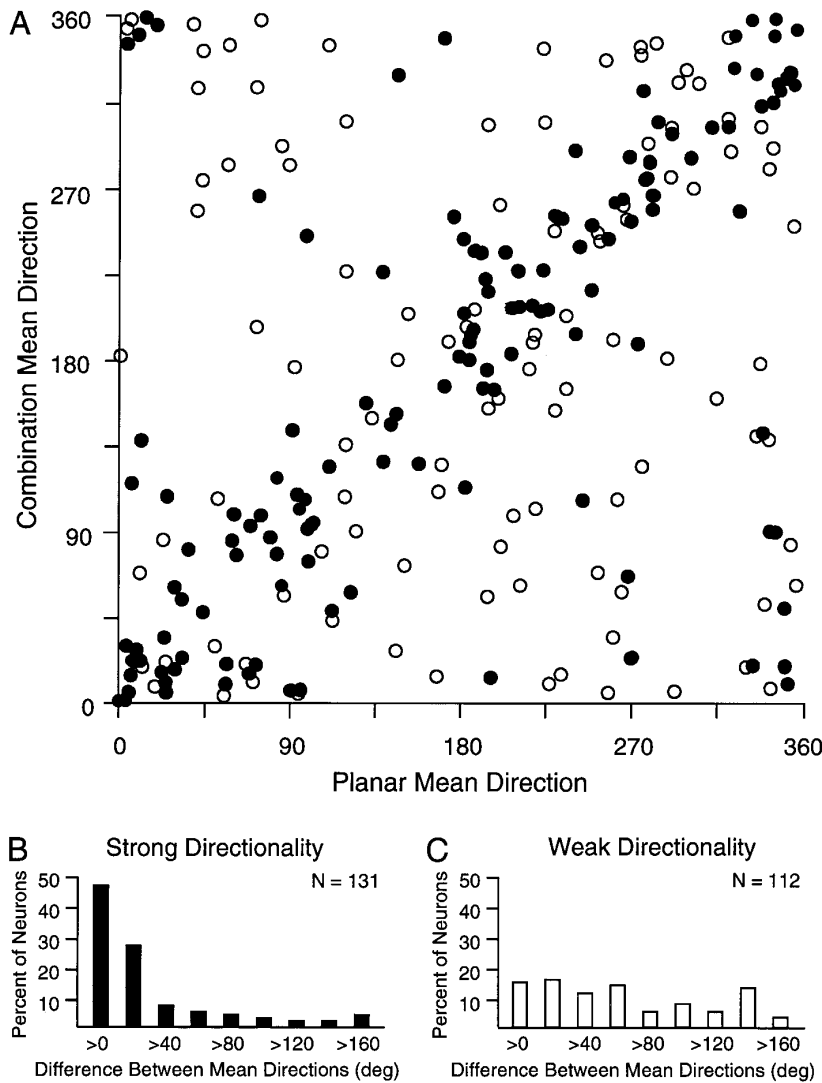


FIG. 5. Comparison of mean directions for planar and vector combination stimuli for all 243 neurons. *A*: scatter plot of directions of net vectors of responses to planar (abscissa) and vector combination (ordinate) stimuli. Each circle represents the responses from 1 of the 243 neurons. Filled circles: strongly directional neurons ( $n = 131$ ), those with a Rayleigh  $Z$  value  $\geq 4$  (see METHODS). Open circles: neurons that were not as strongly directional ( $n = 112$ ), those with a Rayleigh  $Z$  value  $< 4$ . *B* and *C*: bar graphs of the differences between planar and vector combination mean directions. *B*: neurons with strong directional responses, showing that neurons having strong directionality in both studies have similar preferred directions in both studies. *C*: neurons with weak directional responses, showing a relatively flat distribution.

However, the vector combination stimuli with shifted centers of motion, derived from outward radial motion and the eight directions of planar motion, evoke a different response pattern (Fig. 4C). The stimulus combining upward planar and outward radial motion evoked the strongest response, as indicated by the mean resultant length of the net vector (thick line in Fig. 4D). The absence of a planar response is in marked contrast to the response preference for the vector combination stimulus having its center of motion shifted downward by combining upward planar and outward radial motion.

We used descriptive circular statistics to summarize our findings across the sample of neurons. The scatter plot in Fig. 5A compares the mean directions for planar and vector combination stimuli, and each point represents the mean direction of the net vector for the responses to these two stimuli obtained in 1 of the 243 neurons studied. This plot shows wide variation in the preferred directions to the two stimuli, as would be expected given the examples illustrated in Figs. 3 and 4. We divided the sample to separate those neurons that had stronger responses to both planar and vector combination stimuli from those that had weaker responses

to both stimuli or to either one. To do so, we considered both the mean direction and the mean resultant length by the use of the Rayleigh  $Z$  statistic (see METHODS) as a measure of strength of the responses. This approach measures the strength of directional tuning in a response profile; with respect to planar motion, this measure roughly corresponds to a bandwidth in a planar direction tuning curve. We divided the neurons into those that were more strongly directional to both the planar and the vector combination stimuli ( $Z \geq 4$ , Fig. 5A, filled circles) and those that were more weakly directional ( $Z < 4$ , Fig. 5A, open circles). This  $Z$  value was slightly smaller than that for the neuronal response shown in Fig. 2B (where  $Z = 5.4$ ), and roughly divided the sample of neurons into halves. A total of 54% (131 of 243) of the neurons showed the stronger directional responses to both planar and vector combination stimuli and the remaining neurons (112 of 243) had weaker responses. When we now look at the difference in the mean directions for planar and vector combination stimuli, we see clear differences. Figure 5B shows that 48% (63 of 131) of the neurons with stronger preferences had preferred directions within  $20^\circ$  of each other, and 78% (102 of 131) are within  $45^\circ$  of each other. In

contrast, for the remaining 112 neurons (Fig. 5C), there is no such clustering of similar mean directions.

Thus we have found wide variation in the responses to planar motion stimuli and to vector combination stimuli in our sample of MSTd neurons. However, when we consider only those neurons with strong directional responses to both stimuli, we find a clear relationship between the preferred direction to planar motion and the predominate direction of planar motion in the vector combination stimuli. These neurons are probably best understood as responding to the total planar motion in the stimuli and fit with a planar motion mechanism (Fig. 1C). The remaining neurons lack such a clear relationship of directionality to planar and vector combination stimuli and probably fit best with a global pattern motion mechanism (Fig. 1B).

#### Effect of receptive field size and location

One possibility is that the wide variation in the similarity of preferred directions of the planar and vector combination stimuli is due to variation in the size of the receptive fields of the neurons. For example, neurons with planar sensitive receptive fields might respond to radial or circular stimuli whenever an appropriate part of those stimuli happened to fall on the receptive field. If such neurons were a predominant part of our data, larger receptive fields should give more opportunities for such effects, and would be associated with greater similarity between planar and vector combination responses. To test for this possibility, we compared the distributions of receptive field dimensions for the strongly directional (Fig. 6A, left) and weakly directional (Fig. 6A, right) neurons. Both groups show similar percentages of smaller and larger receptive fields, suggesting that receptive field dimensions do not account for the similarity in preferred directions of planar and vector combination stimuli. We also examined the relationship between the strength of directionality in the planar and vector combination studies for individual neurons. The scatter plot in Fig. 6B also shows no clear relationship between receptive field size and directional tuning to planar and combination stimuli.

The location of the receptive fields of the MSTd neurons might also influence the response of the cells to the planar motion component of the combination stimuli: the sensitivity to planar motion might be most evident when the receptive field is positioned such that the motion in the combination stimuli covers it with fairly uniform motion. We investigated this point by studying neurons with receptive fields that should maximize the likelihood of revealing such an effect. We selected those neurons with receptive fields concentrated in just one quadrant of the visual field (shown schematically in Fig. 6C, left). We further selected those neurons in which a clearly preferred direction was evident in the responses to planar motion (as with the downward and rightward motion shown in Fig. 6C, left). If receptive field location is important, we should be able to predict which combination stimulus would be preferred by a neuron once we know the position of its receptive field and its preferred direction of planar motion (Fig. 6C, left). In our sample we had 190 neurons in which visual stimulation in one quadrant evoked the strongest responses, and, of these, 126 showed strongly directional responses (as defined in Fig. 5) in both the planar

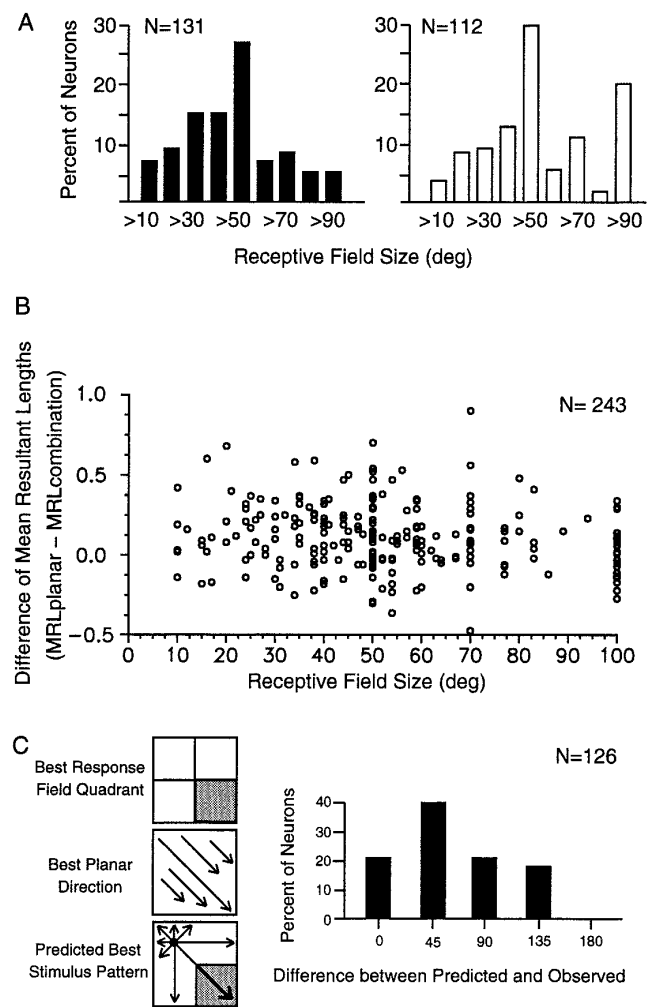


FIG. 6. Relations between strength of directionality and receptive field size and location. *A*: bar graphs showing the distribution of receptive field sizes for strongly directional and weakly directional neurons, as defined in Fig. 5. Both groups show similar percentages of smaller and larger receptive fields, although the weakly directional neurons show a greater percentage of the largest receptive fields. *B*: scatter plot of receptive field sizes and the differences between planar and vector combination mean resultant lengths. Receptive field size in both *A* and *B* is represented on the abscissa by the square root of the receptive field area in degrees and was determined with the use of patterned stimuli (see METHODS). The results analyzed in both *A* and *B* failed to show a relationship between receptive field size and the relative strength of response profile directionality to planar and vector combination stimuli. *C*: relationship of receptive field location and preferred planar direction to preferred direction of vector combination stimuli. *C*, Left: drawings outline the 3 steps used to determine whether vector combination responses reflect planar directional responses in a particular segment of the receptive field. First, 190 neurons that responded best to a stimulus in 1 quadrant of the screen were selected from the total sample (top). Second, 126 of those neurons had significant directionality in both the planar and vector combination studies such that their best planar direction could be compared with the directions of motion in the most responsive quadrant (middle). Third, the vector combination stimulus that most nearly filled the identified quadrant with the preferred direction of planar motion was considered to be the predicted best vector combination stimulus (bottom). *C*, right: bar graph shows the differences between the predicted and observed best vector combination responses (in deg of difference between the planar motion in the predicted best and the observed best vector combination stimuli). Despite these being the best potential cases for clear relations between planar and vector combination responses, only 21% (26 of 126) of the neurons showed a match between the predicted and observed best vector combination stimuli. A total of 39% (49 of 126) of the neurons showed substantial differences of 90 or 135° between the predicted and observed best vector combination responses.

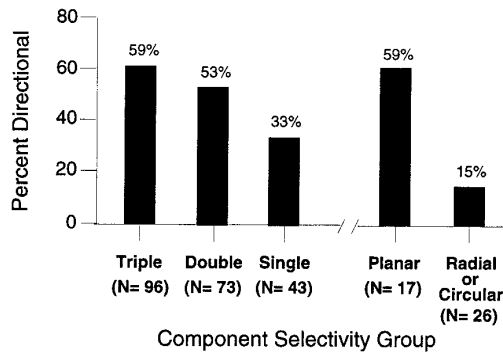


FIG. 7. Bar graph of the percentage of strongly directional neurons in each component selectivity group. Ordinate: percentage of strongly directional neurons in each group, those neurons that had a Rayleigh  $Z$  value  $\geq 4$  for the responses to both the planar and the vector combination stimuli. Triple-component neurons (those that respond to a planar, a radial, and a circular stimulus) show the highest percentage of strongly directional neurons. Single-component neurons (those that respond to either a planar, a radial, or a circular stimulus) show the lowest percentage of strongly directional neurons. Note that a single-component neuron that had no significant response to either of 2 other stimuli (for example, a radial neuron with no significant responses planar or circular stimuli) could still have  $Z$  values  $\geq 4$  on the basis of the profile of planar and/or combination responses. Thus single-component neurons could be, and were, present in the strongly directional group of neurons, but such neurons were less frequent in comparison with the numbers of strongly directional triple-component neurons.

and vector combination studies (Fig. 6C, right). We found good agreement between the predicted and observed best combination responses in only 21% (26 of 126) of the neurons. In contrast, 39% (49 of 126) of the neurons showed substantial disagreement between the predicted and observed best responses; the best vector combination response was based on planar motion with a direction rotated by 90 or 135° from that predicted. Simple planar directionality in a particular part of the receptive field fails to explain the responses of many MSTd neurons to vector combination stimuli.

Another possible relationship is between the strength of the directional response and the number of optic flow components to which a neuron responds (Duffy and Wurtz 1991a). For example, if a neuron responded to planar motion as well as to either radial or circular motion, we would expect that it might be more likely to prefer the same direction of motion in planar and the combined planar/radial vector combination stimuli, as did the neuron in Fig. 3. We found that to be the case. We found that triple-component neurons, those that respond to a planar, a radial, and a circular stimulus, show the highest percentage of strongly directional neurons (Fig. 7, left). In contrast, single-component neurons, those that respond either to a planar, a radial, or a circular stimulus, show the lowest percentage of strongly directional neurons (Fig. 7, left). In addition, the planar single-component neurons (Fig. 7, right), those that respond only to planar motion, show about the same percentage as triple-component neurons. It is the radial and circular single-component neurons, those that respond only to a radial or a circular stimulus, respectively, that show the lowest percentage of neurons with strongly directional responses to both the planar and vector combination stimuli.

In net, we saw no relationship between receptive field size and the similarity of planar and vector combination re-

sponses (Fig. 6, A and B). In addition, in a subset of neurons selected to reveal the effect of receptive field location (Fig. 6C), we see no definitive relation between the location of the receptive fields of the cells and the likelihood that the neuron would respond to the vector combination stimuli, as was the case in our previous study (Duffy and Wurtz 1995). In our view, this suggests that receptive field size and location are unlikely to fully account for the wide range of similarity and dissimilarity between planar and vector combination responses. However there does seem to be a relationship to the single-, double-, or triple-component classification of responses and the strength of the neuron's response to planar stimuli.

#### *Comparison of responses to planar and transparent overlap stimuli*

In a second set of experiments, instead of combining the planar with the radial or circular stimuli, we overlapped them as transparently superimposed stimuli. These transparent overlap stimuli present the same planar motion and radial or circular motion present in the vector combination stimuli, but with no change in the pattern of motion—there is no shift in the center of motion of the radial or circular stimulus as there is in the vector combination stimuli. Many neurons showed similar responses to the planar, vector combination, and transparent overlap stimulus sets. Figure 8 shows the responses of such a neuron, which had significant responses to downward planar motion and outward radial motion (Fig. 8, A and B). This neuron also responded best to both the vector combination stimuli (Fig. 8, C and D), and the transparent overlap stimuli (Fig. 8, E and F) that incorporated downward planar motion. Note that these findings also show that the higher speeds that occur at the edges of the vector combination stimuli do not substantially alter the responses of these neurons, because these higher speeds are not present in the transparent overlap stimuli.

Many neurons showed similar response directionality in planar, vector combination, and transparent overlap studies, with either strong responses to all of these stimuli (Fig. 9A) or weak responses to all of these stimuli (Fig. 9B). Furthermore, examination of the complete sample of responses to planar and transparent overlap stimuli showed a wide range of relations between these responses (Fig. 9C), similar to that seen in comparing planar and vector combination responses (Fig. 5A). As in Fig. 5, we divided the neurons into those that were strongly directional ( $Z \geq 4$ , filled circles) and those that were only weakly directional ( $Z < 4$ , open circles). In the strongly directional group, 63% (51 of 81) showed mean directions within 45° of each other in the two studies; in the weakly directional group, the corresponding value was 43% (52 of 121). Therefore directionality in the transparent overlap studies shows a relationship to planar directionality much like that seen in the vector combination studies.

In cases where the planar and vector combination responses were substantially different from each other, we found that the transparent overlap responses tended to mimic the vector combination responses. Usually, this response pattern consists of directional preferences in either the planar responses or in the vector combination and transparent over-



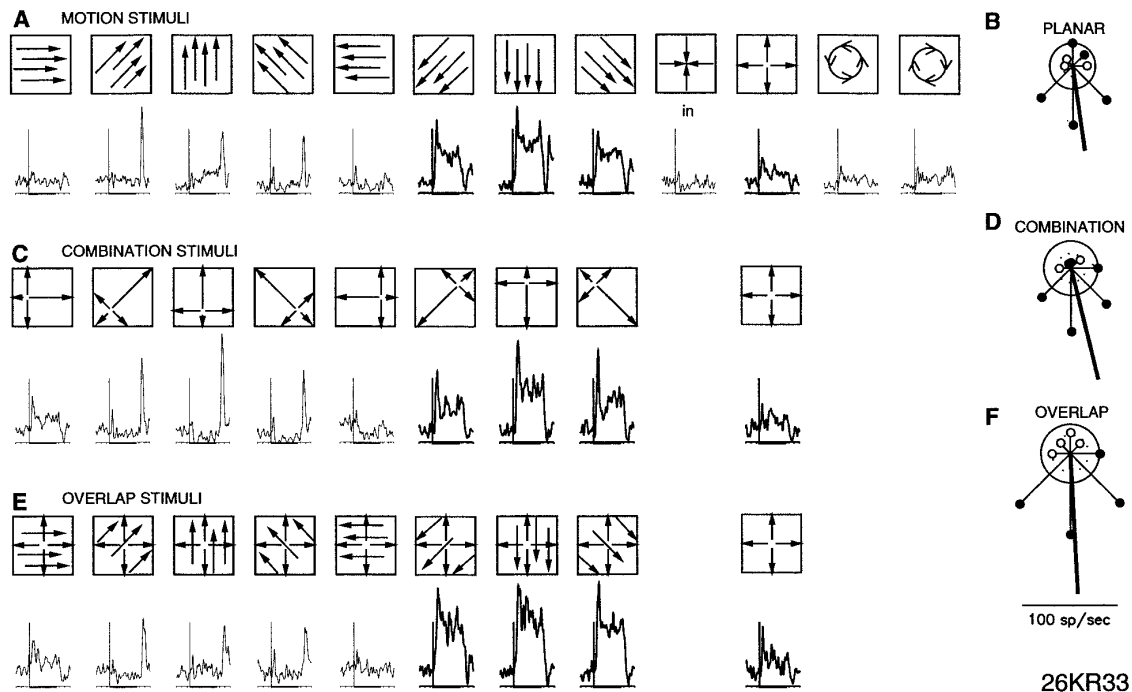


FIG. 8. Response of a neuron to planar, vector combination, and transparent overlap stimuli. Same conventions as in Fig. 7. *A* and *B*: responses of this neuron were strongest to downward planar and outward radial stimuli. *C* and *D*: strongest responses to vector combination stimuli were evoked by the stimulus combining outward radial and downward planar motion. *E* and *F*: strongest responses in the transparent overlap stimuli were evoked by the stimulus overlapping outward radial with downward planar motion. The strong effect of planar directionality is reflected in the large resultant lengths of the net vectors of all 3 stimulus sets.

lap responses, and no directional preferences in the other. Figure 10A shows the responses of one such neuron, with strong leftward directional preferences in the planar study but no directional preferences in the vector combination or transparent overlap studies. This suggests that the vector combination and transparent overlap responses are similar to each other, even when both differ from the planar responses.

The covariation between vector combination and transparent overlap responses, with respect to their differences from the planar responses, is shown in the scatter plot of Fig. 10B for the 202 neurons tested. The ordinate in Fig. 10B is the difference between the planar and vector combination mean resultant length and the abscissa is the difference between the planar and vector combination mean resultant lengths. The regression line for this distribution has a slope of 0.77 and  $r^2 = 0.48$ , which is consistent with covariation between the planar-combination and the planar-overlap differences.

Thus neurons showing similar responses to planar and to vector combination stimuli also have similar responses to planar and transparent overlap stimuli. In the case of the transparent overlap stimuli, all eight have the same center of motion (at the center of the stimulus), and only the direction of planar motion in the vector combination stimuli are mimicked by merely altering the direction of planar motion in the transparent overlap stimuli. These observations are consistent with the idea that planar motion effects make a large contribution to the optic flow field preferences of this subset of MSTd neurons.

#### Role of planar inhibition

We noticed that the responses of many neurons to vector combination and transparent overlap stimuli were smaller than their responses to the radial or circular stimuli presented alone. Unexpectedly, this was even true in neurons that did not show any evidence of inhibition in their responses to planar stimuli. To quantify this point across the sample of neurons, we counted the number of responses to the eight vector combination and transparent overlap stimuli that were significantly larger or smaller ( $t$ -test,  $P < 0.01$ ) than that neuron's activity in response to the the centered-center-of-motion radial or circular pattern. Figure 11 shows that both the vector combination and transparent overlap stimuli more frequently evoked smaller responses: on average there were  $\sim 3$  times as many significantly smaller responses as there were significantly larger responses. The greater numbers of significantly smaller responses in the vector combination and transparent overlap studies suggests that these stimuli might engage an inhibitory mechanism that contributes to their response preferences. The parallels between the vector combination and transparent overlap responses suggest that this mechanism is activated by both stimulus sets.

The transparent overlap studies provided a test of the possibility that inhibition resulting from planar motion might account for differences in neuronal responses to planar and transparent overlap stimuli. If this inhibition is important, neurons with greater differences between their planar and transparent overlap responses should show more inhibition. We therefore compared the differences between responses to planar and overlap stimuli with the number of significant

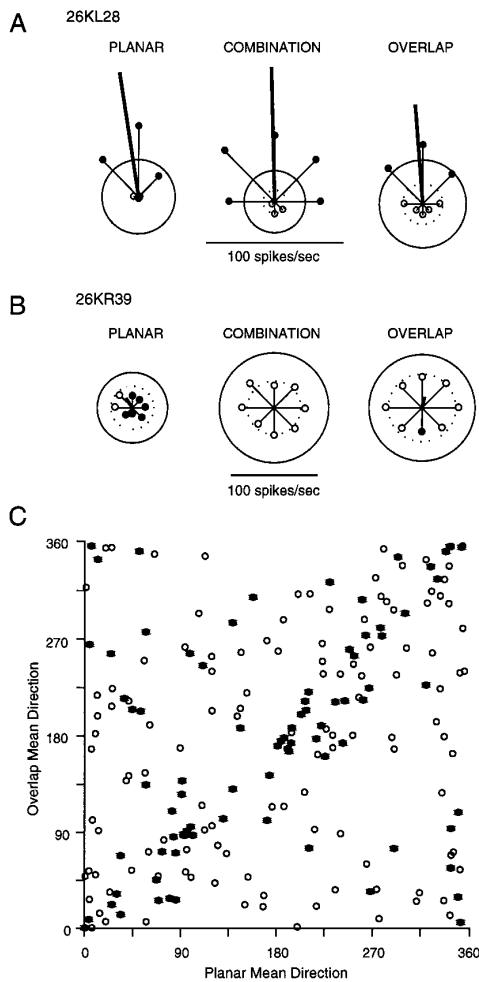


FIG. 9. Transparent overlap stimuli often evoked responses that were similar to those evoked by the planar and vector combination stimuli. *A* and *B*: polar plots of planar (*left*), vector combination (*middle*), and transparent overlap (*right*) response profiles evoked from a neuron showing strong upward preferences with all 3 stimulus sets (*A*) and from a neuron showing little directionality in any of the 3 stimulus sets (*B*). *C*: scatter plot showing that the directions of the net vectors obtained with the planar (abscissa) and transparent overlap (ordinate) stimuli showed the same wide scatter observed when the planar and vector combination stimuli were compared (Fig. 5). Each circle represents the responses from 1 of the 202 neurons. Filled circles: strongly directional neurons ( $n = 81$ ), those with a Rayleigh Z value  $\geq 4$  (see METHODS). Open circles: neurons that were not as strongly directional ( $n = 121$ ), those with a Rayleigh Z value  $< 4$ .

excitatory and inhibitory responses to planar motion (Fig. 12). Neurons having stronger responses to planar than to transparent overlap stimuli showed the most inhibitory responses (Fig. 12, right side of abscissa), whereas neurons having stronger responses to overlap than to planar stimuli showed the fewest inhibitory responses (Fig. 12, left side of abscissa). In contrast, the average number of significant excitatory responses was relatively stable regardless of differences between planar and transparent overlap response profiles. These findings are consistent with a contribution of planar inhibition to differences between planar and transparent overlap response profiles.

*Radial and circular combinations as spiral stimuli*

If MSTd neurons are specialized for specific large field patterns of motion, such as radial or circular stimuli with

centers of motion in different parts of the visual field, these neurons might also respond to other highly specific stimuli. Such special sensitivity has been found for some MST neurons that have been shown to respond to spiral stimuli created by combining radial and circular motion (Graziano et al. 1994). We tested such spiral stimuli on neurons that had significant responses to both radial and circular motion, and then tested to determine whether vector combinations of planar and spiral stimuli had the same preferred directions of planar motion.

We found neurons that responded to such spiral stimuli, and Fig. 13 shows an example of such a neuron. The neuron responded to both inward radial and clockwise circular stimuli (Fig. 13, *A* and *B*), and even more strongly to spiral stimuli resulting from the vector combination of these two radial and circular stimuli (Fig. 13*C*, *right*). The neuron also had a strong response to leftward-upward planar motion, and the planar-spiral vector combination stimulus derived from the leftward-upward planar motion gave the strongest response (compare Fig. 13, *C*, *left*, and *D*). The neuron shows similar preferred directions for the planar motion (leftward-upward) and the planar and spiral vector combination stimulus containing that leftward-upward motion.

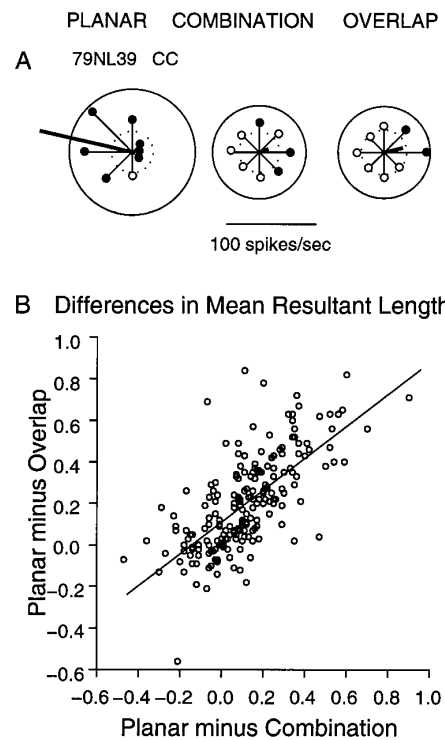


FIG. 10. Comparison of responses to planar, vector combination, and transparent overlap stimuli. *A*: polar plots of planar (*left*), vector combination (*middle*), and transparent overlap (*right*) response profiles from 1 neuron. The vector combination and transparent overlap responses were similar and equally different from the planar responses. This neuron showed strong leftward-upward directional preferences in the planar study, with no responses to the vector combination or transparent overlap stimuli. *B*: scatter plot showing that the vector combination and transparent overlap stimuli generally evoke responses that are similar, even when both differ from the planar responses. Each circle represents the differences between the mean resultant lengths for the planar and vector combination responses (abscissa) vs. the planar and transparent overlap responses (ordinate) from 1 of the 202 neurons studied with all 3 stimulus sets.

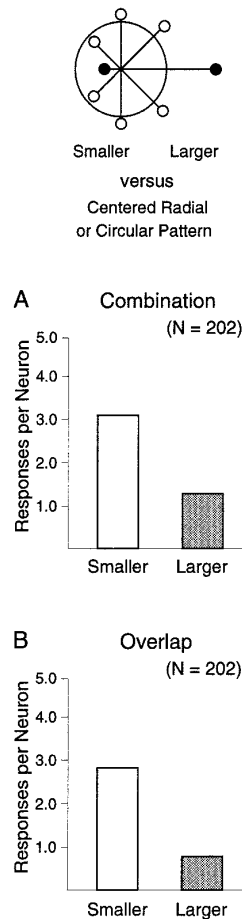


FIG. 11. Mean number of responses per neuron that were significantly larger or smaller than the baseline activity level in the vector combination (A) and transparent overlap (B) studies. *Top*: polar plot shows the basis of our measurements of the responses. *A*: vector combination stimuli evoked an average of 3.2 smaller responses per neuron and 1.3 larger responses per neuron. *B*: transparent overlap stimuli evoked an average of 2.9 smaller responses per neuron and 0.9 larger responses per neuron. Vector combination and transparent overlap responses show similar rates of inhibitory effects.

Figure 14A shows the relative amplitude of the responses to spiral, radial, and circular stimuli for each of the 17 neurons that responded to both radial and circular stimuli. The neurons are arranged so that increasing relative responses to the spiral stimuli are further toward the right. In 10 of these 17 neurons, the response to the spiral was greater than that to the radial or circular stimuli (Fig. 14, neurons labeled 8–17), but for the other neurons the response was better to the radial or circular stimuli alone.

The neurons also responded to planar stimuli and to the planar-spiral vector combination stimulus. Figure 14B compares the direction of the preferred planar motion stimulus with the direction of the best planar-spiral vector combination stimulus. Each circle on the scatter plot represents the responses of 1 of the 17 neurons, and the neurons are again divided into those that had strongly directional responses to both planar and the planar-spiral vector combination stimuli (●) and those that were not as strongly directional (○). Of the 10 strongly directional neurons, 8 had planar and planar-spiral vector combination mean directions within 45° of each

other, but only three of the seven weakly directional neurons did. This is much the same pattern seen for the larger sample of neurons studied with planar and radial/circular vector combination stimuli (Fig. 5).

We next determined whether the neurons giving progressively stronger responses to planar stimuli might also give progressively less similar responses to planar and planar-spiral vector combination stimuli. Figure 14C shows the differences in net vector direction for planar and planar-spiral vector combination stimuli for each of the 17 neurons. No trend in the similarity of direction (ordinate) is evident as strength of the response to the spiral stimulus increases (abscissa). How selective a neuron is for the spiral motion is unrelated to its responsiveness to planar motion.

## DISCUSSION

### *Contribution of planar motion to MSTd responses*

We investigated the contribution of planar motion sensitivity to the selective responses of many MSTd neurons to stimuli whose centers of motion were shifted within the visual field (Fig. 1A). We reasoned that if such sensitivity to planar motion were important, the strongest responses of a neuron should be evoked by stimuli combining the radial or circular motion with the preferred direction of planar motion. We saw evidence for such a relationship in many neurons (Fig. 3). We also saw many neurons whose preferred direction of motion was substantially different to the planar and the combined stimuli (Fig. 4). By dividing our sample of neurons into two groups, those with stronger directionality to planar and vector combination stimuli and those

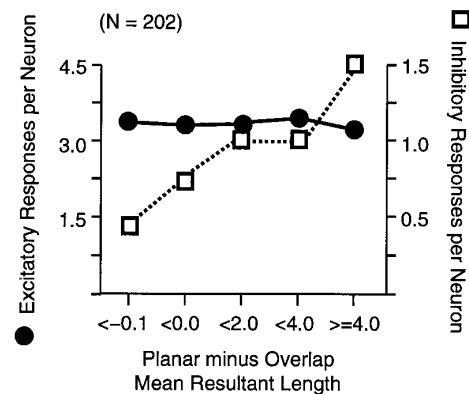


FIG. 12. Comparison of the relative strength of the response to planar motion and the numbers of excitatory (●) and inhibitory (□) responses. *Abscissa*: differences between planar and transparent overlap mean resultant lengths. *Ordinate*: differences in the scale reflect the differences in the average number of excitatory and inhibitory responses to planar motion. The responses on the ordinate are expressed per neuron by dividing the total number of excitatory and inhibitory responses by the number of neurons in the sample (202). The number of excitatory planar responses is stable at ~3 per neuron across groups having mean resultant lengths that are larger to transparent overlap stimuli (less than -0.1), similar for planar and overlap stimuli (<0.0), or larger for planar stimuli (<2.0, <4.0, ≥4.0). The number of inhibitory planar responses increases from 0.5 per neuron among neurons having more transparent overlap selectivity to 1.0 per neuron among having similar planar and transparent overlap selectivities to 1.5 per neuron among neurons having more planar selectivity. Thus the differences in the responses to planar and transparent overlap stimuli are related to the frequency of inhibitory responses.

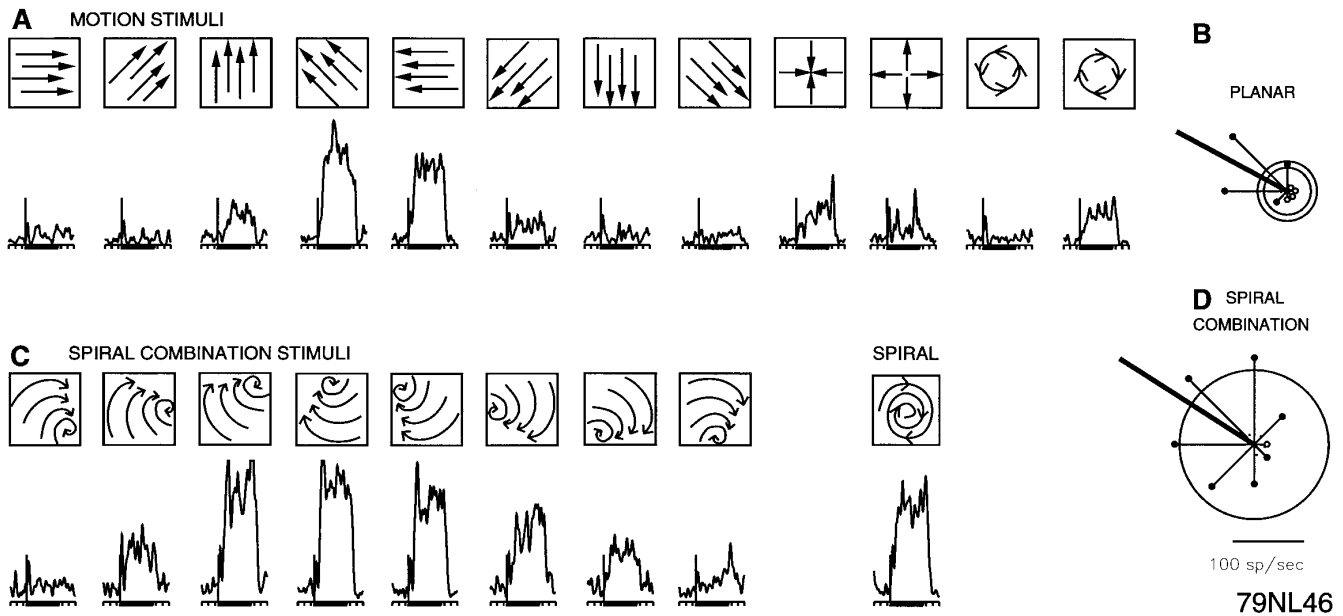


FIG. 13. Responses to spiral stimuli and the vector combination of spiral and planar motion along the top:  $100^\circ \times 100^\circ$  stimulus screen, with the arrows depicting the direction of dot motion on each part of the screen. Spike density histograms below each stimulus: mean responses over 6 presentations of each stimulus. Vertical lines: stimulus onset; height of lines indicates the 100-spike/s discharge rate. Thick horizontal bar: 1-s stimulus period. A: neuron responded best to leftward-upward planar motion, with smaller responses to inward radial and clockwise circular motion. B: polar plot of the planar responses shown in A; the 2 concentric circles show the amplitude of the responses to the radial and circular stimuli. C: response to the spiral stimulus is larger than that to either the inward radial or clockwise circular stimulus from which the spiral was derived. Combinations of the spiral and planar motions produced even stronger responses. D: polar plot of the spiral and vector combination responses. The neuron shows good agreement between the preferred planar motion (leftward-upward) and the planar and spiral vector combination stimulus containing leftward-upward motion.

with weaker directionality, we were able to show that the neurons with the stronger directionality were those that showed the greatest similarity between the preferred direction of motion in both the planar and combined stimuli (Fig. 5B). Thus the responses of those neurons with the stronger directionality to both the motion of planar and vector combination stimuli are most readily understood as responding to the total planar motion in the stimulus, the planar motion mechanism (Fig. 1C).

We tested this distinction by determining whether these MSTd neurons responded in the same way when the planar motion was transparently overlapped by, rather than vector combined with, the radial or circular motion. In the case of these transparent stimuli, the planar motion was present but the center of motion of the radial or circular pattern remained in the center of the screen so that the global pattern remained the same and only the direction of planar motion changed. We found that the neurons that responded most strongly to planar motion when the planar motion transparently overlapped the radial or circular pattern were the same ones that responded best when this motion was vector combined with radial or circular motion (Fig. 10B). This similarity in the response, both when the center of the radial or circular stimuli changes (in the vector combination stimuli) and when it does not (in the transparent overlap stimuli), is consistent with the idea that planar motion makes a large contribution to the response of these neurons.

Not all neurons showed such similarity of preferred direction of planar motion and the predominate planar direction in the vector combination stimuli. These neurons, which had

weaker directional responses (Fig. 5), also showed no such similarity in the preferred directions of planar motion in the transparent overlap stimuli. These neurons fit best with a mechanism dependent on the global motion pattern (Fig. 1B).

One reason that we may see such a range of relationships between sensitivity to planar motion and the shifted-center-of-motion stimuli is that we are drawing our sample of cells from many different anatomic layers of MSTd, and we are therefore looking at the results of successive levels of processing within MSTd. In all of these experiments we have also seen a continuum in the specificity of the response of these cells to one, two, or three of the components of optic flow stimuli (planar, radial, or circular motion) (Duffy and Wurtz 1991a,b, 1995). In this study we have seen that the cells whose responses to the shifted-center-of-motion stimuli are most readily understood in terms of planar motion are those that respond to all three components (planar, radial, and circular; Fig. 7). Those that are least amenable to such a planar basis tend to be those that respond to only one component. One possible interpretation of this observation is that the change in sensitivity to planar motion (at least measured by excitatory responses; see below) reflects a change in the sequence of successive processing stages at which the neuron falls. Because the activity in the preceding visual area (area MT) is so strongly related to planar motion (Lagae et al. 1994; Tanaka et al. 1986), it is tempting to speculate that it is the neurons that are most responsive to planar motion that are the lower-level neurons and that it is the neurons that are least responsive to planar motion and

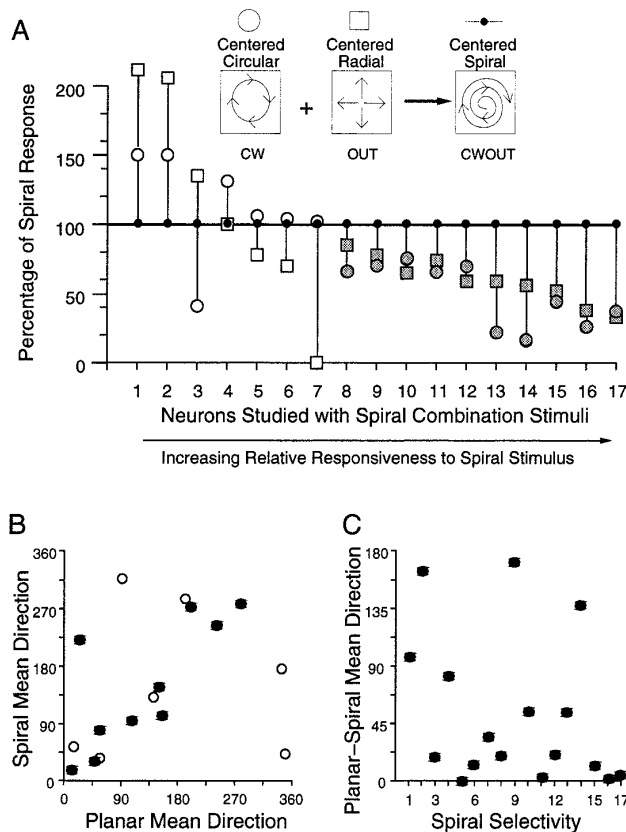


FIG. 14. Comparison of responses to radial, circular, and spiral stimuli. *A*: amplitudes of the response to centered circular ( $\circ$ ) and centered radial ( $\square$ ) stimuli as a percentage of the response evoked by the spiral combination of those 2 stimuli. The outward or inward radial stimulus and the clockwise or counterclockwise circular stimulus that gave the best response for each neuron was used to produce the combination stimulus for that neuron. The responses extend from those that prefer radial or circular stimuli (left side of graph,  $\circ$ ,  $\square$ ) to those that respond best to the spiral stimulus (right side of graph,  $\bullet$ ,  $\boxtimes$ ). *B*: scatter plot of the directions of the net vectors of responses to planar stimuli (abscissa) and planar-spiral combination stimuli (ordinate). Each circle represents the responses of 1 of the 17 neurons; the neurons are divided into those that had strongly directional responses to both planar and the planar-spiral combination stimuli (59%, 10 of 17,  $\bullet$ ) and those that were not as strongly directional ( $\circ$ ) with the use of the same criteria as in Fig. 5 ( $Z$  values  $\geq 4$  for strong responses). Eight of the 10 strongly directional neurons (80%), and 3 of 7 (43%) of the weakly directional neurons had planar and spiral combination mean directions within  $45^\circ$  of each other. *C*: differences in net vector direction for planar and planar-spiral combination stimuli (ordinate) for each of the 17 neurons (abscissa, as in *A* above). Strength of the response to the spiral stimulus is not related to similar preferred directions for planar and planar-spiral combination stimuli.

the most selective for a particular stimulus configuration that are at the highest level of processing. This is a testable hypothesis, because the neurons most sensitive to planar motion should lie in the input layer (layer IV) and should be most frequently orthodromically activated from area MT.

#### Contribution of inhibition

Some MSTd neurons showed little similarity in their preferred direction of motion in the planar and the radial or circular vector combination stimuli. We found that these frequently were also the neurons that responded to only one component of optic flow (Fig. 6*B*), single-component neu-

rons (Duffy and Wurtz 1991b). In contrast, we found that the neurons most likely to respond to the same direction of motion for planar, vector combined, or transparent overlap stimuli were those that responded to multiple components of optic flow (planar, radial, circular motion), triple-component neurons. Thus the observations we have made with the vector combination and transparent overlap stimuli are consistent with the continuum of neuron response types identified previously.

It is tempting to go one step further and argue that single-component neurons, which show dissimilar preferred directions to planar and vector combination stimuli, are largely insensitive to planar motion. We think that this is not the case, but rather that their planar mechanisms are expressed by inhibitory as well as excitatory responses. A role for inhibition in creating the differences between the planar responses on the one hand and the vector combination and transparent overlap responses on the other hand is suggested by the number of responses evoked by each of these stimulus sets. The vector combination and the transparent overlap stimuli evoked 3 times as many responses that were below the centered-center-of-motion baseline than that were above that baseline (Fig. 11, *A* and *B*). This is somewhat surprising in view of the fact that planar stimuli evoked 3 times as many excitatory responses as inhibitory responses, with excitation and inhibition defined as statistically significant difference in comparison with unstimulated control trials. Thus the vector combination and transparent overlap stimuli reveal comparable numbers of inhibitory responses, far in excess of the number of inhibitory responses evoked by planar stimuli.

The impact of planar inhibition is most evident in comparisons between the planar and the transparent overlap response profiles (Fig. 12). This relative clarity of the inhibition in the transparent overlap experiments results from at least two factors: 1) in both the planar and the transparent overlap stimulus sets, the direction of planar motion is the only feature that differentiates the stimuli, because all transparent overlap stimuli have the same center of motion; and 2) the preferred radial or circular pattern is present in all of the transparent overlap stimuli, so that the neurons are more uniformly activated and inhibitory effects might be more evident. We compared the planar and transparent overlap response profiles by the use of the differences between their mean resultant lengths as a measure of the relative strength of their direction preferences. We found that the neurons in our sample had similar numbers of excitatory responses to planar motion regardless of whether their planar and transparent overlap response profiles were similar or very different (Fig. 12, —). In contrast, the number of inhibitory responses to planar motion varied threefold across the range of differences in the planar and transparent overlap response profiles (Fig. 12, - - -). These findings suggest that planar inhibitory mechanisms might account for differences between the planar and transparent overlap response profiles.

When this inhibition is taken into account, it may well be that even those MSTd neurons that we have regarded as least influenced by planar motion are shaped by their directional tuning for planar motion. This interpretation is consistent with our previous suggestion that optic flow field response selectivity in MST neurons is mediated by interac-

tions between excitatory directional tuning and inhibitory directional tuning in partially overlapping zones within the receptive field (Duffy and Wurtz 1991b). Thus, although we find that the strongly directional neurons are most readily understood with the use of planar directional mechanisms (Fig. 1C) and that the weakly directional neurons fit best with a global motion hypothesis (Fig. 1B), this distinction is based largely on the excitatory response of the neurons. If we take into account the inhibitory responses, which are more difficult to experimentally reveal, the response of weakly directional neurons might also eventually be understood as the result of interactions of planar motion sensitivities.

#### *Response to spiral stimuli and the organization of MSTd*

We have confirmed the observation of Graziano et al. (1994) that some MSTd neurons respond to spiral stimuli, including their observation that some respond substantially better to spiral motion than to the component radial and circular patterns. As did Graziano et al., we have observed a continuum of response preferences ranging from neurons that prefer the radial or circular stimulus alone to those that prefer the spiral vector combinations (Fig. 14A).

Many of the neurons studied by Graziano et al. (1994) responded to planar motion, although in 73% of those neurons the planar responses were smaller than the spiral responses. We went on to combine this planar motion with the spiral motion, and found that the responses to planar-spiral vector combination stimuli were very similar to what we had seen for the planar-radial and planar-circular vector combination stimuli: neurons that had strong directionality to both the planar and the planar-spiral vector combination stimuli preferred similar directions of motion for both (Fig. 14B). This was true even for neurons that responded substantially better to the spiral stimulus than to the radial or circular stimuli (Fig. 14C). Thus neurons that are more responsive to spiral stimuli appear to show the same response relations to planar motion as those that are more responsive to radial or circular stimuli.

Although there may be good reasons for maintaining special sensitivity to spiral motion in some neurons (Graziano et al. 1994), we should not consider these neurons to be any more of a separate subpopulation in MSTd than the other MSTd neurons. Rather, their spiral selectivity appears to exist on a continuum of MSTd response selectivities, and this selectivity might depend on planar motion to the same extent as other MSTd neurons.

In our earlier work (Duffy and Wurtz 1991a) we suggested that the stimulus preferences of MSTd neurons can be viewed as varying in a continuum defined by the strength of their responses to planar, radial, and circular optic flow stimuli. That view is inadequate to account for more recent observations, including those of Graziano et al. (1994) on response preferences for spiral stimuli, our more recent observations on planar-radial and planar-circular response preferences (Duffy and Wurtz 1995), and our current observations on planar-spiral response preferences. Our earlier work did, however, suggest that planar motion sensitivity is fundamental to MSTd response to planar, radial, and circular stimuli (Duffy and Wurtz 1991b), and our current work suggests

that this mechanism might underlie response selectivity for the wide variety of optic flow fields studied so far. Together these findings reveal the potential capacity of MSTd neurons to support a neural representation of the optic flow resulting from a wide variety of observer movements in three-dimensional space.

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