Motion Selectivity in Macaque Visual Cortex. II. Spatiotemporal Range of Directional Interactions in MT and V1

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SUMMARY AND CONCLUSIONS
1. We measured the spatial and temporal limits of directional interactions for 105 directionally selective middle temporal (MT) neurons and 26 directionally selective strate (V1) neurons. Directional interactions were measured using sequentially flashed stimuli in which the spatial and temporal intervals between stimuli were systematically varied over a broad range. A direction index was employed to determine the strength of directional interactions for each combination of spatial and temporal intervals tested.

2. The maximum spatial interval for which directional interactions occurred in a particular neuron was positively correlated with receptive-field size and with retinal eccentricity in both MT and V1. The maximum spatial interval was, on average, three times as large in MT as in V1. The maximum temporal interval for which we obtained directional interactions was similar in MT and V1 and did not vary with receptive-field size or eccentricity.

3. The maximum spatial interval for directional interactions as measured with flashed stimuli was positively correlated with the maximum speed of smooth motion that yielded directional responses. MT neurons were directionally selective for higher speeds than were V1 neurons.

4. These observations indicate that the large receptive fields found in MT permit directional interactions over longer distances than do the more limited receptive fields of V1 neurons. A functional advantage is thereby conferred on MT neurons because they detect directional differences for higher speeds than do V1 neurons.

5. Recent psychophysical studies have measured the spatial and temporal limits for the perception of apparent motion in sequentially flashed visual displays. A comparison of the psychophysical results with our physiological data indicates that the spatiotemporal limits for perception are similar to the limits for direction selectivity in MT neurons but differ markedly from those for V1 neurons. These observations suggest a correspondence between neuronal responses in MT and the short-range process of apparent motion.

INTRODUCTION
The middle temporal area (MT) is an extrastriate visual area that is selectively involved in the cortical analysis of visual motion. MT receives ascending visual inputs via a rich set of cortical and subcortical afferents and in turn projects to at least two higher-order cortical areas that provide visual input to posterior parietal cortex (12, 23, 26). One of the major aims of research in MT, or any other extrastriate visual area, is to determine how the output of that area differs from its inputs. In other words, what are the distinctive physiological properties that arise from neural processing within a particular area, and what perceptual or behavioral functions are consequent to the emergence of such properties? Our goal in the present study has been to compare the responses of neurons in MT with those of neurons in a major source of afferent visual input to MT, the striate cortex (V1), in order to begin to answer that question.
Initial studies noted two major differences between MT and V1. The most obvious difference is the increase in receptive-field size. Receptive fields in MT are generally an order of magnitude larger in area than receptive fields at equivalent eccentricities in V1 (e.g., Ref. 8). The second major difference is that a preponderance of neurons in MT are directionally selective (e.g., Ref. 25), whereas V1 contains a minority of such neurons (1). However, recent data indicate that many of the neurons that project from V1 to MT are themselves directionally selective (19). An important question that arises from this observation is whether the direction selectivity of MT neurons simply reflects the properties of its inputs from V1 or whether additional processing occurs that significantly modifies the responses of MT neurons.

In the present experiments we studied the responses of directionally selective neurons in MT and V1 to sequences of stimuli presented in stroboscopic motion in order to see whether MT neurons respond to such stimuli in ways that striate neurons do not. By systematically varying the distance and time interval between successively flashed stimuli, we have been able to measure the spatial and temporal limits for activation of the directionally sensitive subunits within the receptive field. We have found that directional interactions occur over much larger spatial intervals in MT than in V1, while the temporal limits for directional interactions are similar for the two areas. The data suggest that one function of the increased receptive-field size in MT is to permit directional interactions over larger distances, thereby enabling neurons to encode directional information for higher speeds of stimulus motion.

A brief report of this study has appeared previously (15).

METHODS

Behavioral and electrophysiological methods

The methods for monkey training, stimulus presentation, and single-neuron recording were described in the previous paper (16). In the present experiments we also recorded from an additional population of directionally selective neurons in V1 for purposes of comparison. The V1 neurons were located on the lateral surface of the hemisphere and in the calcarine sulcus, covering an eccentricity range from 5 to 30°. We identified the recording site of each striate neuron with respect to the granular layer using the physiological criteria employed by previous investigators (11, 22). Visual stimulation was identical to that used in the study of MT except that the size of the stroboscopic slit was reduced from 3.0° × 0.3° to 2.0° × 0.1°. For neurons that showed appreciable end-stopping, the slit length was adjusted to approximate the optimal length. Striate neurons were also classified as simple or complex according to the spatial overlap of on and off responsive zones within the receptive field (16).

Electrodes tracks were reconstructed after termination of the experiments, and the location of each neuron was confirmed to be in V1.

Data analysis

Neuronal responses were elicited using sequences of flashed stimuli whose spatial and temporal interstimulus intervals were systematically varied during the experiment. The response was measured as follows. For each histogram we calculated the average firing rate within a response window that approximated the duration of the response. The computer program first smoothed the histogram by assigning to each bin a firing rate that was the weighted average of the actual firing rate in that bin and those within three bins on either side. The beginning of the response window was set where the response first exceeded a value twice the standard deviation of the spontaneous firing rate or at a point 40 ms after stimulus onset, whichever came later. The end of the window was set where the response rate, following the maximal response, fell to within two standard deviations of the spontaneous firing rate or 200 ms after stimulus offset, whichever was first.

For blocks of trials in which the spatial separation, Δx, between flashes was held constant and the temporal interval was varied, the total stimulus duration changed from trial to trial, and the response window was calculated separately for each combination of spatial and temporal intervals. Within a block of constant-speed trials, where the ratio of Δx to Δt was held constant, the response window was determined as described above for one histogram, and the same window was subsequently used for the other histograms obtained in a block of trials. When the neuronal response for a particular stimulus condition failed to exceed a value twice the standard deviation of the spontaneous firing rate, the response window was usually set to begin 40 ms after stimulus onset and to end 200 ms after stimulus offset.

After the response window was established for each histogram, the average firing rate during the response window was calculated. The spontaneous firing rate and its standard deviation were calculated for each histogram during an 800-ms period preceding stimulus onset, and the average spontaneous rate was subtracted from the firing rate during the response window to yield a measure of the neuron's
response for each stimulus condition. Average discharge rates were adequate for our purposes here, as opposed to the peak discharge rate used in the preceding paper (16), because our measure of direction selectivity was a ratio of responses in the two directions of motion.

The direction index was then calculated from the response histograms generated by six to eight trials in the preferred and null directions for each stimulus condition. The direction index was computed by the formula: DI = 1 - (response in null/response in preferred). This index yielded a well-behaved measure of directionality with one notable exception: When the response in the preferred direction was very small, minor fluctuations in the response can result in nonsensical values of the direction index. Therefore, we did not calculate a direction index when the averaged response in the preferred direction was less than twice the standard deviation of the spontaneous firing rate.

We displayed the results of this analysis in plots that showed the direction index as a function of spatial and temporal interflash intervals. This analysis is illustrated for one MT neuron in Fig. 1. Figure

![Figure 1](image-url)

**FIG. 1.** Analysis of the spatial and temporal limits of direction selectivity for 1 MT neuron. A: pre-stimulus time histograms for stroboscopic stimuli in the preferred (Pref) and null (Null) directions. The apparent speed was held constant at 16°/s as the temporal interval (Δt) was randomly varied. The Δt for each preferred/null pair of histograms is shown on the left, and the direction index for each pair is given on the right. B: a two-dimensional plot showing the direction index for each pair of spatial and temporal intervals tested for this neuron. Filled circles indicate robust directional interactions; open circles signify intermediate directional interactions; diamonds show that directional interactions were weak or absent (see key). Minus signs indicate that a direction index was not calculated because the response failed to meet minimal criteria (see METHODS). The maximum values of Δx and Δt for which directional interactions were obtained in this neuron are indicated by arrows. Diagonal row of symbols indicated by the asterisk includes the data shown in A.
1.4 shows response histograms obtained in a block of trials in which the apparent speed of the stroboscopic stimuli was held constant at 16°/s. The temporal interval between flashes (∆τ) is given to the left of each preferred/null pair of histograms, and the spatial interval (∆x) covered with the temporal interval, since the apparent speed (dx/∆τ) was held constant. The direction index for each preferred/null pair of histograms is shown to the right. Responses in the preferred and null directions were roughly equivalent for the longest temporal interval (160 ms) but became dramatically asymmetric at shorter intervals. This transition was mirrored by a shift in the direction index from values near zero to values near unity. The index became greater than 1 when inhibition was present in the null direction, and it became negative when the response in the null direction was larger than the response in the preferred direction.

Figure 1B shows the variation in the direction index over the entire range of spatiotemporal intervals tested for this neuron. The value of the direction index is encoded by the symbols as shown in the key at the lower right. The closed circles indicate the region over which robust directional interactions were obtained. Our criterion for such interactions was fairly stringent: We required a direction index of 0.8, which was equivalent to a preferred/null response ratio of 5 to 1. This criterion was somewhat arbitrary, but different criteria did not substantially affect our measurements, since the transition to direction selectivity generally occurred over a narrow range of intervals. For the present comparison of MT and V1 it is only important that the same criterion was used in analyzing data from both areas.

The data in Fig. 1B were obtained in eight blocks of trials in which the apparent speed was held constant at eight different values (2–256°/s). Each diagonal line of symbols in Fig. 1B (lower left to upper right) consists of stroboscopic stimuli of one apparent speed. The asterisk indicates the diagonal for which the apparent speed was 16°/s, and this diagonal includes the data shown in Fig. 1A. From such displays we obtained measurements of the spatial and temporal limits of directional interactions that were used in the present analysis. The maximum spatial separation for direction selectivity is simply the largest value of ∆x for which a criterion directional interaction was obtained, 3.6° in the case of Fig. 1. Similarly, the maximum temporal interval for direction selectivity was 160 ms for this neuron.

Tuning curves were also generated for neuronal responses to smoothly moving stimuli. For these stimuli the response window was calculated for the optimal speed, and the window width was set for nonoptimal speeds by adjusting it for the difference in stimulus duration from that at the optimal speed. Regression lines were fitted using the method of least squares on log values. Correlation coefficients used Pearson’s product-moment correlation, and the significance of differences between regression lines was determined using a Student’s t test.

**RESULTS**

We analyzed the responses of directionally selective neurons in MT and V1. Each neuron included in this analysis had a direction index of 0.8 or greater when tested with smoothly moving stimuli: The response in the preferred direction was at least five times the response in the null direction. In addition, each neuron was studied sufficiently well with stroboscopic stimuli to determine the maximum spatial and temporal intervals for which directionally selective responses could be elicited. We obtained a sample of 105 neurons from MT. It was more difficult to find such neurons in V1, and our sample consisted of only 26 neurons, ~13% of the V1 cells tested. Of the striate neurons, 6 were classified as simple and 20 as complex, with 5 exhibiting significant end-stopping (see METHODS). Nine of these striate neurons were recorded from the supragranular layers and 17 from the infragranular layers. We did not observe any systematic differences in the responses to our stimuli among the small samples in these categories, and we therefore treated the V1 neurons as a single group for the following analysis.

**Spatiotemporal limits to directional interactions**

Figure 2 illustrates the pronounced difference in receptive-field size between the neurons we recorded in MT and V1. The width of each receptive field was measured along its preferred/null axis and is plotted in Fig. 2 as a function of the eccentricity of the receptive-field center. Receptive-field width was highly correlated with eccentricity in both areas, but receptive fields were systematically larger in MT. Over the range of eccentricities covered in our sample (2–30°), the receptive-field widths from MT and V1 were nonoverlapping. The relationship of receptive-field width and eccentricity illustrated in Fig. 2 for MT is similar to that observed in previous studies (8). However, the average receptive-field size of the directionally selective striate neurons appears to be two to three times larger at a given eccentricity than the average receptive-field size.
reported previously for randomly sampled striate neurons (10, 24).

One of our goals was to determine whether the increased size of receptive fields in MT permitted directional interactions to occur over larger distances than in V1. We therefore measured the largest interflash distance (maximum $\Delta x$) for which directional interactions could be obtained for neurons in MT and V1. For example, the maximum $\Delta x$ for the MT neuron in Fig. 1 was $3.6^\circ$ (arrow). Figure 3 shows the relationship between the maximum $\Delta x$ and receptive-field width as measured for both cortical areas. Although there is substantial scatter in the data, the maximum $\Delta x$ was positively correlated with receptive-field width in both areas (MT, $r = 0.57$; V1, $r = 0.53$). The regression lines in Fig. 3 are similar for the two areas, although the slope is somewhat steeper in V1. The maximum $\Delta x$ was substantially larger in MT, with a mean value of $1.3^\circ$ (range 0.2$^\circ$ to 6.0$^\circ$), than in V1, with a mean of 0.59$^\circ$ (range 0.2$^\circ$ to 1.28$^\circ$). Thus neurons in MT were able to respond to directional differences with a $\Delta x$ that was on average three times that in V1, and this capability

![Graph showing receptive-field width vs. eccentricity](image)

**Fig. 2.** Increase in receptive-field size with eccentricity of receptive-field center. In this and subsequent figures, results from MT neurons are indicated by the filled circles and solid regression line, while those from V1 (striate cortex) are shown by the open triangles and dashed regression line. The receptive-field width was measured along the preferred/null axis, and the receptive-field center was taken to be the geometric center of the preferred/null axis. The correlations for both MT and V1 are statistically significant ($P < 0.001$).

![Graph showing maximum $\Delta x$ vs. receptive-field width](image)

**Fig. 3.** Increase in maximum $\Delta x$ with receptive-field width. The maximum $\Delta x$ is the largest spatial interval for which each neuron's response met the minimal criterion for direction selectivity ($DX > 0.8$, see Fig. 1 and METHODS). Correlations for both MT and V1 are statistically significant ($P < 0.001$).
is related to the increase in receptive-field size.

The difference between directional interactions in MT and V1 is seen more clearly in the plot of maximum $\Delta x$ versus eccentricity shown in Fig. 4. The maximum $\Delta x$ increased with eccentricity as would be expected from the relationships shown in Figs. 2 and 3. Although there was some overlap, the mean value of maximum $\Delta x$ in MT was substantially larger than the mean value for V1 at all eccentricities tested.

In contrast with the maximum spatial interval for direction selectivity, the maximum temporal interval, $\Delta t$, was not different for MT and V1 and did not vary with eccentricity. The maximum $\Delta t$ for each neuron is plotted against eccentricity in Fig. 5. The two measures were uncorrelated in both MT and V1. The mean value of maximum $\Delta t$ was in the same range for the two areas: 91 ms in MT and 114 ms in V1. Thus the ability of neurons in both MT and V1 to extract directional information from sequences of stroboscopic stimuli deteriorated substantially when the temporal interval between flashes exceeded 100 ms.

Stroboscopic stimulation and the response to smooth motion

In the preceding analysis we have determined that the maximum spatial interval for direction selectivity is, on average, larger in MT than in V1, while the maximum temporal interval is similar in the two areas. A clear implication of these findings is that MT neurons will discriminate direction for a higher range of speeds ($\Delta x/\Delta t$) than will directionally selective neurons in V1. It has recently been shown (Ref. 25, Fig. 9) that MT neurons have higher preferred speeds than do V1 cells, and one might reasonably infer that MT cells continue to be directionally selective at such higher speeds, although this has not been documented. We therefore measured the maximum speed for which each neuron in MT and V1 gave directionally selective responses to smoothly moving stimuli, and correlated this measure with the maximum $\Delta x$ for direction selectivity as determined with stroboscopic stimuli. We imposed two criteria to determine a neuron’s maximum speed for direction selectivity to smooth motion: a direction index of 0.8 and a response in the preferred direction at least half that for the optimal speed.

Figure 6 illustrates the relationship between the maximum speed for direction selectivity elicited by smooth motion and the maximum $\Delta x$ for direction selectivity elicited by stroboscopic trains. The two measures were positively correlated in both MT and V1 ($r = 0.64$, $r = 0.75$), and the maximum speed for direction selectivity was clearly displaced to higher speeds in MT. The mean of the maximum speeds in MT was 98°/s (8°–25°/s), while the mean in V1 was 43°/s (4°–128°/s), about half that in MT. It would appear, therefore, that
one physiological concomitant of the increased receptive-field size and increased directional interaction distances in MT is the extension of direction selectivity to a higher range of speeds.

An unexpected result of the analysis illustrated in Fig. 6 was the clear displacement of the MT regression line above the V1 regression line. This displacement shows that in addition to absolute differences in maximum Δx and the maximum speed for direction selectivity in the two areas, there are also differences in the relationship between these two measures. In other words, some differences must exist in the temporal properties underlying direction selectivity in MT and V1. This result was surprising to us, since the mean value of the maximum Δx was similar for the two areas as shown in Fig. 5. However, the maximum Δx generally occurred at some small value of Δt, and rarely, if ever, at the maximum Δt (see, for example, Fig. 1B). Thus, Fig. 6 indicates that the temporal interval relating maximum Δx and the maximum speed for direction selectivity was, on the average, longer in MT than in V1. This effect actually constrained the increase in maximum speed for direction selectivity observed in MT. If the temporal properties were identical for MT and V1, the regression lines for MT and V1 would superimpose, and the data points from MT would be displaced to even higher speeds (to the right) in Fig. 6.

A closer analysis suggested that the same temporal factor also varied within MT as a function of eccentricity. To determine this factor, we divided the maximum Δx by the maximum speed for direction selectivity to obtain a “derived Δt,” which is plotted as a function of eccentricity in Fig. 7. There was a weak, but significant (r = 0.33, p < 0.001 level) relationship between the two measures: The
derived Δt became longer with eccentricity. The mean value of the derived Δt for MT was 21.7 ms with a range of 3.5–80 ms. Clearly, then, changes occur in the temporal properties of MT neurons, both as a function of eccentricity within MT and compared with striate neurons. However, these changes are small with respect to the more dramatic variations in spatial properties.

DISCUSSION

Directional interactions

We have identified differences in the processing of motion information in V1 and extrastriate area MT by comparing the responses of directionally selective neurons in these areas to sequences of stroboscopically flashed stimuli. Our major finding is that MT neurons detected directional differences over spatial intervals that were, on average, three times larger than those detected by V1 neurons. This increase in maximum Δx was positively correlated with receptive-field size and with the maximum speed for which directionally selective responses could be obtained with smoothly moving stimuli. Although the circuitry underlying these changes in physiological properties is not yet known, the increased speed for direction selectivity in MT neurons is likely to be the direct result of the increased spatial interval for directional interactions (speed = Δx/Δt). The small increase in temporal properties that we measured in MT actually worked against the increase in maximum speed for direction selectivity. We conclude that one of the primary consequences of neural processing between V1 and MT is to extend direction selectivity to higher stimulus speeds by increasing the spatial width of the receptive-field subunits that detect directional differences.

There are two limitations that must be kept in mind when evaluating these results. First, although we have gathered our sample of V1 neurons from a population that is likely to project to MT, we have not positively identified individual projection neurons by antidromic activation. It is conceivable, therefore, that the average maximum Δx of the V1 neurons that actually project to MT is larger than the average of our sample as a whole. Even if this were so, however, additional processing would still be required to generate the responses observed in MT, since the largest values of maximum Δx we observed in V1 were smaller than the mean value in MT at all eccentricities (Fig. 4). It would seem that despite this limitation, our data demonstrate a substantial increase in maximum Δx between V1 and MT. A second limitation is that there are multiple anatomical pathways by which afferent information can reach MT from V1 (12). While we have shown that MT neurons do not simply reflect the properties of their direct afferents from V1, it remains possible that the increase in maximum Δx actually occurs in a second extrastriate area, which in turn projects to MT. Possible candidates for such a role would include V2 and V3. We think it possible that such indirect pathways indeed play a role in the observed increase in maximum Δx, but it also seems likely that processing within MT augments that increase, since MT receptive fields are known to be larger than receptive fields in V2 and V3 at equivalent eccentricities (Ref. 8; Felleman and Van Essen, in preparation).

Comparison with psychophysics

SPATIAL AND TEMPORAL PROPERTIES. Several recent psychophysical studies have employed apparent motion stimuli to characterize the neural detectors that mediate motion perception in the human visual system. The random dot patterns used as visual stimuli in most of these studies differ from the oriented slits used in the present study, but the effect of the visual stimulation is comparable in that a perception of motion was elicited by successive step displacements of otherwise stationary images. It is interesting to compare the properties of the motion detectors inferred from psychophysical experiments with those observed in the present physiological study.

The recent psychophysical studies of Baker and Braddick (3, 4) appear to be most comparable to our physiological experiments. They measured the maximum spatial and temporal intervals for which apparent motion was perceived for a range of eccentricities, a portion of which overlapped with the range of eccentricities from which our physiological data were obtained. Figure 8 compares the physiological and psychophysical measures of maximum spatial interval over the common range of eccentricities. The physiological data show the maximum Δx obtained from neurons in
MT and V1 as previously displayed in Fig. 4, and the psychophysical data show the maximum spatial separation for which human subjects perceived motion in the study of Baker and Braddick (Ref. 3, Fig. 3). The maximum $\Delta x$ from psychophysics and from both cortical areas increases as a function of eccentricity, a finding that has been confirmed in psychophysical experiments by Nakayama and Silverman (20). It is clear that the psychophysical data fall near the mean of the physiological data obtained from MT and that there is little, if any, overlap between the psychophysical data and the performance of striate neurons. In general, the psychophysical observers were able to detect motion for larger spatial separations than could the best striate neurons in our sample. Despite the species difference in the two studies, this observation establishes MT as a likely candidate to mediate the sensation of apparent motion at large spatial intervals.

Although MT neurons may underlie the perception of apparent motion for the largest spatial intervals at each eccentricity, these data do not inform us about the neural substrate for spatial intervals below the upper threshold. Obviously, human observers perceive motion for a wide range of spatial intervals and apparent speeds below the upper threshold, and it is possible that neurons in V1 may underlie the effect over much of this range. If this is the case, the perception of apparent motion may depend upon neural activity in different cortical areas in a manner determined by the spatial separation between successive stimuli. Data presented in the next paper in this series (21) suggest that this is in fact the case.

Interesting comparisons of physiology and psychophysics can be made in the temporal domain as well. Baker and Braddick reported that motion was never seen when the interstimulus interval exceeded a maximum value of $\sim 100$ ms. This is comparable to the mean values of maximum $\Delta t$ that we measured for neurons in MT (91 ms) and V1 (114 ms). In addition, Baker and Braddick (4) reported that the perception of apparent motion was optimal for interstimulus intervals of 20–40 ms, and similar values have been reported by Morgan and Ward (17) and by Burt and Sperling (7). This value corresponds nicely to the mean $\Delta t$ of 23 ms that was derived from the maximum $\Delta x$ and the maximum speed for direction selectivity in MT (see Fig. 7). Baker and Braddick (4) also found that the temporal properties cited above were invariant with eccentricity, a finding that is reasonably congruent with our physiological observations, since the variations in temporal properties that we observed were small compared with the variations in spatial properties.

**LONG- AND SHORT-RANGE PROCESSES IN MOTION PERCEPTION.** A distinction between two processes underlying perception of motion has
been proposed by Braddick (5, 6), and it is useful to consider whether the physiological mechanisms we observe in MT might correspond to one of these processes. Braddick's proposal was derived from experiments using random dot displays in contrast to most classical studies of apparent motion, which used discrete stimuli such as alternating slits of light. Perhaps the key point in Braddick's hypothesis was that the short-range process acted over distances of 15 min of arc for foveal stimuli, whereas classical experiments reported apparent motion over as much as 10°. The subsequent experiments of Baker and Braddick (Ref. 3, which we considered above) have shown that the short-range process operates over larger distances as the eccentricity of stimulus presentation increases. A second characteristic is that the short-range process fails if the interval between stimuli exceeds 80-100 ms, whereas light flashes in classical apparent motion can be separated by as much as 300 ms (6). From the above comparison, the mean values of maximum Δx and maximum Δt for MT neurons correspond quite well to the results of Baker and Braddick (3, 4), and based on this comparison we conclude that MT neurons are likely to be closely related to the short-range process.

A serious complication in identifying MT neurons with the short-range process is that the short-range process is severely compromised when successive stimuli are presented to different eyes (5). This observation suggests that the neurons mediating the detection of motion are monocular and are likely to represent the first stage in V1 where direction selectivity occurs. This conclusion contrasts with our data, which suggest that neurons at a higher-level cortical area such as MT, which are predominantly binocular, underlie the perception of apparent motion for large spatial intervals. We currently do not see a satisfactory solution to this conflict. Both the psychophysical observations and the physiological observations, however, are based on limited experimental evidence, and further experiments at both levels may resolve the problem.

**SEQUENTIAL RECRUITMENT.** Recent studies have found that several successive displacements of an apparent-motion stimulus provide more information to psychophysical observers than the often-used single-displacement stimulus. Nakayama and Silverman (20) reported that multiple displacements increase the maximum spatial separation for which subjects perceive motion, and McKee and Welch (14) have observed an enhanced sensitivity to temporal parameters for multiple displacements. The term "sequential recruitment" has been employed to describe this phenomenon (13), and we have observed a possible physiological correlate in our experiments. We used multiple displacements ("stroboscopic trains") throughout this study precisely because we noted in preliminary experiments that many MT neurons (but not all) that were strongly directional in response to smooth motion or to multiple displacements of a stationary stimulus were poorly selective for single dis-
placements of a stationary stimulus (two-flash experiments). It would seem, then, that multiple displacements are necessary to elicit optimal direction discrimination from many MT neurons.

The data in Fig. 3 can be used to calculate the number of stimuli that fell within each neuron's receptive field when the neuron yielded its "best" spatial performance. We divided the width of the receptive field by the maximum $\Delta x$ and plotted this ratio against eccentricity in Fig. 9. The mean value was about four to six displacements for receptive fields in the central 5° of the visual field, and the value increased to eight to ten displacements for receptive fields beyond 20° of eccentricity. Interestingly, these values correspond well to the psychophysical observations of McKee and Welch (14) that the enhanced sensitivity to temporal parameters in apparent motion became asymptotic at five to eight displacements. This correspondence suggests that the sequential recruitment noted in psychophysical experiments may be a rather direct correlate of the stimulus configuration that elicits maximal physiological performance in the pool of neurons underlying the perceptual effect.

Comparison of MT and V1

There is now a lengthening list of properties that distinguish the likely contributions of neurons in MT and V1 to the perception of visual motion. Movshon et al. (10) showed that 15–20% of the neurons in MT are capable of responding to the unitary motion of complex patterns, whereas neurons in V1 respond to the oriented components that compose such patterns, and Albright (1) reported changes in orientation tuning that may accompany the response to pattern motion. Van Essen (23) observed that the optimal speeds for stimuli moving in the preferred direction are higher in MT than in V1. Allman et al. (2) demonstrated the existence of directionally selective, antagonistic surrounds in MT neurons, which may enable some MT neurons to distinguish figure from ground on the basis of relative motion. Similar effects have been observed in V1, but additional processing must occur between V1 and MT since the surrounds in MT are extremely large, frequently crossing into the ipsilateral hemifield (J. M. Allman, personal communication). To this list can now be added the present finding that directional interactions occur over substantially larger distances in MT than in V1 and that this increase extends direction selectivity to higher speeds of motion. Each of these findings supports the hypothesis that MT is involved in the cortical analysis of moving images, and each provides a specific example of the role MT may play in that analysis. In general, such response properties that distinguish the output of a particular visual area from its inputs are most instructive for understanding the functional consequences of neural processing within that area. Profiles of such distinctive properties obtained from the various extrastriate visual areas should eventually permit a functional mapping of information flow within the complex set of cortical pathways originating in V1.

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