

Motion Selectivity in Macaque Visual Cortex.

III. Psychophysics and Physiology of Apparent Motion

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SUMMARY AND CONCLUSIONS

1. We have conducted physiological and psychophysical experiments to identify possible neural substrates of the perception of apparent motion. We used identical sequences of flashed stimuli in both sets of experiments to better compare the responses of cortical neurons and psychophysical observers. Physiological data were obtained from two cortical visual areas, striate cortex (V1) and the middle temporal area (MT).

2. In the previous paper (13) we presented evidence that neuronal thresholds for direction selectivity in extrastriate area MT were similar to psychophysical thresholds for motion perception at the largest effective interflash interval, and thus speed, for a given eccentricity. We now examine physiological and psychophysical thresholds for a broad range of speeds to determine whether such a correspondence exists for speeds below the upper threshold considered in the previous paper.

3. Stimuli were presented in stroboscopic motion of constant apparent speed while the spatial and temporal interflash intervals were systematically varied. For each neuron we measured the largest spatial interval that elicited directionally selective responses at each of several apparent speeds. We calculated the composite performance of neurons in both MT and V1 by averaging the spatial interval necessary for direction selectivity at each apparent speed.

4. We employed the same apparent-motion stimuli for psychophysical experiments with human subjects in which we measured the spatial interval necessary for the perception of

motion over a similar range of apparent speeds. We obtained a composite profile of psychophysical performance by averaging thresholds across subjects at each apparent speed.

5. For high apparent speeds, physiological data from MT, but not V1, corresponded closely to the psychophysical data as suggested in the preceding paper. For low apparent speeds, however, physiological data from MT and V1 were similar to each other and to the psychophysical data. It would appear, therefore, that neurons in either V1 or MT could mediate the perceptual effect at low speeds, whereas MT is a stronger candidate for this role at high speeds. We suggest that the neuronal substrate for apparent motion may be distributed over multiple cortical areas, depending upon the speed and spatial interval of the stimulus.

INTRODUCTION

Visual illusions have been important in the development of visual science because a stimulus that gives rise to an illusory perception typically contains only a few critical features of the stimulus that normally elicits that perception. By manipulating these critical features in a systematic fashion, psychophysicists can determine the stimulus attributes that are necessary for a particular perception. For example, it is well known that a sequence of stationary lights can elicit a strong impression of motion if the lights are flashed at appropriate intervals in space and time. This phenomenon of "apparent motion" can be induced in a variety of ways and has been highly useful for

analyzing the mechanisms that underlie the perception of continuous motion (for review see Nakayama, Ref. 15).

The intent of the present study was to explore the possible relationship between the discharge of cortical neurons and the perception of apparent motion. We recorded from directionally selective neurons in two visual areas of the monkey's cortex: the primary visual area, striate cortex (V1), and the middle temporal area (MT), an extrastriate area that is selectively involved in motion processing. We also conducted psychophysical experiments in humans using the same visual stimulation as in the physiological experiments. We systematically varied the spatial and temporal intervals between successive stimuli in our apparent-motion displays, and we then compared the intervals that elicited motionlike responses in cortical neurons with those that elicited a perception of motion in human observers. Our goal was to identify possible neural substrates of this perceptual phenomenon by determining which neurons responded in a manner most closely congruent with the psychophysical observers.

In the preceding paper (13), we showed that the maximum spatial intervals for which MT neurons extracted motion information corresponded to the maximum spatial intervals for which the short-range mechanism of apparent motion is operative (1). There was little or no overlap between the psychophysical data and the physiological responses of neurons in striate cortex. We therefore concluded that directionally selective neurons in MT were a likely neural substrate for the psychophysical responses at *maximum* spatial separations. It is obvious, however, that the perception of apparent motion generally occurs over a range of spatial intervals below the maximum, and the analysis presented in the preceding paper is not informative concerning correspondences between physiology and psychophysics in this range.

This issue has been addressed previously in psychophysical experiments by van Doorn and Koenderink (24, 25) and by Nakayama and Silverman (16). These investigators employed random dot displays of constant eccentricity to measure the spatial and temporal interflash intervals necessary for the perception of apparent motion at different apparent speeds. By measuring the critical interflash intervals *as a*

function of apparent speed, these investigators obtained threshold measurements for a broad range of spatiotemporal intervals below the absolute maximum possible at a given eccentricity. Following their lead, we have measured physiological and psychophysical thresholds as a function of apparent speed. In contrast to previous notions, our results suggest that neurons in different cortical areas may mediate the perception of apparent motion for stimuli of differing speeds and spatial intervals.

A brief report of some of these experiments has appeared previously (17).

METHODS

Physiological experiments

We recorded the physiological responses of single neurons in three awake, behaving rhesus monkeys (*Macaca mulatta*). The monkeys were trained on a visual-fixation task, and receptive fields were studied while the monkey fixated a spot of light in the center of the screen. Methods for monkey training, visual-stimulus presentation, and single-unit recording were detailed in the first paper of this series (12).

We restricted our sample to neurons that were directionally selective in response to smoothly moving stimuli (direction index ≥ 0.8). We also limited the sample of neurons in MT and V1 to those having receptive-field centers between 5 and 25° eccentricity.

When a neuron was determined to be direction selective, we proceeded to study its responses to stroboscopically flashed sequences of stimuli that traversed the entire receptive field in the preferred and null directions (13). The stimuli were rectangular slits of light 3.0° (MT) or 2.0° (V1) in length, except when neurons with clear end-stopping were encountered, in which case the slit length was adjusted to the optimal value. Slit width was 0.3° for MT neurons and 0.1° for V1 neurons.

We collected data in blocks of trials in which the apparent speed ($\Delta x/\Delta t$) of the stroboscopic stimulus was held constant, and the strobe rate was varied randomly from trial to trial. With this procedure the spatial interval between flashes (Δx) could vary from 0.01° to 10.2°, (during study of a particular neuron). Five to eight presentations were usually obtained for each combination of spatial and temporal interval tested. We then determined the maximum Δx for which the neuron was directionally selective. Subsequent blocks of trials repeated this process for different apparent speeds until a satisfactory range of speeds was tested or until the neuron was lost. We then obtained a composite representation of the responses of MT and V1 neurons

by averaging the maximum Δx for direction selectivity for each apparent speed.

Psychophysical experiments

The psychophysical experiments were conducted in the same apparatus, with identical visual stimuli and under the same conditions of ambient illumination as the physiological experiments. The subjects sat in a chair and faced the tangent screen 1.5 rad distant. A chin rest provided for constant head position for all subjects. Since the centers of the receptive fields included in this study were beyond 5° of eccentricity, stimuli were presented at an eccentric location (5°) in each observer's visual field while he fixated a central target. The quality of fixation was spot-checked for each subject by monitoring eye movements with EOG electrodes during the psychophysical task. Fixation was accurate for all subjects, and the data obtained during EOG recording were indistinguishable from those obtained with no fixation control. In most experiments we therefore relied on the subject to maintain steady fixation during stimulus presentation. The apparent-motion stimulus traversed 10° of the visual field in an upward direction with the path length centered on the horizontal meridian. Slit orientation was always orthogonal to the direction of motion.

We measured the threshold spatial interval for which motion was perceived at five different apparent speeds. Subjects were the three authors and two colleagues who were unfamiliar with the physiological experiments. All observers experienced a strong sensation of motion for high strobe rates and experienced no motion at low rates. They were asked to report "motion" or "no motion" for each stimulus presentation during the threshold determination. We used a staircase method of threshold measurement in which the observer reported motion or no motion by pressing one of two switches whose closure was detected by the computer. All trials within a particular block were presented at a constant apparent speed, and the first stimulus within a block was presented with a sufficiently low strobe rate so as to appear as successive flashes (no motion) to all observers. Thereafter a response of no motion by the subject resulted in a higher flash frequency on the following trial, whereas a motion response resulted in a lower flash frequency on the following trial. The frequency steps were of a fixed amplitude and were the same for all observers. When the subject oscillated between two adjacent frequencies on three successive trials, the highest frequency of the pair was identified as the threshold for motion, and the entire process was repeated two additional times. After three threshold determinations were obtained for a particular apparent speed, succeeding blocks of trials repeated the process for apparent speeds ranging from 2 to $32^\circ/\text{s}$. Judgments at $32^\circ/\text{s}$ were difficult, and speeds higher than $32^\circ/\text{s}$

were impractical because the stimuli passed so quickly that the observers could not make a meaningful motion/no-motion judgment. Each subject was given 1 day of practice, and actual data collection began the following day.

RESULTS

In the first section we derive a composite profile of the direction selectivity of MT and V1 neurons for a range of apparent speeds. In the second section we describe psychophysical performance over the same range of speeds, and we compare psychophysical performance to the composite responses of cortical neurons.

Physiology: conditions for direction selectivity

The spatial intervals necessary for maintaining directional selectivity in cortical neurons were determined at each speed. This process is illustrated for one MT neuron in Fig. 1. The apparent speed of the stroboscopic stimuli was held constant at $32^\circ/\text{s}$ while the spatial interval (Δx) between stimuli varied between 0.45° and 3.60° . The histograms show the responses obtained in the preferred and null directions for each spatial interval. This neuron yielded directionally selective responses for values of Δx up to 2.56° , but became nonselective at a Δx of 3.60° . We quantified this transition using a direction index: $DI = 1 - (\text{response in the null direction}/\text{response in the preferred direction})$. The null direction was always considered to be the direction opposite to the quantitatively determined preferred direction. The value of the direction index is shown below each pair of histograms in Fig. 1A. The index ranged from values near 0.0 for nondirectionally selective responses to values near 1.0 for directionally selective responses. The direction index therefore provided an objective measure of the neuron's direction selectivity as a function of spatial interval for each apparent speed tested.

Figure 1B shows how the direction index varied as a function of spatial interval for four different apparent speeds, and these data illustrate two major points. First, the transition from a directional to a nondirectional response for any given speed was abrupt, normally occurring within two spatial interval units at most. Thus any one value of the direction index selected as a criterion for direction selectivity, although arbitrary, did not yield grossly

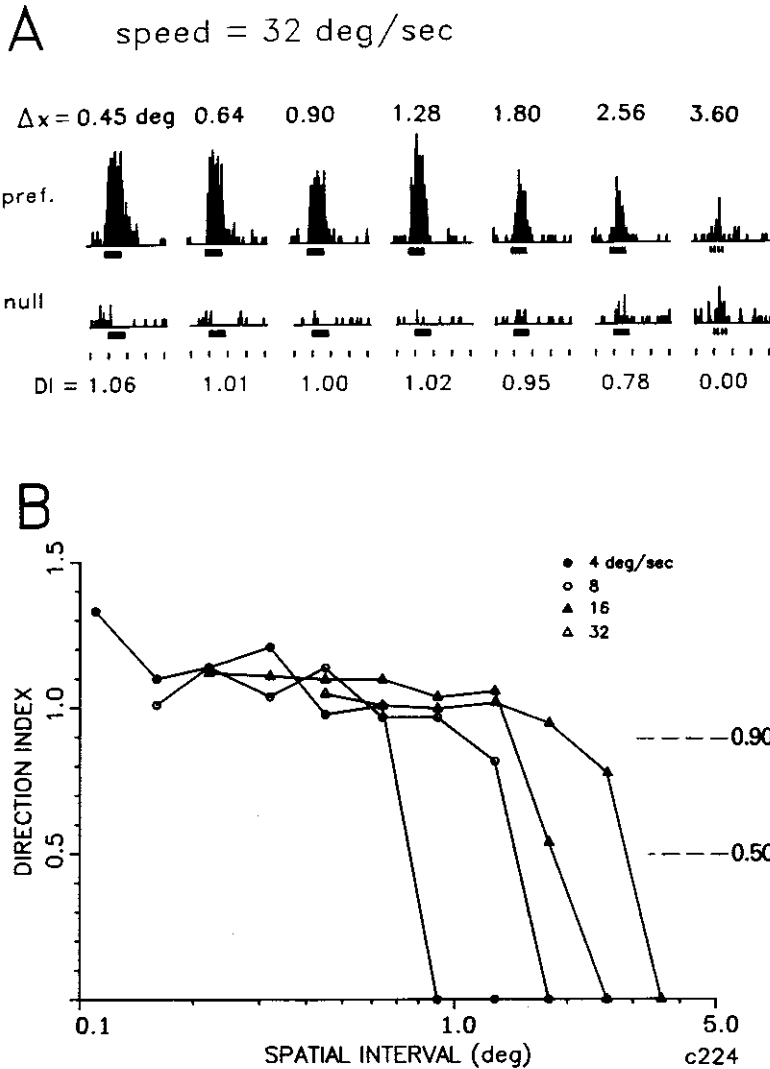


FIG. 1. Measurement of the spatial limits for direction selectivity as a function of apparent speed. *A*: responses of an MT neuron to stroboscopic motion in the preferred (pref.) and null (null) directions for spatial intervals ranging from 0.45 to 3.60°. The apparent speed ($\Delta x/\Delta t$) was held constant at 32°/s. Histograms show summed responses for 8 trials; bin width is 20 ms; individual stimulus flashes are indicated by the vertical tic marks under each histogram (fused together for shorter intervals). The tic marks on the time scale are 500 ms apart. The direction index (DI) fell precipitously from 0.78 to 0 between 2.56° and 3.60°. *B*: direction index as a function of spatial interval for 4 apparent speeds (4, 8, 16, and 32°/s). For all speeds the decline in the directional index was abrupt. The spatial limit for direction selectivity was taken to be the spatial interval for which the neuron's response reached a criterion level of the direction index such as 0.50 or 0.90 (right).

different results from other reasonable values. Secondly, the spatial interval at which the transition occurred varied with apparent speed. Directionally selective responses were obtained for larger spatial intervals at higher apparent speeds. We observed a similar pattern of responses for most neurons.

After performing this analysis for each MT neuron, we averaged the results across the population of neurons to obtain a "composite profile" that could be easily compared with similar data from V1 and with psychophysical data. We employed an arbitrary value of the direction index as a criterion for direction se-

lectivity, and then identified the spatial interval for which the neuron reached the criterion level at each apparent speed tested. The spatial interval necessary for direction selectivity was then averaged across all the neurons for which data were available at a given apparent speed. This process was repeated for each apparent speed tested during these experiments, and the composite spatial interval values were plotted against apparent speed in Fig. 2A. The graph in Fig. 2A actually contains a family of curves, each curve illustrating the result when a different value of the direction index was used as the criterion for direction selectivity. The values of the direction index employed in generating these curves were 0.9, 0.8, 0.67, and 0.5, which represented preferred/null response ratios of 10, 5, 3, and 2, respectively. Since all

speeds were not tested for each neuron, n varied for each of the points on the graph and is indicated for each speed below the abscissa of the graph in Fig. 2C.

The data in Fig. 2A show that MT neurons, on the average, make the transition from weak direction selectivity ($DI = 0.5$) to strong direction selectivity ($DI = 0.9$) over a narrow range of spatial intervals. It is also clear that directional interactions occurred over progressively larger spatial intervals as the apparent speed of the stroboscopic stimulus increased. The data from V1 are shown for comparison in Fig. 2B. Although the same general trends are present in the V1 data, there are important quantitative differences between MT and V1. At high speeds, MT neurons were, on average, directionally selective for

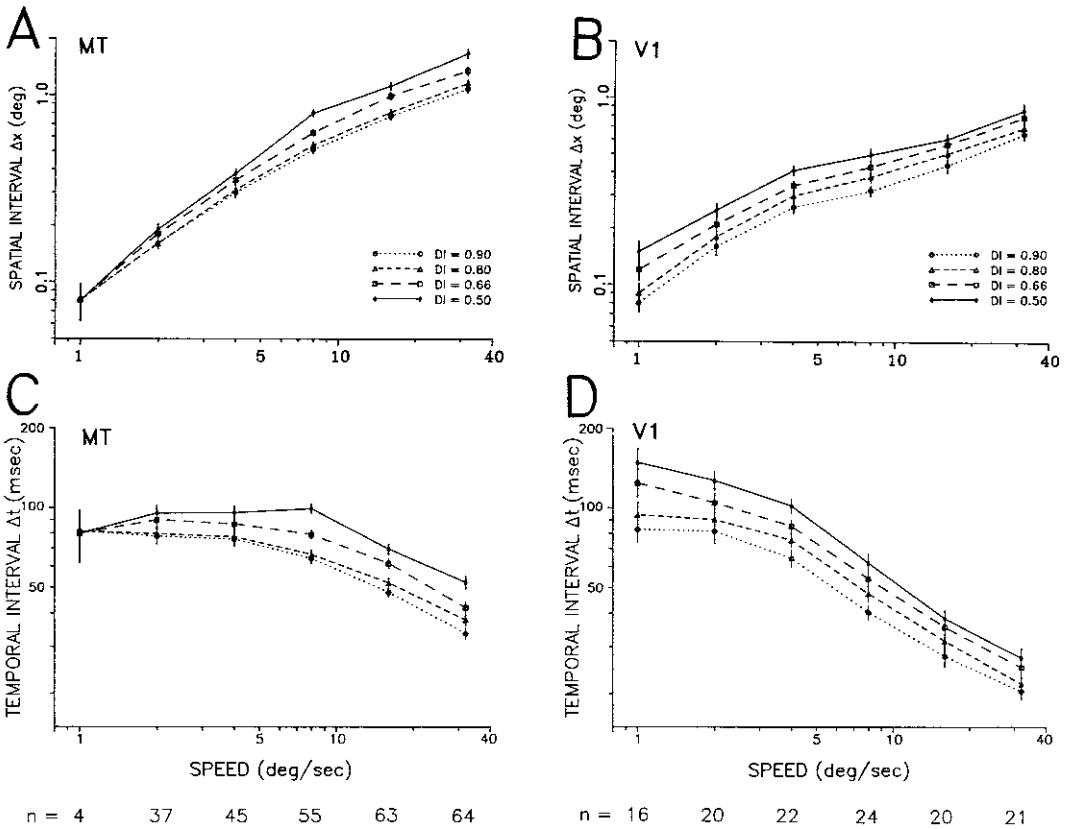


FIG. 2. Composite profiles of the spatial and temporal limits of direction selectivity for each of several apparent speeds. Each curve indicates the points for which neurons, on average, met a particular criterion level of the direction index (see key). Vertical bars indicate standard errors for each point. The number of neurons for which data were obtained at each speed is shown below the abscissa in C (MT) and D (V1). A: spatial limits for MT neurons; B: spatial limits for V1 neurons; C: temporal limits for MT neurons; D: temporal limits for V1 neurons.

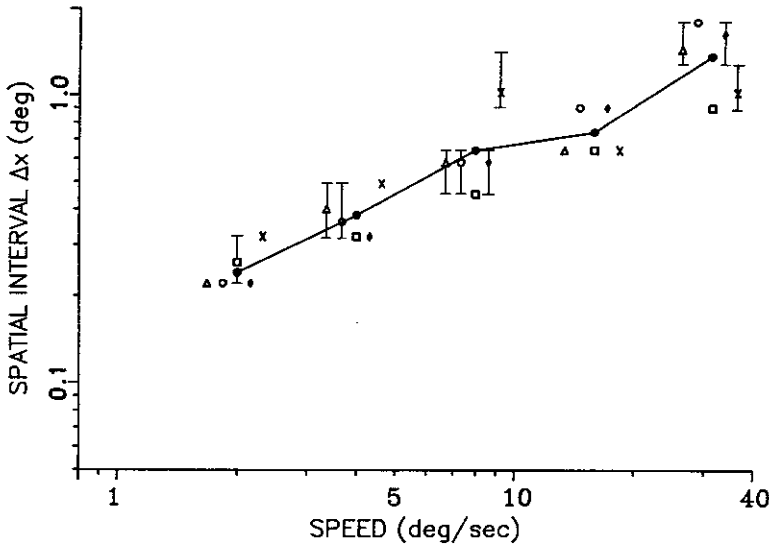


FIG. 3. Maximum spatial interval for perception of apparent motion for 5 human observers. Each *open symbol* shows the logarithmic mean of 3 threshold determinations made at each speed. A *vertical bar* associated with a *symbol* shows the range of the 3 threshold measurements; absence of the *vertical bar* indicates all 3 measurements were identical. *Solid circles* show the mean across subjects.

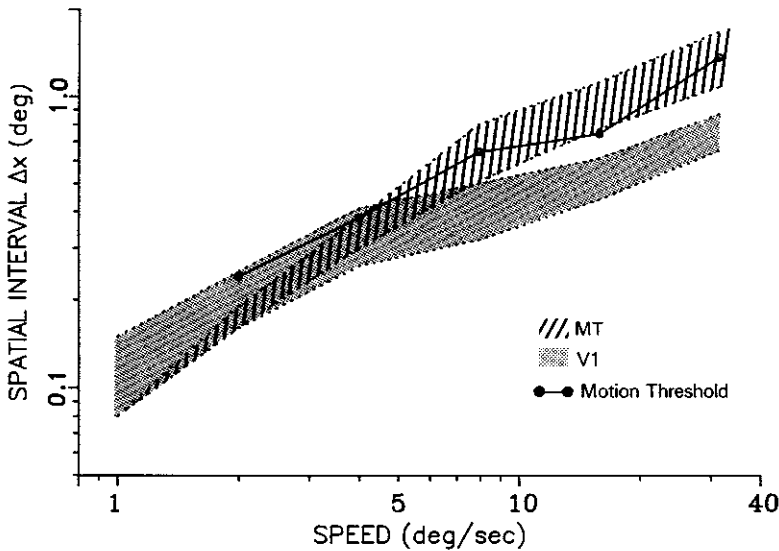
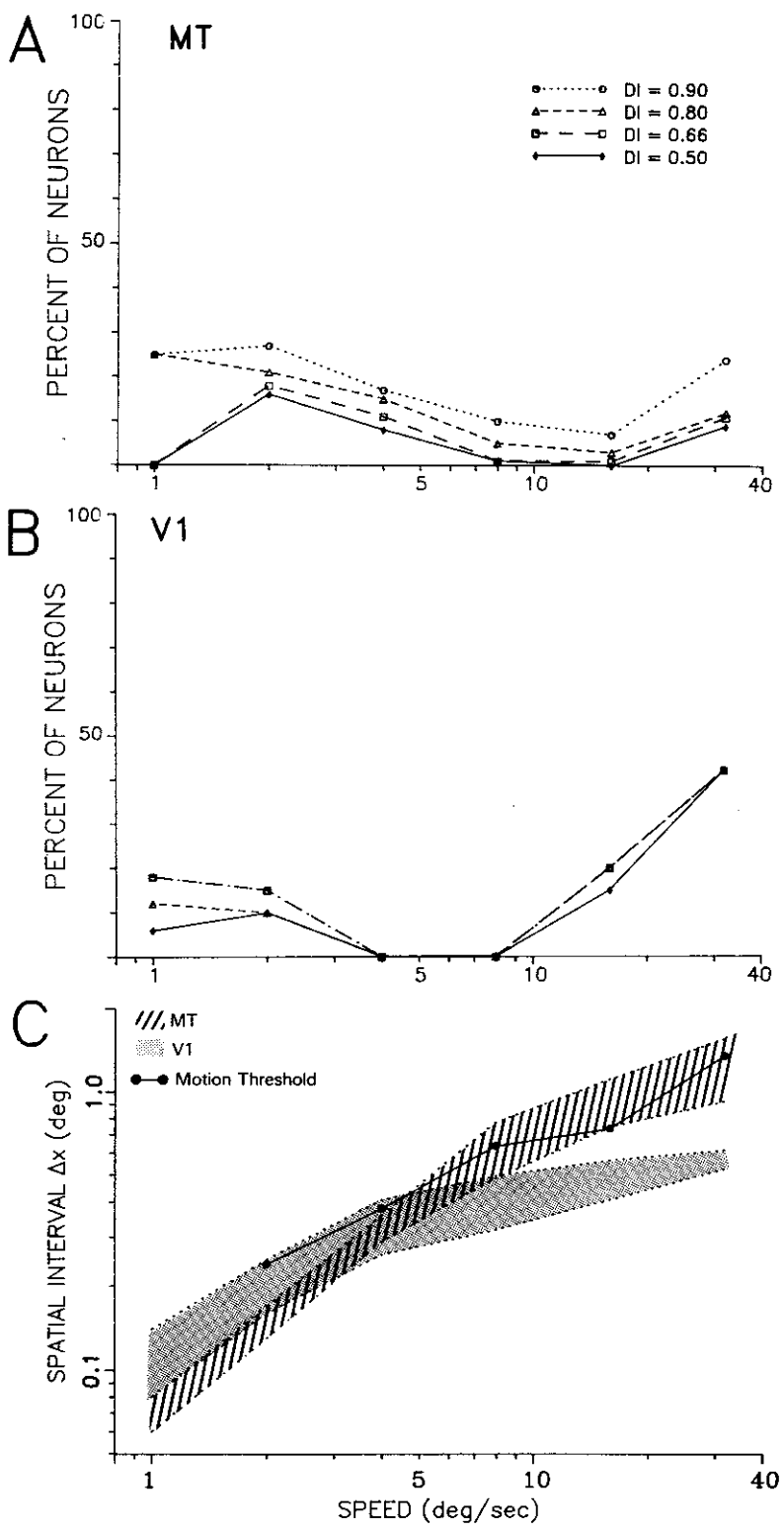


FIG. 4. Comparison of composite physiological responses with psychophysical thresholds for apparent motion. *Hatched region* shows the envelope of direction index curves produced for MT neurons in Fig. 2A. These curves indicate the range of spatial intervals at each apparent speed over which MT neurons, on the average, undergo a transition from directional (*below envelop*) to nondirectional (*above envelop*). *Stippled region* shows the equivalent transition area for directionally selective V1 neurons (from Fig. 2B). The *solid circles* connected by *line segments* show the psychophysical thresholds for perception of apparent motion by human observers. Observers saw motion for spatial intervals and apparent speeds below the line but did not see motion for points above the line.



larger spatial intervals than were V1 neurons. At 32°/s for example, the transition in directionality occurred between 1.1 and 1.8° in MT in contrast to between 0.6 and 0.9° in V1. This result was not surprising in light of the increase in receptive-field size in MT compared with V1 (13). At low speeds, however, V1 neurons were directionally selective for a similar range of spatial intervals as the MT neurons despite their small receptive fields. V1 neurons seemed somewhat better than MT neurons at the lowest speed tested (1°/s): V1 neurons were directional for spatial intervals up to 0.14°, whereas MT neurons became nondirectional, on average, at 0.08°.

The data in Fig. 2, *A* and *B*, show the dependence of direction selectivity on spatial interval for different apparent speeds. However, changes in the spatial interval between flashes were always accompanied by proportional changes in the temporal interval in these experiments, since the apparent speed was held constant. The physiological data from MT and V1 have been replotted to show the *temporal* limits for direction selectivity at each apparent speed in Fig. 2, *C* and *D*. Comparison of panels *A* and *C* in Fig. 2 shows that the maximum Δx in MT increased monotonically with speed from 1–4°/s, whereas the maximum Δt was roughly constant at 80–90 ms. This suggests that the temporal interval is limiting for MT neurons over this range. At higher speeds, however, a *combination* of spatial and temporal intervals limited directional interactions since both values varied with apparent speed. In V1, the limits for directional interactions were due to a combination of spatial and temporal factors over the entire range of speeds tested.

Psychophysics: conditions for motion perception

The conditions for which human observers perceive apparent motion were studied with

the same visual stimuli as in the physiological experiments. Three threshold determinations were made at each apparent speed for five subjects (see METHODS), and the data are shown in Fig. 3. The three measurements for a particular observer never differed by more than one spatial-interval unit, and the general increase of threshold spatial interval with apparent speed was similar for all observers. The solid circles indicate the mean of all 15 threshold measurements at each speed and provide a composite measure of human performance.

We calculated a regression line for the logs of the data shown in Fig. 3, and the power function relating spatial interval (Δx) and apparent speed (\dot{x}) is

$$\Delta x = k\dot{x}^{0.58}$$

The exponent, 0.58, which is the slope of the regression line relating spatial interval and apparent speed, is similar to the values of 0.60 and 0.56 derived independently by van Doorn and Koenderink (24) and by Nakayama and Silverman (16), respectively. Thus, while the psychophysical judgment used in our experiments was subjective, our data are comparable with those obtained with very different psychophysical paradigms.

A comparison of the psychophysical and physiological results is shown in Fig. 4. The hatched area shows the threshold range of spatial intervals for direction selectivity in MT neurons (from Fig. 2*A*). MT neurons were, on average, directionally selective in the space below the hatched region and nondirectionally selective above. The stippled region indicates the equivalent transition zone for V1 neurons (from Fig. 2*B*). The solid circles connected by lines are the means of the human psychophysical responses illustrated in Fig. 3.

The salient point of this comparison is that psychophysical performance was closely matched by the physiological data, but neurons that provided the closest match were not

FIG. 5. Percentage of neurons which failed to give directionally selective responses to stroboscopic motion at each speed. *A*: MT; *B*: V1. These neurons met criterion levels of directionality for some speeds, but not for others. Data for apparent speeds at which a neuron failed to meet criterion levels were dropped from the analysis since no threshold was measurable. Failure to meet criterion levels was due, in part, to equipment limitations that prevented us from creating stimuli with temporal intervals <10 ms. *C*: analysis of physiological data adjusted to compensate for the limitation on the strobe rate. Format is the same as for Fig. 5. See text for details.

necessarily in the same cortical area over the full range of speeds. Interestingly, human psychophysical performance corresponded consistently to the "best" physiological responses in that the corresponding neuronal population at each speed was that which detected directional differences for the largest spatial intervals. Thus, at 32°/s, humans perceived motion for spatial intervals at which MT neurons were directionally selective but V1 neurons were not. Below 8°/s, the physiological transition occurred over similar ranges in V1 and MT and overlapped the psychophysical thresholds.

A source of error in this comparison of physiology and psychophysics arose because we occasionally recorded from neurons that were directionally selective at certain speeds but not for others for either smooth or stroboscopic motion. This problem was particularly troublesome for very high or low apparent speeds and for relatively demanding criteria for direction selectivity ($DI = 0.9, 0.8$). When this problem was encountered, the data for that apparent speed were simply dropped from further consideration, and such data were therefore not included in Fig. 4. The percentage of cells excluded for this reason for each value of the direction index at each speed is shown for the MT and V1 neurons in Fig. 5, *A* and *B*, respectively. The number of neurons excluded was generally <20% except at the highest apparent speed for V1 neurons. The percentage of data excluded was, predictably, lower for less demanding values of the direction index.

This problem was almost certainly due in part to the fact that we could not create stimuli with temporal intervals <10 ms because of the finite time required to recharge the stroboscope's capacitors. We tried to estimate the potential effect of this problem on our conclusions by reanalyzing the data in the following manner. We assumed that all such neurons would have been directionally selective at the problematic speed had we been able to present temporal intervals of 5 ms. We assigned appropriate threshold values for direction selectivity in such cases: $\Delta t = 5$ ms; $\Delta x = (5 \text{ ms}) \times (\text{apparent speed})$. Recalculation of the composite physiological profiles following this procedure yielded the result shown in Fig. 5*C*. This adjustment actually worked in favor of our main conclusions, since its only

effect was to separate further the MT and V1 data envelopes at the highest and lowest speeds. We feel, therefore, that the limitation on the strobe rate did not seriously compromise our observations.

DISCUSSION

This study provides the first direct comparison of physiological and psychophysical responses to stroboscopic motion. We determined thresholds for motion selectivity in cortical neurons by measuring the spatial limits for directionality over a range of apparent speeds. Using the same stimuli, we obtained thresholds for human observers by measuring the spatial limits for the perception of apparent motion over the same range of speeds. Our sample of neurons was taken from two cortical visual areas: the primary visual area, V1 or striate cortex, and extrastriate area MT. We found that psychophysical thresholds corresponded closely to neuronal thresholds over the entire range of tested speeds, suggesting that the threshold for directional selectivity in cortical neurons is a correlate of the psychophysical threshold for perception of apparent motion. Moreover, a comparison of psychophysical data from V1 and MT suggests different roles for the two areas in this perceptual effect. MT data corresponded to psychophysical data over the entire range of speeds, with the possible exception of 2°/s. Neuronal responses in V1 on the other hand, corresponded to the psychophysical responses only for speeds below 8°/s. These observations suggest that MT is a likely neural substrate at high speeds, while the requisite neuronal capabilities exist in *both* V1 and MT at low speeds. The point of divergence between MT and V1 responses seems to be 4–8°/s at the intermediate eccentricities employed in this study. These results raise the possibility that the neuronal substrate for apparent motion is distributed over more than one cortical visual area depending upon the speed and interflash intervals of the stimulus.

While the case for such a distribution of function is not yet strong, it is supported by the recent study by Zihl, Von Cramon, and Mai (26) of a human patient with a selective deficit for visual motion. The patient suffered bilateral lesions of parietal-occipital cortex in

a region where a human analog of MT might exist. The patient had striking deficits in perceiving and responding to visual motion, but the deficits were far more severe for high speeds than for low speeds. A similar relation between physiological and psychophysical responses has been reported for flutter-vibration sensitivity in the somatosensory system by Talbot et al. (22). They found that separate populations of afferents were likely to mediate the perceptual response at high and low stimulation frequencies.

Although we have studied neuronal responses in only two visual areas, it seems reasonable to suppose that directionally selective neurons in other cortical areas such as V2 and V3 might also respond to the apparent-motion stimuli. If so, the distribution of neurons mediating the psychophysical response may actually include several cortical areas, with each area making its greatest contribution within a particular range of speeds.

Previous studies have discussed many of the difficulties and assumptions underlying a comparison between psychophysical responses and single-neuron responses (see for example, Refs. 2, 23), and some of these difficulties may be sources of error in this study. Certain problems arise because no consensus exists about proper methodology for exploring the relation of psychophysical capabilities to neuronal response properties. Other problems arise because of specific aspects of our experiments. We will consider four major problems that may have introduced errors into our analysis.

First, we required any cortical neuron included in our study to be directionally selective. We imposed this restriction because direction selectivity is the property of cortical neurons that seems most unambiguously related to the motion of a stimulus: It is difficult to imagine that the neural circuitry underlying direction selectivity exists for any other reason than to extract information about the motion of a target. Recent behavioral evidence supports this view, since destruction of directionally selective neurons by lesion or by environmental manipulation results in motion-related behavioral deficits (18, 19). Psychophysicists have also considered directionally selective cortical neurons to be the likely neural substrate for the short-range process in apparent motion (3-5, 14). A directionally selective

substrate seemed necessary to explain many of these psychophysical observations, since the visual system was forced to solve a correspondence problem that depended upon correct identification of the direction of displacement of random texture patterns. It remains true, however, that our conclusions may be compromised to the extent that the neural substrate of apparent motion includes neurons that we have systematically excluded from our study.

A related problem in interpreting our data arises from the fact that our measurement of neuronal thresholds involved an explicit comparison of *two* directions of motion (preferred and null), whereas our psychophysical thresholds involved judgments of a *single* direction of motion. This difference is not as paradoxical as it might seem, however, since psychophysical experiments suggest that judgments concerning motion in a particular direction involve a summation of activity among neurons that respond preferentially to opposite directions of motion. For example, the well known "waterfall" illusion shows that motion in a particular direction can be perceived as a result of adaptation of neurons that respond preferentially to motion in the opposite direction.

A second source of error arises in our measurement of neuronal threshold for direction selectivity. At the extremes of the speed range which we tested, some neurons failed to become directionally selective for any stroboscopic stimulus that we could present, although they were directionally selective at intermediate speeds. Data from the problematic apparent speeds were simply dropped from our analysis (Fig. 5, *A* and *B*). It is not clear that this procedure was appropriate, since we don't know the significance for visual processing of the failure of these few neurons to reach threshold at these speeds. However, we do not believe that this uncertainty severely compromises our main conclusions; these problematic cases were few enough that inclusion of them in the analysis did not substantially change the results (Fig. 5*C*).

A third source of error in our analysis is the species difference in psychophysical and physiological subjects. We are not overly concerned about this species difference, however, since recent psychophysical experiments indicate that the perception of motion in the macaque monkey is similar to that of man (9). This ob-

servation extends an extensive list of previous studies that document the many similarities in visual capabilities of these two species (6-11, 20, 21).

Finally, a lack of control for retinal eccentricity of the stimuli could introduce error in our analysis. In the previous paper (13) we showed that the maximum spatial interval for direction selectivity in MT neurons varied with eccentricity and corresponded to psychophysical measures of the maximum spatial interval versus eccentricity. However, the goal of the present study was to perform a more complete physiological analysis by ascertaining the necessary conditions for direction selectivity as a function of speed while eccentricity was controlled. This approach compares with that taken in previous psychophysical analyses (15, 25). The problem, of course, was to obtain a sufficiently large sample of neurons at a controlled eccentricity. The neurons in this study ranged from 5-25° of eccentricity in both V1 and MT. While this range is not as narrow as we might have liked, it excludes all neurons from foveal and perifoveal eccentricities as well as from the far periphery. In addition, the range of eccentricities we sampled was similar for V1 and MT, so it seems unlikely that the important differences illustrated in Figs. 2 and 4 can be attributed to eccentricity differences in our samples of neurons.

Although we do not think it likely that any single source of error described above has se-

riously compromised our conclusions, it is possible that small errors from a number of sources have had a cumulative effect that is not negligible. For this reason numerical results such as the exact speed for divergence between V1 dominance and MT dominance should be considered as our best estimate of an actual value that may be somewhat higher or lower.

The greatest virtue of these experiments may be that they lead to an eminently testable hypothesis concerning the neural substrate for apparent motion. We would expect that an MT lesion would compromise a monkey's ability to detect apparent motion at high speeds and large interflash intervals while having relatively little effect on its performance at low speeds and small interflash intervals. With recently developed techniques for making selective MT lesions (18), this experiment appears practical and should provide a decisive behavioral test of the conclusions suggested by this study.

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