Neuronal Mechanisms of Motion Perception

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An enduring problem for sensory neurophysiology is to understand how neural circuits in the cerebral cortex mediate our perception of the visual world. In part, the problem endures because it is difficult; the circuits in visual cortex are formidable both in their number and in their complexity. Of equal importance, however, is that investigation of the visual system has yielded a stream of fascinating insights into the nature of cortical information processing. Perhaps foremost among these insights is that individual cortical neurons, in contrast to retinal photoreceptors, respond selectively to perceptually salient features of the visual scene. For example, neurons in striate cortex (or V1) respond selectively to the orientation of local contours, to the direction of motion of a visual stimulus, or to visual contours that fall on disparate locations in the two retinae (for review, see Hubel 1988).

Selective neurons of this nature are often thought to be related to specific aspects of visual perception. For example, orientation-selective neurons could provide the basic information from which we perceive shape and form, direction-selective neurons might play a prominent role in seeing motion, and disparity-selective neurons could mediate the sensation of stereoscopic depth. Although straightforward links between neuronal physiology and visual perception are intuitively appealing, the evidence for such links is generally indirect (see, e.g., Teller 1984).

The goal of our research is to explore—in as direct a manner as possible—the relationship between the physiological properties of direction-selective cortical neurons and the perception of visual motion. All of the physiological experiments were conducted in the middle temporal area (MT, or V5) of rhesus monkeys, a higher-order visual area that lies near the junction of the occipital, parietal, and temporal lobes as illustrated in Figure 1. We chose MT for these experiments because it contains a conveniently organized population of direction-selective neurons. More than 90% of the neurons in MT are direction-selective (Zeki 1974; Maunsell and Van Essen 1983), and they reside in a series of "direction columns" that systematically represents direction of motion at each point in the visual field (Albright et al. 1984). MT is thus a logical site to investigate the role of direction-selective neurons in motion perception.

Our general strategy is to conduct physiological experiments in rhesus monkeys that are trained to discriminate the direction of motion in a random-dot motion display. In such experiments, we can simultaneously monitor physiological events and perceptual performance. The psychophysical task is designed so that good performance depends on signals of the kind carried by direction-selective cortical neurons. We asked three basic questions during the course of the investigation: (1) Is performance on the direction discrimination task impaired following chemical lesions of MT? (2) Are cortical neurons sufficiently sensitive to the motion signal in the random-dot display to account for psychophysical performance? (3) Can we influence perceptual judgments of motion by manipulating the discharge of directionally selective neurons with electrical microstimulation? The answer to each of these questions is "yes" (Newsome and Paré 1988; Newsome et al. 1989a,b; Salzman et al. 1990); we therefore conclude that under the conditions of our experiments, perceptual judgments of motion direction rely heavily on information carried by direction-selective neurons in MT.

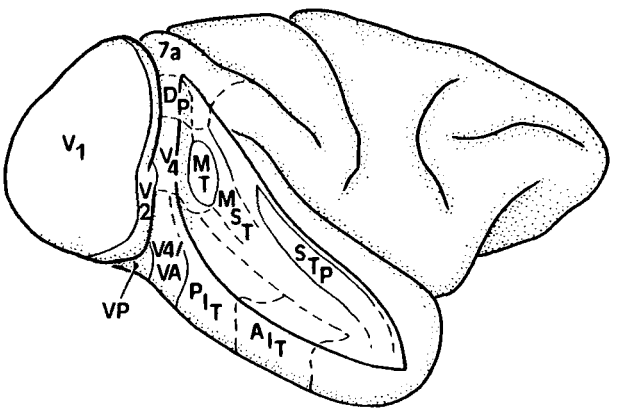

Figure 1. Organization of extrastriate visual areas in the macaque monkey. The middle temporal visual area (MT) is located in the depths of the superior temporal sulcus, which has been opened in this drawing so that normally hidden areas are visible. Thin solid lines indicate borders of visual areas that are known with a reasonable degree of certainty. Dashed lines represent borders that are less well documented. (AIT) Anterior inferotemporal area; (DP) dorsal prelunate area; (MT) middle temporal area; (MST) medial superior temporal area; (PIT) posterior inferotemporal area; (STP) superior temporal polysensory area; (VA) ventral anterior area; (VP) ventral posterior area. (Reprinted, with permission, from Maunsell and Newsome 1987.)

METHODS

We trained five rhesus monkeys (*Macaca mulatta*, three males and two females) on the psychophysical task described below. Prior to training, we surgically implanted each monkey with a search coil for measuring eye movements (Robinson 1963; Judge et al. 1980) and a stainless steel device for immobilizing the head during experiments. After training, a stainless steel recording cylinder was surgically attached to the skull above a craniotomy that permitted microelectrode access to MT. The animals were comfortably seated in a primate chair during daily experimental sessions, and they were returned to their home cages afterward.

Physiological recording. Our general methods for electrophysiological recording in alert monkeys were adapted from those of Wurtz and his colleagues (see, e.g., Mikami et al. 1986). Briefly, the monkey's head was immobilized, and tungsten microelectrodes were advanced into MT using a hydraulic microdrive mounted on the recording cylinder. Action potentials from single MT neurons were isolated, windowed, and displayed on an oscilloscope. The time of occurrence of each action potential, as well as other significant events such as stimulus onset and offset, was stored on a computer disk for subsequent analysis.

Visual stimuli. Each monkey was trained to discriminate the direction of correlated motion in a dynamic random-dot display presented on a CRT screen. The essential feature of this display is that we can vary systematically the signal-to-noise ratio of a unidirectional (or correlated) motion signal within a masking motion noise. The display consists of a stream of randomly positioned dots plotted within a circular aperture. Each dot survives for a brief period of time before being replaced by a partner dot. In one extreme configuration, illustrated in the left-hand panel of Figure 2, each partner dot appeared at a random location on the screen, thus creating random motion noise lacking a correlated motion signal. At the other extreme, illustrated in the right-hand panel of Figure 2, each dot appeared with a fixed displacement in space and time with respect to its partner so that the motion of each dot was identical across the entire display (100% correlation state). Typically, the monkeys viewed a display that was intermediate between these two extremes. In the display illustrated in the middle panel of Figure 2, for example, 50% of the dots carry the correlated motion signal and 50% of the dots provide a masking motion noise.

Psychophysical procedures. The goal of the psychophysical procedures was to measure the lowest correlation value at which the monkey could successfully discriminate one direction of motion from the direction 180° opposed. The procedures have been described in detail by Newsome and Paré (1988) and are illustrated in Figure 3. On each trial, the monkey was required to maintain its gaze on a central fixation point (FP, Fig. 3A) while attending to the random-dot pattern presented within a display aperture at a peripheral location (large circle). After viewing the display for a brief period, the monkey indicated its judgment of motion direction by making a saccadic eye movement to one of two target LEDs (Pref LED and Null LED) corresponding to the two possible directions of motion. The monkey received a liquid reward for correctly reporting the direction of motion.

Figure 3B illustrates the temporal sequence of events in a single trial. The fixation point appeared at time T1, and the monkey centered its gaze on the fixation point (eye-position trace). After the monkey achieved fixation, the visual display appeared at time T2 and remained visible for 1 or 2 seconds. At time T3, the fixation point and the visual display were extinguished, and the two target LEDs appeared. The monkey indicated its judgment of motion direction by transferring its gaze to the corresponding LED. If the monkey broke fixation prematurely, the trial was aborted and the data were discarded.

In a typical block of trials, the monkey performed the direction discrimination at several correlation levels near psychophysical threshold. The correlation levels were chosen so that the monkey's performance varied from near chance (50% correct) to near perfection.

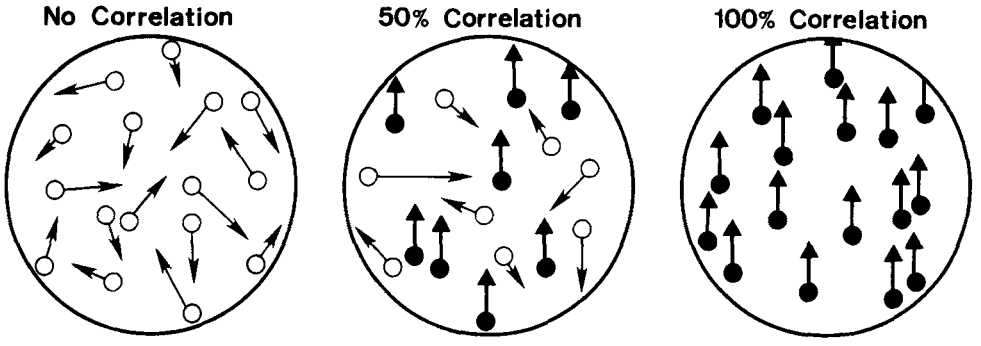

Figure 2. Dynamic random-dot visual display used in the present study. The strength of the motion signal in the display is controlled by specifying the percentage of dots in correlated motion. At 0% correlation (*left* panel), the motion is completely random. At 100% correlation (*right* panel), the motion is completely unidirectional. See text for details. (Reprinted, with permission, from Newsome and Paré 1988.)

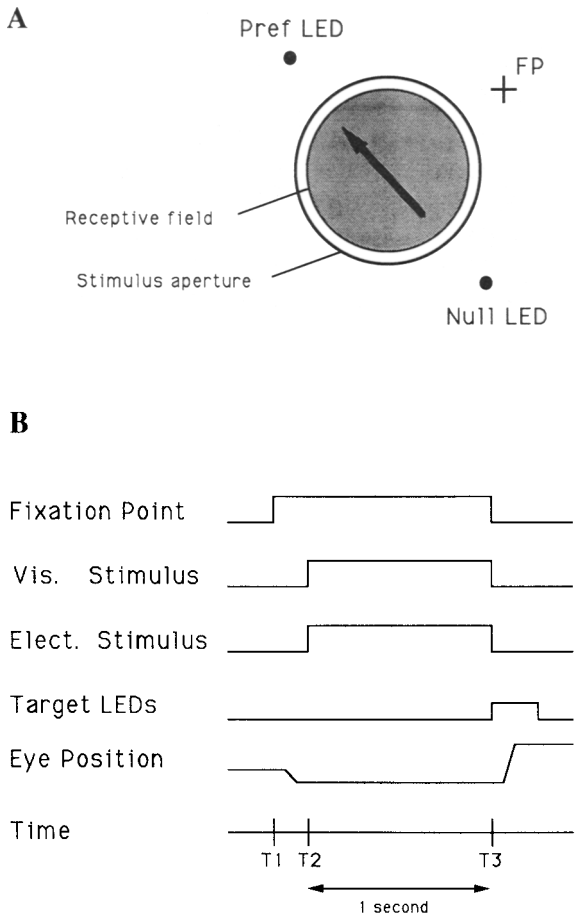

Figure 3. Psychophysical methods employed in the present study. (*A*) Spatial layout of the fixation point (FP), receptive field, stimulus aperture, and target LEDs (Pref LED and Null LED). (*B*) Temporal sequence of events during a single trial. See text for description. (Reprinted, with permission, from Salzman et al. 1990.)

The psychophysical data were compiled into psychometric functions, and sigmoidal curves were fitted to the data. Threshold was considered to be the correlation level at which the monkey made correct decisions on 82% of the trials.

In the single-unit recording experiments, the display aperture was placed directly over the receptive field (shaded circle, Fig. 3A) of the neuron being studied, and the dimensions of the aperture were matched as closely as possible to the dimensions of the receptive field. On each trial, motion was presented in the preferred direction of the neuron (arrow, Fig. 3A) or in the opposite, or null, direction. The speed of the dots in correlated motion was set equal to the preferred speed of the neuron. In this manner, we attempted to create a situation in which the monkey's judgments of motion were likely to depend in part on the responses of the recorded neuron.

In the microstimulation experiments, physiological recordings were obtained from multineuron clusters. The location of the display aperture and the direction and speed of the motion signal were therefore matched to the properties of the multineuron receptive field. On half of the trials, a train of stimulating pulses (10 μA, 200 Hz, biphasic pulses) began and ended simultaneously with the onset and offset of the random-dot display. Microstimulation effects were assessed by comparing the monkey's performance on stimulated and nonstimulated trials.

In the lesion experiments, it was not necessary to match the visual display in a precise manner to the properties of an individual neuron or group of neurons. Rather, the display aperture was always 10° in diameter and was centered 7° eccentric on the horizontal meridian. Motion was either upward or downward on a given trial, and the direction was randomly chosen from trial to trial. Lesions of MT were made by injecting small volumes (1–4 μl) of the neurotoxin, ibotenic acid (Olney 1983), into MT. The injections were made under physiological control so that the lesion was accurately placed at a point in the visual field map that corresponded to the location in visual space of the stimulus aperture. Histological reconstruction revealed that a single injection of ibotenic acid usually resulted in a lesion restricted to 2–3 mm^2 of cortex.

RESULTS

Figure 4A shows the effect of a unilateral MT lesion on direction-discrimination thresholds in the visual hemifield contralateral to the lesion. Psychophysical threshold is plotted as a function of the speed of the correlated motion signal. The prelesion data, illustrated by the solid curve, represent the mean and standard error of at least ten different threshold measurements at each speed. The postlesion data (dashed line) depict the results of single threshold measurements at three different speeds on the day following the injection of ibotenic acid into MT. MT lesions had a substantial effect on direction-discrimination performance, elevating thresholds by a factor of 3–8 above the mean prelesion level at each speed. Figure 4B shows that the lesion had *no* effect on direction-discrimination thresholds measured at the same time in the hemifield ipsilateral to the lesion. Thus, the threshold elevation illustrated in Figure 4A resulted from the lesion and not from anomalous behavioral variables such as attentional state or degree of water satiation.

This monkey was also trained on an orientation-discrimination task in which he was required to report the orientation of a stationary sine-wave grating that appeared within the same visual display aperture used for the random-dot patterns. We measured contrast thresholds by determining the minimum grating contrast at which the monkey could successfully discriminate orthogonal orientations. Figure 4C shows that the MT lesion had no effect on contrast thresholds measured on the same day as the motion threshold illustrated in Figure 4, A and B. Thus, the MT lesion resulted in striking threshold elevations that appeared to be selective for motion vision and for the hemifield contralateral to the MT lesion. This pattern of results

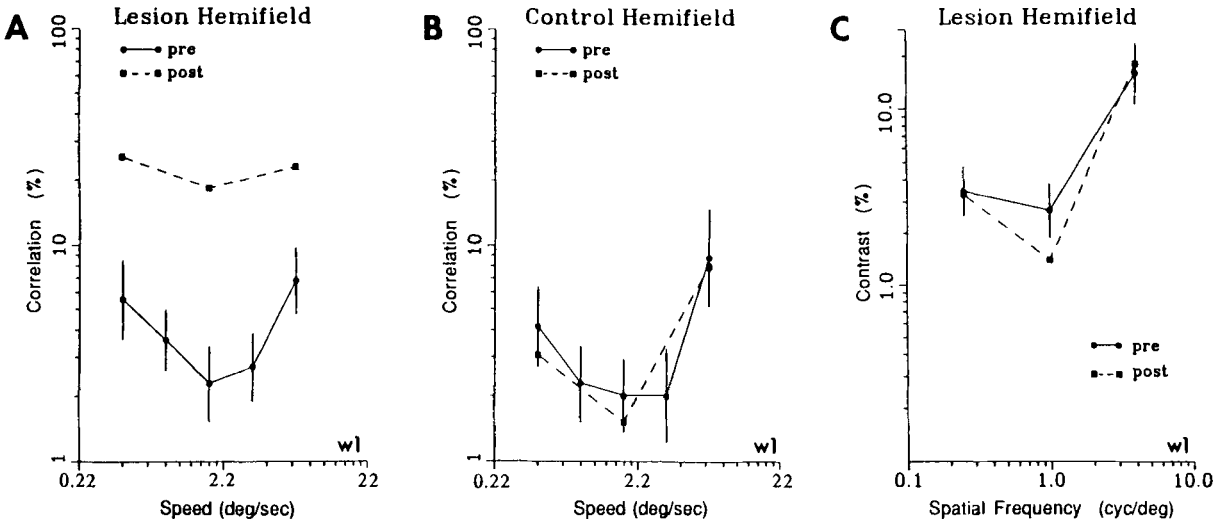

Figure 4. Effects of an MT lesion on psychophysical performance. (*A*) Elevation of direction-discrimination thresholds in the hemifield contralateral to the lesion. The symbols connected by the solid line show the mean of at least ten prelesion thresholds (in percentage of correlated dots) measured for five different stimulus speeds. The error bars indicate standard deviations. The symbols connected by the dashed line show thresholds obtained at three speeds on the first day after an injection of ibotenic acid into MT. (*B*) Lack of effect on direction discrimination thresholds in the ipsilateral hemifield (symbols as in *A*). (*C*) Lack of effect on contrast thresholds in the contralateral hemifield. Thresholds were measured at three different spatial frequencies (symbols as in *A*). (Reprinted, with permission, from Newsome and Paré 1988.)

was observed in a second monkey as well (Newsome and Paré 1988).

The deficit illustrated in Figure 4A was not permanent; with daily practice, the monkey recovered to prelesion performance levels within 1 week of the lesion. That recovery was both quick and complete is partly attributable to the small size of the lesion caused by a single injection of ibotenic acid (2–3 mm^2 of cortex). In another monkey, we made a complete unilateral MT lesion with multiple injections of ibotenic acid. Direction-discrimination thresholds were permanently elevated in this monkey, although the permanent deficit was smaller than the acute deficit observed during the first week postlesion. Thus, some recovery appears to be mediated by pathways outside MT.

Although the lesion experiments demonstrate that neuronal activity in MT contributes selectively to motion perception, they do not specify the nature of that contribution. A plausible, although extreme, interpretation might hold that MT merely supplies a tonic, nonspecific drive to another visual area, where the critical signals for directional judgments are located. We therefore conducted electrophysiological experiments to determine whether the directional signals in MT could support direction-discrimination performance in our task.

Neuronal Responses during Perceptual Discriminations

We recorded the responses of MT neurons while the monkeys performed a direction-discrimination task that was well matched to the physiological properties of each neuron (see Methods). A block of trials contained motion stimuli presented in random order in the neuron's preferred or null direction at a range of correlation levels spanning psychophysical threshold. The resulting psychometric function provided a measure of perceptual sensitivity to the motion signal under the conditions of each individual experiment. At the same time, we recorded the response of the MT neuron to the visual stimulus presented on each trial.

Figure 5a illustrates the responses we obtained from one MT neuron during an experiment of this nature. The three histograms show for three correlation levels the number of trials on which the neuron yielded any particular response. In these experiments, the visual stimulus remained on for 2 seconds, and the neuron's response was considered to be the number of action potentials that occurred during the period of stimulus presentation. The hatched bars indicate responses to motion in the neuron's preferred direction, and the solid bars depict responses to motion in the null direction. At the highest correlation level illustrated, 12.8%, the neuron was highly directional: The preferred and null response distributions had little overlap. At the lowest correlation level, 0.8%, the distributions were indistinguishable.

We analyzed these response distributions to obtain a metric of neuronal sensitivity that is directly comparable to the perceptual sensitivity captured by the psychometric function. For this purpose, we employed a simple decision rule to compute the expected performance of an observer who bases his judgments of motion direction on the responses we recorded from the MT neuron under study (Newsome et al. 1989a,b). This expected performance characterizes the sensitivity

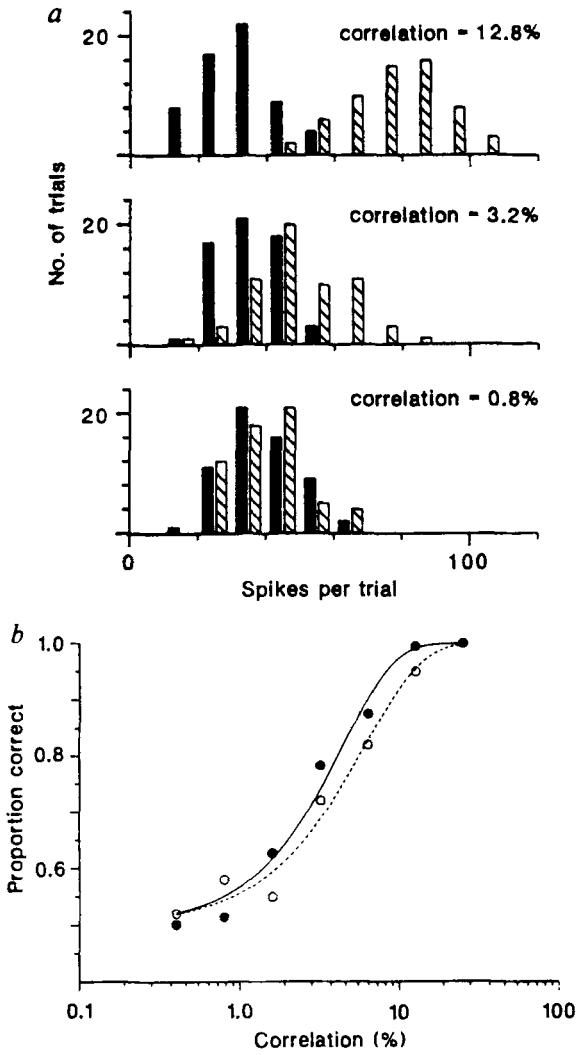

Figure 5. Physiological and psychophysical data obtained simultaneously from an alert rhesus monkey. (*a*) Responses of an MT neuron at three correlation levels near psychophysical threshold. The hatched distributions show responses to motion in the preferred direction; the solid distributions indicate responses to motion in the null direction. Responses were obtained from 60 trials in each direction for each correlation level. As described in the text, we used these response distributions to compute a neurometric function that describes the sensitivity of the neuron to the motion signals in the display. The neurometric function is directly comparable to the psychometric function computed from the monkey's behavioral responses. (*b*) Neurometric (solid symbols, solid curve) and psychometric (open symbols, dashed curve) data obtained on the same set of trials. The psychometric data show the proportion of correct responses obtained from the monkey at each correlation level. Threshold, considered to be the point at which the fitted curve reached 82% correct, was 4.4% correlation for the neuron and 6.1% correlation for the monkey. In other words, the neuron was slightly more sensitive than the monkey. (Reprinted, with permission, from Newsome et al. 1989a.)

of the neuron and may be compared to the actual performance of the monkey on the same block of trials.

We assume that on each trial, a "decision element" compares the responses of two neurons: the one under study and an "antineuron" that differs only in that it prefers the opposite direction of motion. Thus, the histograms in Figure 5a represent the responses of both the neuron and the antineuron; the preferred and null directions are simply reversed for the antineuron. If the response of the neuron is larger than that of the antineuron on a particular trial, the decision element chooses motion in the preferred direction of the neuron. If the response of the antineuron is larger, the decision element chooses motion in the preferred direction of the antineuron. At each correlation level, then, the probability of a correct decision is simply the probability that a randomly drawn response from the hatched distribution is larger than a randomly drawn response from the solid distribution. Clearly, this decision rule would yield excellent performance for the data obtained at 12.8% correlation in Figure 5a, while yielding performance near chance (50% correct) at 0.8% correlation.

Using a method derived from signal-detection theory (Green and Swets 1966), we calculated this choice probability at each correlation level for which we obtained data. The resulting neurometric function characterizes the sensitivity of the MT neuron to directional signals in the motion display and is commensurate with the psychometric function that characterizes perceptual sensitivity to the same signals (Tolhurst et al. 1983; Bradley et al. 1987). We obtained both neurometric and psychometric data for a population of 60 neurons in two monkeys. We fitted each data set with a sigmoidal curve according to the method introduced by Quick (1974), and we considered threshold to be the correlation level at which the fitted curve reached 82% correct.

Figure 5b illustrates the neurometric function (closed circles, solid line) computed for the example neuron as well as the psychometric function (open circles, dashed line) obtained on the same set of trials. The two sets of data were statistically indistinguishable ($p > 0.05$). This neuron therefore encoded directional signals with a sensitivity and reliability equal to that with which the monkey discriminated the signals perceptually.

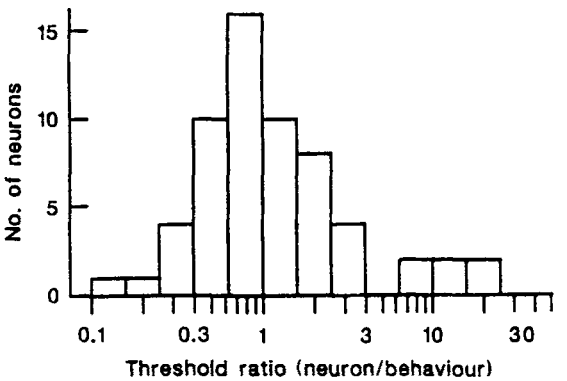

Figure 6. Ratio of neuronal threshold to psychophysical threshold measured during recording experiments from 60 MT neurons. A value of unity indicates perfect correspondence between neurometric and psychometric data. Values near unity were common in our sample. (Reprinted, with permission, from Newsome et al. 1989a.)

Figure 6 illustrates the ratio of neuronal threshold to psychophysical threshold for each of the 60 neurons studied. Neuronal threshold was within a factor of two of psychophysical threshold for 76% of the cells; the neuron illustrated in Figure 5 was therefore typical of the population as a whole.

The physiological data summarized in Figure 6 show that single MT neurons encode directional signals with sufficient sensitivity to account for psychophysical performance. When considered together with the results of the lesion study (above), the data strongly support the notion that perceptual judgments of motion direction are based in large part on the directional signals carried by MT neurons. If this hypothesis is correct, it should be possible to influence judgments of motion direction in a predictable manner by manipulating the responses of MT neurons while a monkey performs the direction-discrimination task. The last experiments were designed to test this possibility.

Influence of Electrical Microstimulation on Perceptual Decisions

In these experiments, we attempted to enhance the representation of a particular direction of motion within the visual cortex by selectively stimulating a population of MT neurons whose preferred directions were similar. Obviously, the major methodological challenge in these experiments was to restrict the microstimulation effects to a physiologically homogeneous group of neurons. The experiment was feasible because MT is organized in a columnar fashion so that neighboring neurons have a common preferred direction. The preferred direction of motion shifts in an orderly manner from column to column so that a complete representation of motion direction exists for each point in the visual field (Albright et al. 1984).

To enhance the representation of a particular direction of motion, we therefore employed microstimulation parameters that activated neurons over distances similar to the dimensions of a typical direction column. We chose parameters (10 μA, 200 Hz, biphasic) that, in a previous study, restricted direct neuronal activation to within approximately 85 μm of the electrode tip (Stoney et al. 1968), and we performed microstimulation experiments at sites in MT where multi-unit recordings maintained a constant preferred direction over at least 150 μm of electrode travel.

Although we attempted to match these dimensions as closely as possible, the exact distribution of stimulated neurons was uncertain. In particular, our physiological exploration of the local geometry of direction columns was restricted to one dimension—the line of electrode travel. We do not know, for example, how the preferred direction may have changed 50 μm to the left or right of the line of electrode travel. In some experiments, then, microstimulation almost certainly affected direction columns other than the target column. In addition, the effects of microstimulation may have spread to other columns, or indeed to other visual areas, by *trans*-synaptic pathways. However, *trans*-synaptic spread does not necessarily imply a loss of functional selectivity. Recent experiments in striate cortex (T'so and Gilbert 1988; Gilbert and Wiesel 1989) have shown that individual orientation columns are anatomically connected in a patch-like fashion to other columns with the same preferred orientation. If a similar pattern of local connections exists in MT, it is reasonable to suppose that microstimulation in our experiments activated a *circuit* of neurons related to a particular direction of motion.

Measurements of psychophysical threshold were carried out in our usual manner (see Methods; Fig. 3). The location of the stimulus aperture, the preferred-null axis of motion, and the speed of the correlated dots were matched to the properties of the multi-unit receptive field at the stimulation site. On half of the trials in a block, we applied a train of stimulating pulses that began and ended simultaneously with onset and offset of the random-dot display. The remaining trials provided control measurements of the animal's behavior in the absence of microstimulation. The trials within a block were presented in random order so that the monkey could not anticipate the presence of the stimulating current, the direction of motion, or the correlation level on any given trial.

If MT neurons provide the signals for perceptual judgments of motion direction, we would expect selective microstimulation to bias the animal's decisions toward the preferred direction of the stimulated neurons. Figure 7 shows the results of two experiments in which we observed such an effect. The plots show the proportion of "preferred" decisions (ordinate) as a function of the strength of the motion signal expressed as the percentage of correlated dots (abscissa). A preferred decision is defined as a judgment by the monkey that motion on a particular trial occurred in the preferred direction of the stimulated neurons. Similarly, a "null" decision is a judgment in favor of the null direction. On the abscissa, positive correlations indicate that the stimulus motion was in the preferred direction; negative correlation values signify motion in the null direction. Thus, strong motion signals lie at either end of the abscissa, and weak motion signals fall near the center. The closed symbols illustrate choice performance on stimulated trials and the open symbols depict performance on unstimulated trials. In both experiments, microstimulation caused an increase in the proportion of preferred decisions at each correlation level tested. Summing across correlation levels, microstimulation resulted in a total increase of 43 preferred decisions in Figure 7A and 118 preferred decisions in Figure 7B.

In each experiment illustrated in Figure 7, microstimulation shifted the psychometric function leftward. The magnitude of the leftward shift, expressed in the percentage of correlated dots, provides a measure of the microstimulation effect in units of the visual stimulus. In other words, the leftward shift indicates the visual stimulus that would have yielded a change in choice behavior equivalent to that caused by micro-

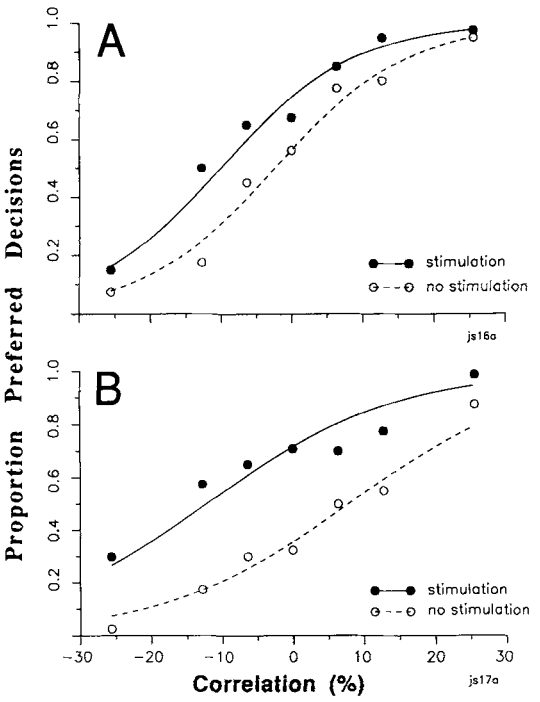

Figure 7. Effect of electrical microstimulation in MT on the performance of a rhesus monkey in a direction-discrimination task. The proportion of preferred decisions is plotted against the strength of the motion signal in percentage of correlated dots. Positive correlation values indicate stimulus motion in the preferred direction; negative correlation values represent motion in the null direction. A preferred decision is a judgment by the monkey that stimulus motion on a particular trial was in the preferred direction of the neuron. The open symbols and dashed line represent the monkey's performance on nonstimulated trials; the closed symbols and solid line depict performance on stimulated trials. (*A*) Microstimulation caused a moderate-sized effect in this experiment, shifting the psychometric function leftward by 7.7% correlated dots. (*B*) Microstimulation caused a much larger effect in this experiment; the psychometric function shifted leftward by 20.1% correlated dots. Both effects were statistically significant (logistic regression, $p \leq 0.0001$). (Reprinted, with permission, from Salzman et al. 1990.)

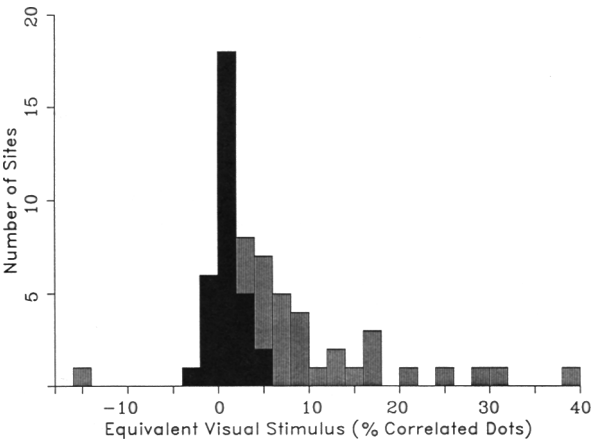

Figure 8. Distribution of microstimulation effects obtained in 62 experiments from three monkeys. In each experiment, the effect of microstimulation was considered to be the shift of the psychometric function in percentage of correlated dots. Positive values on the abscissa indicate leftward shifts (increased preferred decisions); negative values represent rightward shifts (decreased preferred decisions). Experiments that yielded statistically significant shifts (logistic regression, $p < 0.05$) are shown by striped columns. The psychometric function was shifted leftward in 29 of the 30 experiments in which a significant effect was obtained. (Reprinted, with permission, from Salzman et al. 1990.)

stimulation. We fitted the data in each experiment with sigmoidal curves and used logistic regression analysis (Cox 1970) to estimate the size and statistical significance of the stimulation-induced shift of the psychometric function. In the experiment of Figure 7A, microstimulation caused a leftward shift equivalent to the addition of 7.7% correlated dots to the visual stimulus. The effect was larger in the experiment of Figure 7B, having a stimulus equivalence of 20.1% correlated dots (for both experiments, $p \leq 0.0001$).

We performed such experiments at a total of 62 stimulation sites in three monkeys (Salzman et al. 1990). We observed statistically significant effects ($p < 0.05$) of microstimulation at 18 of 38 sites in one monkey, at 9 of 16 sites in a second monkey, and at 3 of 8 sites in a third. Figure 8 shows the distribution of effects across the entire sample. Positive values correspond to leftward shifts of the psychometric function; negative values indicate rightward shifts. The striped bars represent experiments in which the effect of microstimulation was statistically significant. In 29 of the 30 experiments with significant effects, the psychometric function was shifted leftward. Thus, microstimulation biased the monkeys' decisions toward the preferred direction of the stimulated neurons in 97% of the experiments in which a significant effect occurred. This result indicates that focal microstimulation selectively enhanced the neural signal related to a particular direction of motion and that the monkey responded to this signal in a meaningful way in the context of the behavioral paradigm.

It is worth noting that a wide range of preferred directions and receptive field locations are represented in the experiments of Figure 8. Within broad limits, we performed the experiment at the first acceptable stimulation site encountered during an experiment without regard to the actual preferred direction or the location of the receptive field. Thus, the metrics of the saccades to the preferred and null target LEDs varied broadly across experiments and were not systematically associated with a particular direction of motion. For this and several other reasons discussed elsewhere (Salzman et al. 1990), it is highly probable that the microstimulation effects resulted from changes in the sensory signals related to motion direction, rather than from changes in motor signals related to the monkey's operant response, a saccadic eye movement.

During this investigation, we were actually surprised that such large perceptual effects could result from a current level that ostensibly activates a region of cortex whose dimensions approximate those of a single column. To interpret the finding properly, it is important

to assess the effective spread of the microstimulation current within MT. Two lines of evidence suggest that the effects were well localized. First, we occasionally encountered points in an electrode penetration where the preferred direction of the cluster of neurons shifted abruptly to the opposite direction following a 100-μm advance of the electrode tip. In one penetration, we carried out microstimulation experiments on *both* sides of such a transition point, successfully biasing the monkey's choice behavior in *opposite* directions at stimulation sites separated by only 250 μm. In this experiment, then, direct activation of neurons by the microstimulation current was clearly weighted toward the target column.

Although *direct* excitation appears to be quite local, it may be possible for microstimulation effects to spread *trans*-synaptically within MT, as suggested above. To test this possibility, we required the monkey to perform the psychophysical task in the usual manner, but we applied microstimulation at a topographically noncorresponding site in MT. For example, the stimulating electrode could be placed in the upper quadrant representation in MT while the display aperture was placed in the lower quadrant of the visual hemifield. Under these conditions, the effect of microstimulation was greatly attenuated or eliminated entirely. Microstimulation consistently influenced the monkey's choice behavior only when there was overlap of the display aperture with the receptive field at the microstimulation site. This observation suggests that lateral propagation of directional signals by *trans*-synaptic mechanisms was not widespread within MT, if present at all.

DISCUSSION

The present series of experiments explored the relationship between the responses of direction-selective neurons in extrastriate area MT and the perception of visual motion. We applied several physiological techniques in conjunction with a psychophysical task that required rhesus monkeys to discriminate the direction of motion in a dynamic random-dot display. In an initial set of experiments, lesions of MT caused a selective elevation of thresholds in the direction-discrimination task. The monkeys recovered fully from the effects of partial MT lesions, but a complete unilateral lesion of MT resulted in a permanent impairment. This finding indicates that MT is *necessary* for optimal performance on the direction-discrimination task. In a second set of experiments, a signal-detection analysis of neuronal responses showed that the directional information encoded by MT neurons is *sufficient* to account for psychophysical performance near threshold on the direction-discrimination task. Finally, we found that microstimulation of columns of direction-selective MT neurons can *cause* dramatic changes in a monkey's performance on the direction-discrimination task. When such effects occurred, judgments of motion direction were almost always biased toward the preferred direction of the stimulated neurons.

Although each of these findings suggests further experiments that will permit more precise interpretation, the pattern of results provides compelling evidence that perceptual judgments of motion direction in our psychophysical paradigm are based in part on the activity of direction-selective MT neurons. An important question for future research concerns the neuronal mechanisms that convert such sensory signals into a decision. In our paradigm, the monkey indicates its decision by a saccadic eye movement to one of two locations in space. Clearly, then, neuronal responses in motor centers such as the superior colliculus will reflect the monkey's decision, rather than the strength of the visual stimulus as encoded in the responses of MT neurons. Using anatomy as a guide, it should be possible to determine where this transition occurs in the pathways that link visual cortex to eye movement control centers. Such studies may help localize the decisional mechanisms that integrate sensory and motor functions.

It should be recognized that our results do not require that all, or even most, motion perception is based on the responses of MT neurons. To maximize the chances of establishing a direct link between physiology and perceptual performance, we deliberately selected a visual stimulus that would elicit directional signals in MT neurons in as robust and selective a manner as possible while providing as little information as possible to nondirectional mechanisms. Furthermore, we adjusted the stimulus to be optimal for each neuron or group of neurons that we studied. However, MT is only one locus on an extended cortical pathway that analyzes visual motion information (see Maunsell and Newsome 1987). Whether similar links between neuronal activity and motion vision can be demonstrated at other loci on the pathway is an open and important question.

Finally, it will be of interest to determine whether the general approach employed in the current investigation can be applied to a broader range of questions concerning the physiological basis of visual perception. For example, can we demonstrate that the activity of orientation-selective neurons actually influences perceptual judgments of contour orientation? Can we alter perceptual judgments of relative depth by manipulating the responses of disparity-selective neurons? Clearly, the immediate of goal of such investigations would be to test the intuitive linking assumptions that underlie contemporary research in the physiological basis of vision. A more intriguing possibility, perhaps, is that such investigations will reveal new relationships between physiology and perception that are not apparent at present.

ACKNOWLEDGMENTS

We are grateful to Judy Stein for technical assistance during the course of these experiments. The work was supported by the National Eye Institute (EY-5603 and EY-2017), the Office of Naval Research (N00014-88-K-

0161), and by a McKnight Development Award to W.T.N. C.D.S. is supported by a Medical Student Research Training Fellowship from the Howard Hughes Medical Institute.

REFERENCES

Albright, T.D., R. Desimone, and C.G. Gross. 1984. Columnar organization of directionally selective cells in visual area MT of the macaque. *J. Neurophysiol.* **51:** 16.

Bradley, A., B.C. Skottun, I. Ohzawa, G. Sclar, and R.D. Freeman. 1987. Visual orientation and spatial frequency discrimination: A comparison of single neurons and behavior. *J. Neurophysiol.* **57:** 755.

Cox, D.R. 1970. *Analysis of binary data.* Methuen, London.

Gilbert, C.D. and T.N. Wiesel. 1989. Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *J. Neurosci.* **9:** 2432.

Green, D.M. and J.A. Swets. 1966. *Signal detection theory and psychophysics.* Wiley, New York.

Hubel, D.H. 1988. *Eye, brain and vision.* Scientific American, New York.

Judge, S.J., B.J. Richmond, and F.C. Chu. 1980. Implantation of magnetic search coils for measurement of eye position: An improved method. *Vision Res.* **20:**535.

Maunsell, J.H.R. and W.T. Newsome. 1987. Visual processing in primate extrastriate cortex. *Annu. Rev. Neurosci.* **10:** 363.

Maunsell, J.H.R. and D.C. Van Essen. 1983. Functional properties of neurons in the middle temporal visual area (MT) of the macaque monkey. I. Selectivity for stimulus direction, speed and orientation. *J. Neurophysiol.* **49:** 1127.

Mikami, A., W.T. Newsome, and R.H. Wurtz. 1986. Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *J. Neurophysiol.* **55:** 1308.

Newsome, W.T. and E.B. Paré. 1988. A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *J. Neurosci.* **8:** 2201.

Newsome, W.T., K.H. Britten, and J.A. Movshon. 1989a. Neuronal correlates of a perceptual decision. *Nature* **341:** 52.

Newsome, W.T., K.H. Britten, J.A. Movshon, and M. Shadlen. 1989b. Single neurons and the perception of visual motion. In *Neuronal mechanisms of visual perception* (ed. D. Lam and C.D. Gilbert), p. 171. Portfolio, The Woodlands, Texas.

Olney, J.W. 1983. Excitotoxins: An overview. In *Excitotoxins* (ed. K. Fuxe et al.), p. 82. Macmillan, London.

Quick, R.F. 1974. A vector magnitude model of contrast detection. *Kybernetik* **16:** 65.

Robinson, D.A. 1963. A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans. Biomed. Eng.* **10:** 137.

Salzman, C.D., K.H. Britten, and W.T. Newsome. 1990. Cortical microstimulation influences perceptual judgments of motion direction. *Nature* **346:** 174.

Stoney, S.D., W.D. Thompson, and H. Asanuma. 1968. Excitation of pyramidal tract cells by intracortical microstimulation: Effective extent of stimulating current. *J. Neurophysiol.* **31:** 659.

Teller, D.Y. 1984. Linking propositions. *Vision Res.* **24:** 1233.

Tolhurst, D.J., J.A. Movshon, and A.F. Dean. 1983. The statistical reliability of signals in single neurons in cat and monkey visual cortex. *Vision Res.* **23:** 775.

T'so, D.Y. and C.D. Gilbert. 1988. The organization of chromatic and spatial interactions in the primate striate cortex. *J. Neurosci.* **8:** 1712.

Zeki, S. 1974. Functional organization of a visual area in the superior temporal sulcus of the rhesus monkey. *J. Physiol.* **236:** 549.