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Vision During Saccadic Eye Movements. I. Visual Interactions in Striate Cortex

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SUMMARY AND CONCLUSIONS

1. Psychophysical experiments have demonstrated that the brief stimulation during saccadic eye movement is masked by visual stimuli before and after the saccade. We investigated the physiological correlates of this masking effect by studying the response of single cells in the primary visual (striate) cortex of awake monkeys trained to fixate and make saccadic eye movements.

2. Cells of striate cortex were not easily driven by stimuli moving at saccadic velocity. In order to obtain reliable responses to stimuli moving at saccadic velocity, it was usually necessary to use stimuli moving in the direction of the long axis of the receptive field and elongated in the same direction. Only about 45% of the cells above the granular layer responded to stimuli of saccadic velocity; about 95% of the cells below the granular layer responded. Supragranular cells were also more persnickety to drive either with stationary or rapidly moving stimuli.

3. All cells showed an attenuation of the response to visual stimulation during a saccade when the saccade was preceded by a stimulus falling on the receptive field of the cell. Discrete stimuli falling on the receptive field of the cell were generally more effective than visual noise patterns, but both types of stimuli produced an attenuation. The attenuation occurred whether the stimulus movement resulted from saccades across stationary stimuli or from equivalent rapid movement of the stimuli. Psychophysical experiments with stimuli similar to those used in the physiological experiments showed a clear forward masking effect of stationary stimuli on a discrete stimulus swept at saccadic velocity.

4. Stimuli falling on the receptive field following the saccade usually did not attenuate the response to stimulation during a saccade. Instead the responses to stimuli occurring during a saccade and after a saccade usually merged indistinguishably as though there were a single stimulus, with onset at the time of the stimulus during the saccade and offset at the time of offset of the postsaccadic stimulus. This merging of the responses to a moving stimulus and a stationary stimulus following it after an interval of less than 50 ms occurred whether the stimulus movement resulted from saccades across stationary stimuli or from equivalent rapid movement of the stimuli. Psychophysical experiments made under similar stimulus conditions showed that these moving stimuli are not detected. Thus, when the responses of the two stimuli were merged, the brain was apparently not able to distinguish between them.

5. Under the conditions of our experiments the stimulus interaction effects we studied were more powerful than any input to striate cortex occurring as a corollary to generation of saccades (a central inhibition) or resulting from a suppression due to movement of stimuli in the peripheral visual field (a periphery or shift effect). The effect is powerful enough to be an important physiological mechanism underlying the lack of perception during saccadic eye movements made in contoured environments.

INTRODUCTION

It is a remarkable fact that the jerklike or "saccadic" eye movements with which we shift our gaze from one point to another

are so little evident in our visual experience. Objects are perceived as positionally stable even though their images are displaced to different regions of our retina by each saccade. Furthermore, we normally do not experience a transient blurring of the visual scene as the eyes move saccadically across it. These two features of vision during eye movements—its stability and its clarity—need to be sharply distinguished if confusion is to be avoided. In this paper we concern ourselves only with the latter problem of the clarity (or lack of blurring) of vision and do not address the problem of visual stability.

Holt (19) was one of the first to ask why vision during saccades was not blurred. He noted that in the view from a rapidly moving railway car the foreground is blurred, and suggested that the reason that we do not perceive a blurred image during saccadic eye movements (which involve similar retinal image velocities) is that there is an "anesthesia" of vision during eye movements. Holt's hypothesis was rejected by Dodge (10, 11), who showed that if care were taken to equalize the retinal stimuli delivered to the stationary and saccadically moving eye, the thresholds obtained were quite similar. Dodge suggested that the reason one did not perceive a blur during saccades was that the brief intrasaccadic stimulation was masked by the stronger stimulation from the stationary images present before and after the saccade.

The subject lay dormant until Volkmann (45), using more precise methods than those available to Dodge, showed that there was a small elevation of visual threshold for spots of light presented during saccades. Whatever the origin of the small elevation of threshold (usually 0.5 log unit or less (33)), it seems to us that this "saccadic suppression" is too slight an effect to account for the lack of perception of saccadic blur. Similarly, the threshold-elevating effect of peripheral contour displacement (30) is also a small effect (23) and so is unlikely to be a major factor in accounting for the invisibility of saccadic blur. Thus some kind of masking mechanism, as first suggested by Dodge, is likely to be the major factor—at least in the patterned surroundings that are our normal environment.

Alpern (1) and Matin et al. (34) suggested that metacontrast or backward masking may play a major role in decreasing the visibility of intrasaccadic stimuli, that is, the pattern falling on the retina after a saccade diminishes the visibility of the stimuli present during the eye movement, a hypothesis that has received considerable attention (5). Campbell and Wurtz (8) demonstrated that either forward- or backward-masking effects are sufficient to eliminate perception of saccadic blur in a normal contoured environment. By illuminating the surroundings only during saccades, they were able to make saccadic blur strikingly apparent to subjects. Extending the period of illumination either to include the period immediately before or just after the saccade made the saccadic blur imperceptible.

While several experiments have been performed in search of an extravisual input that would decrease the sensitivity of the visual system in anticipation of saccadic eye movement (3, 7, 36–38, 41, 48, 49) and several investigations of possible physiological correlates of backward masking in the visual system have been made in the anesthetized cat (6, 9, 42), there have been no studies that have directly investigated the role of temporal interactions between successive visual stimuli in diminishing the sensitivity of visual neurons during saccades.

In the experiments on single cells in the striate cortex of awake monkeys that we describe in this report, we have not attempted to replicate exactly the conditions that produce saccadic blur. Instead, we simplified the conditions in order to see the nature of the visual interactions between stimuli present during saccades and stimuli falling on the receptive fields before and after saccades. We find that many cells in striate cortex do not respond to stimuli moving at saccadic velocities and that the responses of those cells that do respond are greatly decreased by stimuli preceding and following the saccade. Using stimuli similar to those used in the physiological experiments, we also performed psychophysical experiments that demonstrated a pronounced forward-masking effect in humans. We think that the physiological interactions contribute to the visual masking effects that are an important factor controlling vision during saccadic eye movement in a contoured environment.

An abstract of these experiments has been published previously (24).

METHODS

Behavioral and recording procedures

Three male rhesus monkeys (*Macaca mulatta*) were trained on a fixation task described previously by Wurtz (47). When the monkey depressed a bar, a spot of light (0.05° in diameter) appeared on a tangent screen 57 cm in front of it, stayed on for a randomly varied interval of several seconds, and then dimmed, usually for 400 ms. If the monkey released the bar during the time the light dimmed, it received a drop of water from a spout positioned near its mouth. Release of the bar earlier or later produced no such reward and simply started a 0.5- to 2-s delay period preceding the next fixation trial.

The monkeys were easily taught a variation of this task in which the original fixation point disappeared to be replaced by a target point at another place on the screen. After a delay, this target point would either dim or itself be replaced by the original fixation point (which would then dim after a delay). By this means the monkeys could be induced to make saccades of a predictable size and direction.

During experiments the screen background luminance was 1 cd/m^2. Visual stimuli were of luminance 5–10 cd/m^2 (i.e., never more than 1 log unit above background). The monkey sat in a primate chair that restricted movement only at the neck, and was returned to his home cage at the end of each recording session. In order to help insure the health of the monkeys, records of daily water consumption and weight were kept during periods of training and recording.

During recording sessions the monkey's head was restrained using implanted bolts (16) connected to a common receptacle that was attached to the primate chair. Eye movements were recorded via implanted silver-silver chloride electrodes (4). Extracellular responses of single neurons were recorded with glass-insulated platinum electrodes (46) advanced through a cylinder permanently implanted for chronic recording (15, 16). Details of the behavioral and recording procedures are similar to those described previously (17, 35, 47).

The experiments were controlled by an on-line digital computer in ways comparable to those described in detail previously (35). The current experiments used a PDP-11-40 computer. The computer controlled the sequence of visual stimuli presented to the monkey and allowed rapid switching from one kind of behavioral paradigm to another or adjustment of the parameters of any particular task. Single-unit discharges were converted to standard pulses using an amplitude discriminator. Using these standard pulses (sampled once per millisecond), the computer displayed dot patterns (rasters) and histograms aligned on one of several behavioral responses or stimulus triggers. These rasters and histograms were photographed automatically on 35-mm film and stored on magnetic disks.

The computer digitized the eye-position signals every 4 ms and showed a moving display (35) of the eye movements, behavioral task indicators, and cell discharges. In the later experiments the computer also monitored the quality of the fixation using the digitized eye movement signal and automatically removed from the raster display any cell discharges during trials in which either an unwanted eye movement occurred or in which the monkey prematurely released the bar.

Cell classification

The cells studied were in the striate cortex, on the dorsal surface, or in the second gyrus encountered after penetrating the dura (i.e., in the lateral bank of the ascending limb of the medial calcarine sulcus). Receptive fields were generally located 5–13° from the fixation point. The second gyrus was selected for intensive study so that the analysis of receptive fields would be less influenced by small eye movements. An incidental advantage of this procedure was that "dimpling" of the cortex by a toughening intact dura, which might have affected recording in the gray matter on the dorsal surface, appeared to have minimal effect on recordings from the second bank. A scattering of cells also were studied from the dorsal surface (receptive fields 4–5° from fixation point) and the third bank (receptive fields 11–20° from the fixation point).

We classified cells by their general receptive-field types (nonoriented, simple, complex), by their location in the striate cortex (above layer IV, supragranular, or below it, infragranular), and by their discharge characteristics to a stationary stimulus (sustained or transient). For each cell studied we first located the receptive field and determined the effective stimulus; less than 2% of the cells were omitted from the sample because of inability to determine these general stimulus characteristics. We then determined the response of the cell to rapid stimulus movement and the visual interactions between two stimuli and, finally, the receptive-field type of the cell. This procedure meant that some cells were thoroughly studied during rapid stimulus movement but were lost before the details of the receptive-field organization were determined.

For classifying cells by receptive-field type we used the following criteria, which are generally comparable to the classical description of Hubel and Wiesel (20, 22). Cells with nonoriented receptive fields responded as well or better to a stationary spot of light as to a slit of light. Such cells responded to a slit centered on the field regardless of the orientation of the slit. Slow

movement of a spot of light in any direction across the receptive field was about equally effective. Cells with simple receptive fields required a slit of light with a specific orientation and in a particular position; a slit to one side or the other of the optimum position reduced the response substantially. These cells also responded to spots of light if they fell in the area of the optimum slit. Cells with complex receptive fields also required an oriented slit for maximal activation. For these cells the slit of light could be placed in several positions and still produce a strong response; covering the whole area occupied by the slits individually produced a reduced response. We sometimes observed a "stopped-end" effect but did not designate a separate hypercomplex category or categories (12, 21, 22, 25).

In later experiments we determined whether the cell was supragranular, granular, or infragranular by using the spontaneous activity of the multiple-cell discharges always present in the background (22, 39). We listened to the spontaneous discharge and its modulation by visual patterns as we advanced the microelectrode through the cortex. We found an area a few hundred micrometers in extent in which the background discharge rate was strikingly high, not strongly modulated by a visual pattern, and insensitive to orientation of visual stimuli. Microelectrode marks (5 mA for 5 s, electrode positive) at the start of this area of high discharge rate showed, as had Hubel and Wiesel (22) and Poggio et al. (39), that this was the granular layer (layer IV). Cells between this area and the cortical surface are referred to as supragranular cells; cells between this layer and white matter are referred to as infragranular cells.

Finally, we categorized each cell type as sustained or transient according to the persistence of its discharge to stationary stimuli 2.5 s in duration. We found that neither sensitivity to rapidly moving stimuli nor visual interaction effects were different for sustained and transient cells and will consider these categories no further.

Psychophysical methods

Three subjects participated in psychophysical experiments in which the experimental arrangements were similar to those of the physiological experiments. The monkey chair was removed from the recording room and replaced by a chair on which the subject sat facing (at a distance of 57 cm) the same screen used in the physiological experiments. The subjects binocularly fixated a small spot of light, and during this fixation period stimuli of the same luminance and of similar size and eccentricity to those used in the physiological experiments were projected onto the screen. The task was to detect these stimuli; blank trials were used to determine the false positive rate and the detectability, H, was calculated according to the formula, $H = (P - F)/(1 - F)$, where P is the correct positive-response rate and F the false positive rate. The mean false positive rate was 20%.

RESULTS

Cell sensitivity during saccades

We noticed early in the experiments that it was difficult to obtain visual responses during saccades from cells with oriented receptive fields unless the eye moved in a direction parallel to the long axis of the field center and the stimulus was elongated along this axis. In order to investigate this phenomenon, we moved stimuli in various directions in front of the stationary eye, using a high stimulus velocity (900°/s) to simulate saccadic movement and a low velocity (usually 12°/s) for comparison with more conventional stimulus velocities used in physiological experiments. Figure 1*A* shows the familiar selective sensitivity of a cell with an oriented field center to slow movement of a bar in a direction perpendicular to its long axis (transverse movement). At velocities of 900°/s the cell failed to respond to transverse movement of a bar at any orientation (Fig. 1*B*). For movement of a bar in a direction parallel to its long axis (axial movement), not only did the cell respond to movement over the long axis of the receptive-field center at low velocities (Fig. 1*C*), but it continued to respond to such movement at 900°/s (Fig. 1*D*). An elongated stimulus moving axially over the long axis of the receptive-field center was the most effective rapidly moving stimulus for all cells studied, presumably because the lengthwise orientation of stimulus and direction of movement keeps the light on the receptive-field center and off its flanks for the longest period of time. Cells responded better to longer stimuli than to shorter ones; we generally used a stimulus about twice the length of the receptive-field center. Since Wurtz (48, 49), in previous studies, did not have difficulty in activating cells using transverse movement, we think that it is likely that the earlier study was based mainly on cells with receptive fields that were nonoriented and lacked powerful surrounds. Such cells are drivable with transverse movement.

Of 254 cells we have studied in striate

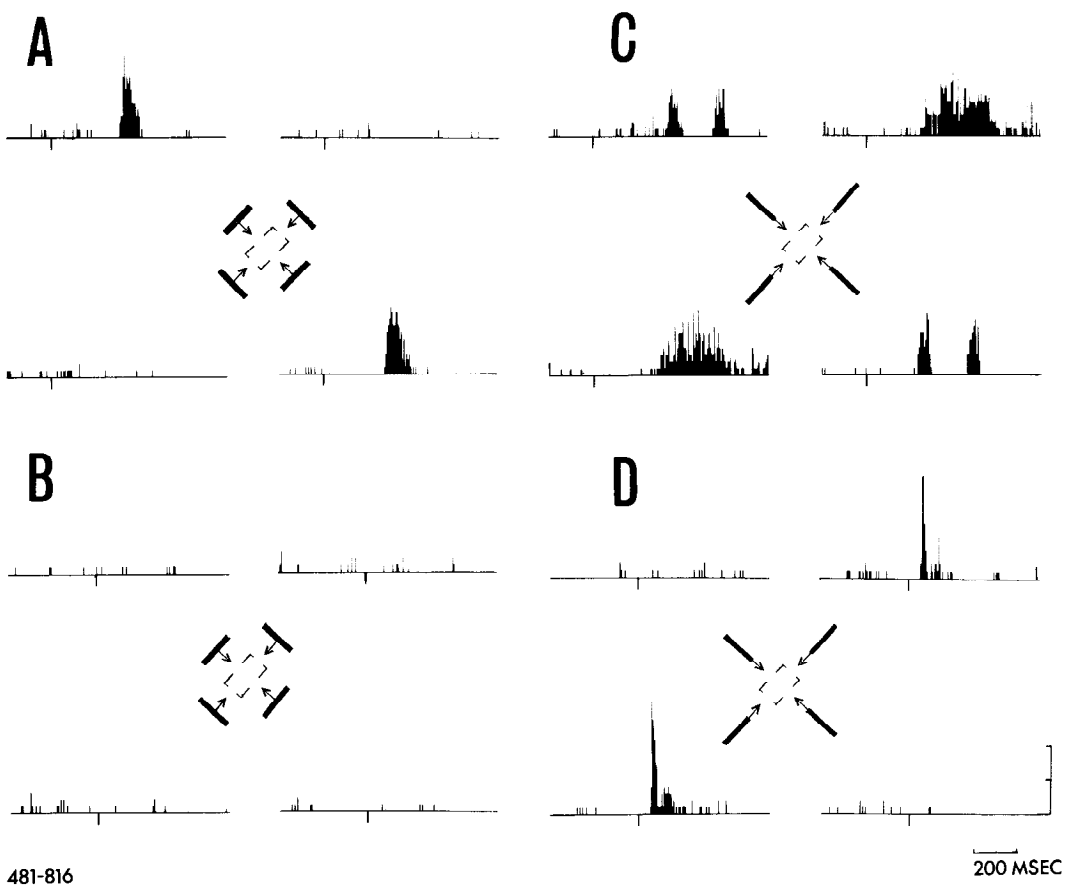


FIG. 1. Comparison of the response of a striate cortex cell to slow (12°/s) and rapid (900°/s) stimulus movement. The cell responded to a slit of light moved slowly in transverse (*A*) or axial directions (*C*) across the receptive field. At high speeds the transverse movement (*B*) was no longer effective, while one direction of axial movement (*D*) still was. The response to each different stimulus is shown in the histogram nearest to the diagrammatic representation of the stimulus. Thus, for example, in *A* the histogram at the bottom right is the response to the stimulus moved transversely in the 10 o'clock direction. The trigger line on the histogram represents the start of the 20°-long sweep of the stimulus; the interval between the trigger and the response of the cell results in part from time taken for the stimulus to reach the receptive field. The cell had a complex-type receptive field and was located in the supragranular layers. The moving slit of light (represented by a dark bar) was 2.5° x 0.5°. Each histogram is the sum of eight trials. Bin width is 6 ms and each division on the ordinate indicates a discharge rate of 100 discharges per second per trial; full scale is 200 discharges per second per trial.

cortex, about 50% responded to rapid axial movement of an elongated stimulus. For a group of 110 of these cells, the location above or below the granular layer (layer IV) was determined by using the intensity of the background activity and its modulation by light as the indicator of the granular layer. The difference in response to rapid movement was striking; 96% of the infragranular cells responded to rapid stimulus movement while only 44% of the supragranular cells responded (Fig. 2). Nearly all of the infragranular cells in our sample had complex receptive fields. The supragranular cells in our sample had nonoriented, simple, or complex receptive fields in about equal proportion, so that supragranular cells were more heterogeneous in both receptive-field type and response to rapid movement. While tuning curves for direction of movement were not obtained, it was obvious that the supragranular cells were particularly fussy about direction of stimulus motion; slight changes in stimulus direction eliminated the response. In some cases, supragranular cells that did not respond to rapidly moving stimuli

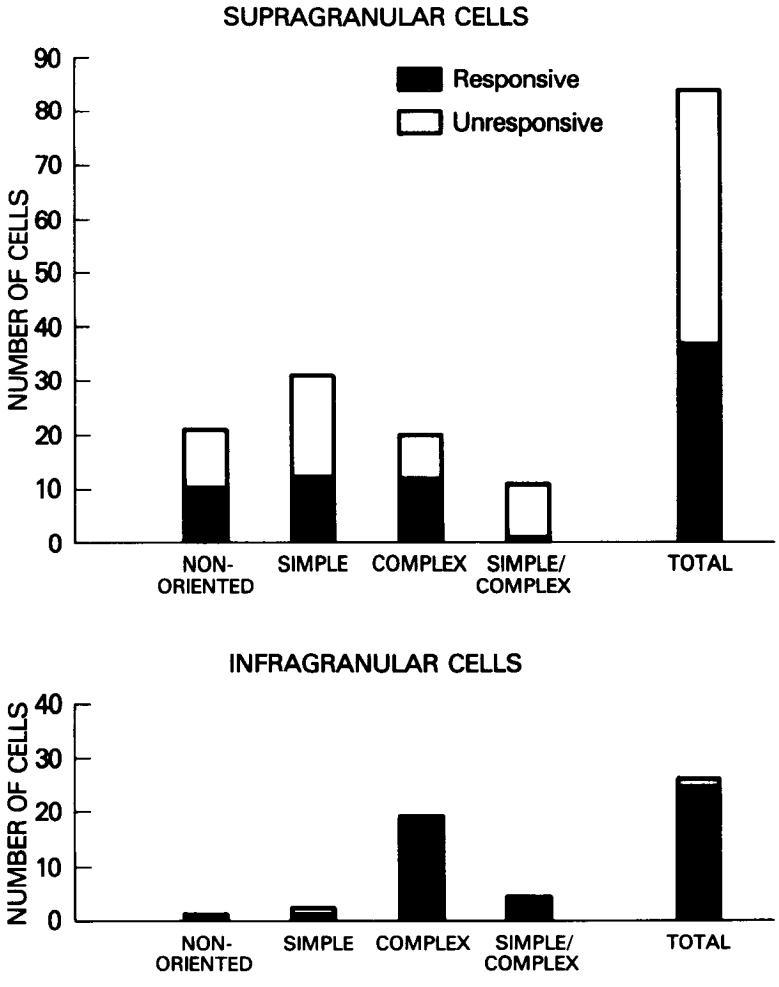


FIG. 2. Number of cells in supragranular layers (upper bar graph) and infragranular layers (lower graph) responsive to rapidly moving stimuli. Almost all infragranular cells (96%) responded to stimuli moving at 900°/s, whereas less than half (44%) of the supragranular cells responded.

were found to be hypercomplex in that their response to an optimally oriented slit was reduced by lengthening the slit, but many cells that did not respond to rapidly moving stimuli showed no such end-inhibition effects. Granular layer cells were not isolated although some cells at the margin of the layer may be included in the sample of supragranular cells.

To determine how far above threshold these responses to rapid stimulus motion were, we reduced the intensity of the stimulus in experiments on 10 supragranular and 7 infragranular cells. Reduction of the stimulus intensity from our standard level of 10 cd/m^2 on a 1 cd/m^2 background to 4.6 cd/m^2 (a ⅓ log unit decrease) reduced the response of all but one cell. The mean decrease in response was 32 ± 17% SD. When the stimulus intensity was decreased to 2.1 cd/m^2 (⅔ log unit below the standard level), many cells failed to respond (mean reduction in response 82 ± 19%), and at an intensity of 1.6 cd/m^2 (0.8 log unit below the standard level), only one cell showed any response. The stimuli used in these experiments were, therefore, often less than 0.6 and nearly always less than 0.8 log units above the threshold for striate cortex cells.

Two points emerge from this analysis of the response of striate cortex neurons to stimuli moved at saccadic velocities, and

these points effect our subsequent experiments on neural correlates of visual masking. The first is that neurons with oriented receptive fields responded best to movement in the direction of the receptive-field axis (i.e., to axial movement of the stimulus on the retina). Since we were interested in studying the response of striate cortex cells during eye movement, we generally picked the most effective discrete stimulus for activation of a cell during an eye movement —a slit oriented with its long axis in the direction of the saccade. The second point is that of the cells we sampled, many fewer supragranular cells than infragranular responded during rapid stimulus movement. The latter point is particularly interesting since it is primarily the supragranular cells that project to prestriate cortex (28), whereas the infragranular cells project mainly to subcortical areas (especially the superior colliculus and the lateral geniculate nucleus). We assumed that the activity of cells that project to higher cerebral cortical areas is more likely to be closely related to perception than is the activity of cells that project mainly to subcortical areas. We therefore concentrated our experiments on stimulus interactions on the supragranular cells.

Stimulus interactions: discrete stimuli

While we designed our experiments to search for a physiological basis of visual masking, we do not wish to presume from the outset that the physiological effects are necessarily a correlate of the psychophysical phenomena. Thus, we will reserve the term masking for the psychophysical phenomenon and use the term visual interaction for the physiological effects.

In these experiments we first determined how the responses of cells to stimuli swept across the receptive field during a saccade were altered by stimuli falling on the receptive field before and after a saccade. We used discrete stimuli—slits of light oriented appropriately for the cell under study. Next we determined whether the visual interactions seen with saccades were also evident with comparable stimulus movements while the monkey was fixating. We then compared these visual interaction effects studied physiologically in the monkey to the masking effect studied psychophysically in man.

SACCADIC STIMULATION. Figure 3*A* and *B* shows the arrangement of stimuli used in these experiments. Each section of Fig. 3 shows on the left the spatial arrangement of the stimuli on the screen and on the right, the temporal sequence of stimulation. For each cell we first determined whether there was a response as a saccadic eye movement swept the receptive field across the stationary stimulus (Fig. 3*A*). We shall refer to this stimulus as the saccadic stimulus; its size and orientation and the direction of the saccadic eye movement were adjusted to produce the maximum response by the cell. Those cells that responded to the stimulus during the saccade were then tested by adding an effective stimulus on the receptive field before (presaccade stimulus) and after (postsaccade stimulus) the eye movement. The shutters controlling whether the pre- and postsaccade stimuli were visible on the screen were both opened at least 500 ms before the saccade. We checked that the postsaccade stimulus was not on the receptive field before the saccade. The pre- and postsaccade stimuli were stationary on the receptive field before and after the eye movement (Fig. 3*B*) and were selected to be appropriate in size and orientation to produce a vigorous response. It should be noted that if the effect of the pre- and postsaccade stimuli is substantial against such a saccadic stimulus, one would expect it to be at least as strong against the weaker responses to less well-positioned saccadic stimuli.

The effects of the pre- and postsaccade stimuli were dramatic, as illustrated in Fig. 4. While the cell responded clearly to a saccadic stimulus present during an eye movement across an otherwise blank screen (Fig. 4*A*), when the pre- and postsaccade stimuli were present, the response was obliterated (Fig. 4*B*). How completely the response to the saccadic stimulus was reduced is indicated by comparing Fig. 4*C*, where the saccadic stimulus was not present, with Fig. 4*B*, where the saccadic stimulus was present; little difference is evident.

By presenting the presaccade or postsaccade stimuli separately rather than in conjunction, we determined the relative contribution of each. Figure 5*A*–*C* shows the striking effect of the presaccade stimulus; it is difficult to tell the difference between

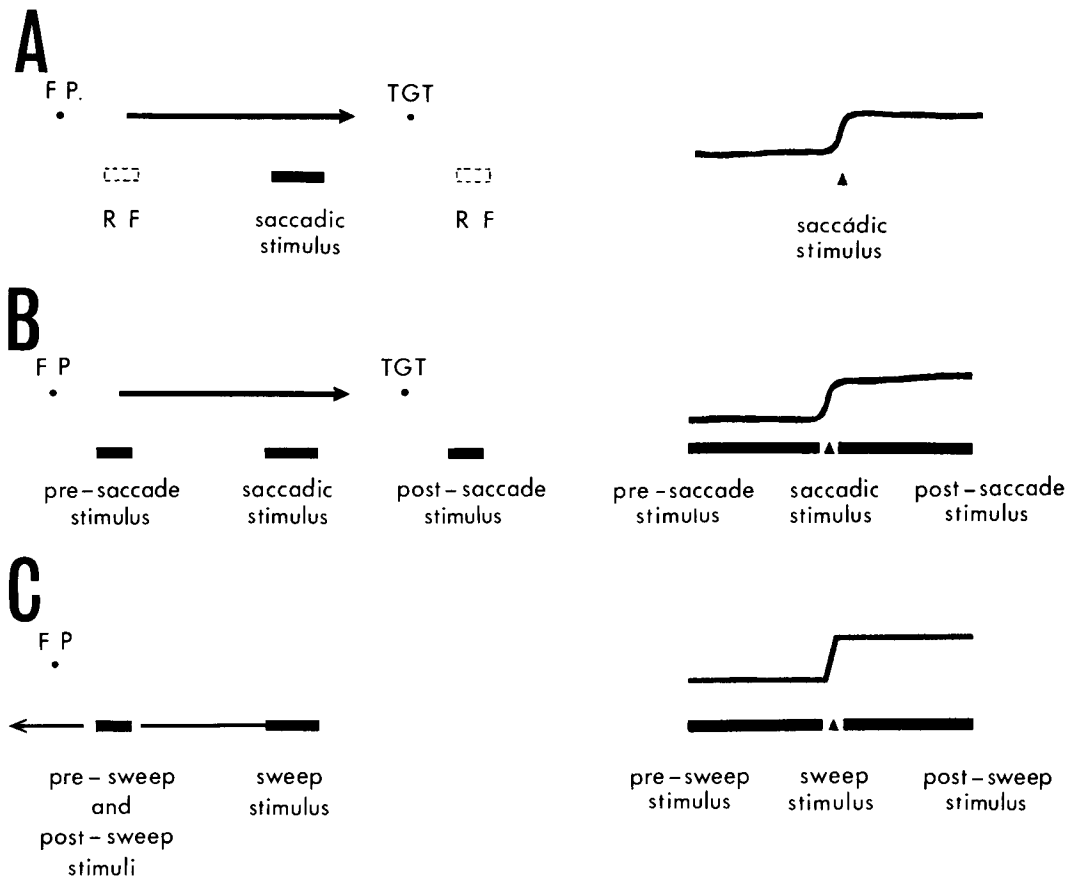


FIG. 3. Stimulus configuration in visual interaction experiments. *A* shows the arrangement of stimuli when the monkey made saccades across a stationary stimulus on an otherwise uniform screen. On the left is the location of a typical receptive field (RF, dashed lines) before and after a saccade, fixation point (FP), target point for the saccade (TGT), and the stimulus across which the receptive field moved during the saccade (saccadic stimulus). On the right is the temporal relation of the eye movement (indicated by a schematic EOG trace) and the approximate time the saccadic stimuli intersected the visual receptive field (indicated by a triangle). *B* (on the left) shows the stimulus configuration for visual interaction experiments, which is similar to that shown in *A* but with the addition of stimuli that are on the receptive field before the saccade (presaccadic stimulus) and after the saccade (postsaccade stimulus). All these stimuli were on the screen at least 500 ms before the saccade. *B* (right) shows the temporal sequence of events; the time between the stimuli is shown somewhat exaggerated for illustrative clarity since the real time interval between pre- and postsaccadic stimuli should be exactly equal to the duration of the eye movement. *C* (on the left) shows the stimulus configuration for experiments in which the monkey looked at the fixation point and made no eye movement but, instead, the stimulus (sweep stimulus) was moved across the receptive field at 900°/s. In this case the presweep and postsweep stimuli fell on the receptive field before or after the sweep stimulus. *C* (right) shows the temporal sequence of the stimuli. The triangle representing the saccadic or sweep stimulus and the dark bars representing the presence of the pre- and postsaccade or sweep stimuli will be used in subsequent figures.

Fig. 5*B*, where the saccadic stimulus is present, and Fig. 5*C*, where it is not. This powerful effect was common; 80% of 35 cells studied showed this complete attenuation (comparable to that in Fig. 5*B*), while 95% of the cells showed attenuation of response by at least 50%.

The effect of the postsaccade stimulus is more subtle. Comparison of Fig. 5*E*, where saccades made over the saccadic stimulus were followed by the postsaccade stimulus on the receptive field, with Fig. 5*F*, where only the postsaccade stimulus was present, shows little apparent difference in the amplitude of the response of the cell when the saccadic stimulus was present and when it was not. Examination of the timing of the responses, however, reveals that in Fig. 5*E*

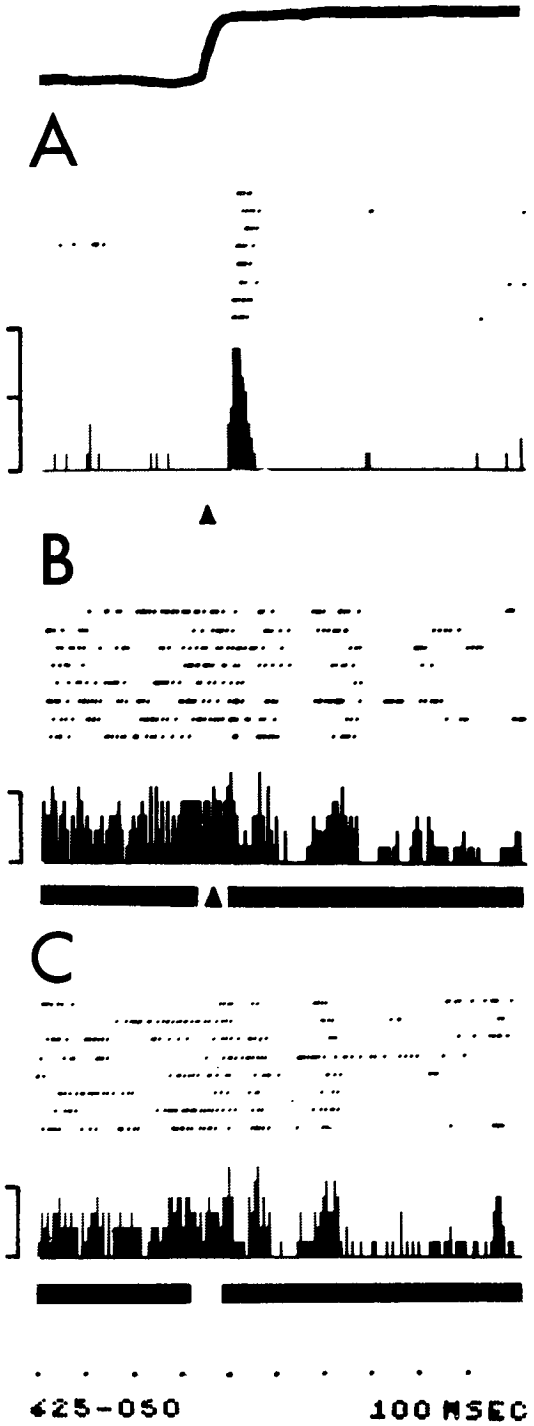


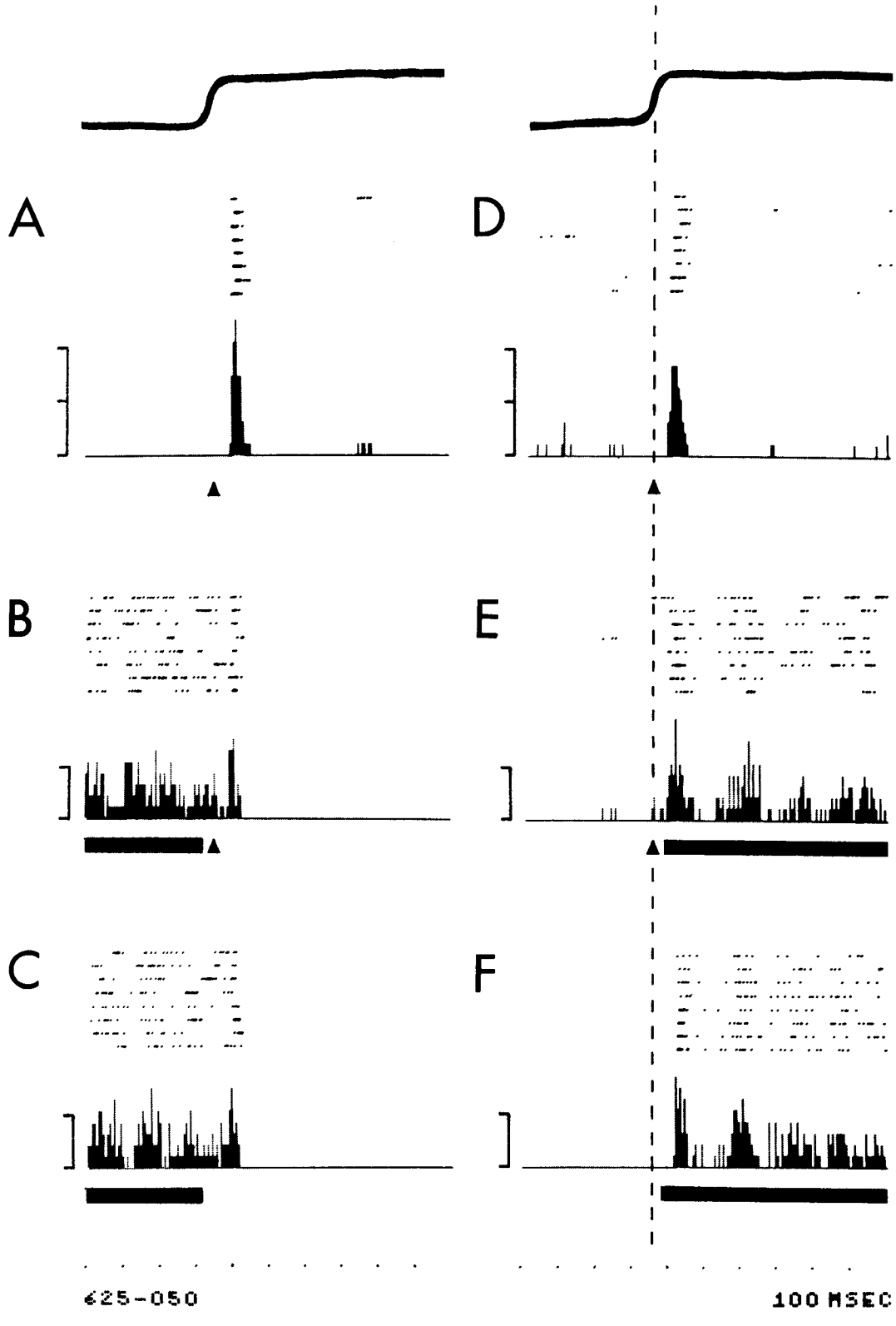
FIG. 4. Obliteration of the response of a cell to a stimulus present during an eye movement. *A* shows the response of the cell to the stimulus present during a 20° saccade, while *B* shows that this response is obliterated when presaccade and postsaccade stimuli are also present on the receptive field. In *C* only these pre- and postsaccade stimuli are present. Since the cell response in *C*, where the saccadic stimulus is not present, looks like the response in *B*, where the saccadic stimulus is present, we conclude that this neuron could not detect the presence of the stimulus during the eye movement. The presaccade stimulus was usually turned on 500 ms before the saccade target appeared. Since these rasters and histograms are aligned relative to the time of the saccade, which occurred at a variable time after the onset of the stimulus, we do not attempt to show the response to the onset of the presaccade stimulus. The cell had a complex receptive field and was located in the supragranular layers; the stimuli were 2° x 1°. Each dot represents the discharge of the cell, and successive lines represent successive stimulus presentations. The histogram below each raster shows the sum of data from the raster; bin width is 6 ms, and each division on the scale to the left indicates a discharge rate of 100 discharges per second per trial; full scale is 200 discharges per second per trial. Time between dots on the time base is 100 ms. The monkey and cell numbers are indicated at the bottom of the figure.

the response starts about 25 ms before the response in Fig. 5*F*. The onset latency with the saccadic stimulus present (Fig. 5*E*) coincides with the latency of the response to the saccadic stimulus alone (Fig. 5*D*), indicating that the initial response in Fig. 5*E* is to the saccadic stimulus rather than to the postsaccade stimulus. The response to the saccadic stimulus merges into (and indeed may even attenuate) the response to the postsaccade stimulus.

The majority (76%) of the 21 cells studied continued to respond to the saccadic stimulus when a stimulus was present after the saccade, as shown in Fig. 5*E*. A minority of cells (19%) clearly failed to respond at a latency appropriate to the saccadic stimulus (for the remaining cell the results were unclear).

The stimulus interaction effects were highly consistent. Whereas in almost all cells stimuli present only before the saccade were sufficient to eliminate the response to stimuli during saccades (a forward effect), few cells showed a loss of responsiveness produced by stimuli present after the saccade (a backward effect). These forward and backward visual interaction effects were observed in cells of all receptive-field types and in all cortical layers; cells with nonoriented, simple, or complex receptive-field types in both the supragranular and infragranular layers of striate cortex showed the visual interaction effects with discrete stimuli.

PSEUDOSACCADIC STIMULATION. In order to determine the time course of the visual



interactions, in the next series of experiments we used rapid stimulus movement across a stationary receptive field rather than the rapid movement of the receptive field across a stationary stimulus produced by a saccadic eye movement. We will call this rapidly moving stimulus the sweep stimulus. The arrangement of the sweep stimulus and the pre- and postsweep stimuli falling on the receptive field of the cells is shown in Fig. 3*C*. The response to such a sweep stimulus alone is comparable to the response to a saccadic stimulus present during a saccade, as can be seen by comparing Fig. 6*A* and *D*. Figure 6 shows also that the forward stimulus interaction effect is comparable when the eye moves and when it does not. Figure 6*A–C* shows that a presaccadic stimulus attenuates the response of the cell to a saccadic stimulus. A similar response attenuation is seen in Fig. 6*D–F* where no eye movement occurred, but a presweep stimulus (the same stimulus as in Fig. 6*A–C*) was turned off and 50 ms later the sweep stimulus crossed the receptive field. While the sweep alone produced a clear response (Fig. 6*D*), when the sweep was preceded by a stationary stimulus on the receptive field, there was no better response (Fig. 6*E*) than when only the presweep stimulus was present (Fig. 6*F*).

To study the time course of the attenuation effect, we varied the interval between the stationary pre- or postsweep stimulus and the sweep stimulus. Figure 7*A* shows a decline in amplitude of the response to the sweep stimulus as the interval between it and the presweep stimulus decreased. When the interval between the presweep stimulus and the sweep stimulus was 150–200 ms, there was a slight reduction in the response to the sweep stimulus. The response to the sweep stimulus was obliterated by the time the interval was reduced to 50 ms.

Figure 8*A* (left) shows quantitative data on the time course of the forward attenuation effect for seven supragranular cells. Clearly in some cells the magnitude of the effect is less dramatic than that shown in Fig. 7, but in most cases responses of cells to the sweep stimulus are greatly attenuated by a presweep stimulus extinguished 50 ms before the sweep.

Figure 7*B* shows that there is no effect of a postsweep stimulus on the response to the sweep stimulus until the responses to the two stimuli overlap in time. For an interstimulus interval of 50 ms, the sweep response is unaffected. Contrast this lack of backward response attenuation with the dramatic forward effect seen in Fig. 7*A* at the same 50-ms interstimulus interval.

For interstimulus intervals that are so small that the responses to the two stimuli overlap, the responses do not sum additively, as can be seen in Fig. 7*B* and on the right of Fig. 8*A*. What is plotted as ordinate in Fig. 8*A* (right) is the difference between the response to the postsweep stimulus alone and the response to the postsweep stimulus when accompanied by the sweep stimulus. The fact that this response decreases for interstimulus intervals of 50 ms and less does not necessarily mean that the response to the sweep stimulus is attenuated by the presence of the postsweep stimulus. On the contrary, it may well be that the presence of the sweep stimulus attenuates the response to the postsweep stimulus since the early phase of the response to the sweep stimulus is unaffected by the presence of the postsweep stimulus. Hence, although the response to the sweep stimulus was rarely eliminated by the postsaccade stimulus, the

FIG. 5. Reduction of the response to a saccadic stimulus by a presaccade stimulus (*A–C*) but not by a postsaccade stimulus (*D–F*). The response to the saccadic stimulus (*A*) is greatly reduced when it is preceded by a stimulus falling on the receptive field (*B*). The response is the same in *B* where the saccadic stimulus is present as in *C* where only the presaccade stimulus is present. When the saccadic stimulus (*D*) is followed by a stimulus falling on the receptive field (*E*), there is little change in the response of the cell to the saccadic stimulus. While little difference is apparent between the response amplitude in *E* (where the saccadic stimulus is present) and *F* (where it is not), examination of the time of onset of responses shows that the response in *E* has a latency appropriate for a stimulus during the saccade, while in *F* the latency is appropriate for a stimulus following the saccade. The difference between the response latencies in *E* and *F* is aproximately 20 ms, which is what one would expect of a saccade with a duration of 40 ms crossing the saccadic stimulus halfway through the saccade. Same cell and stimuli as in Fig. 4.

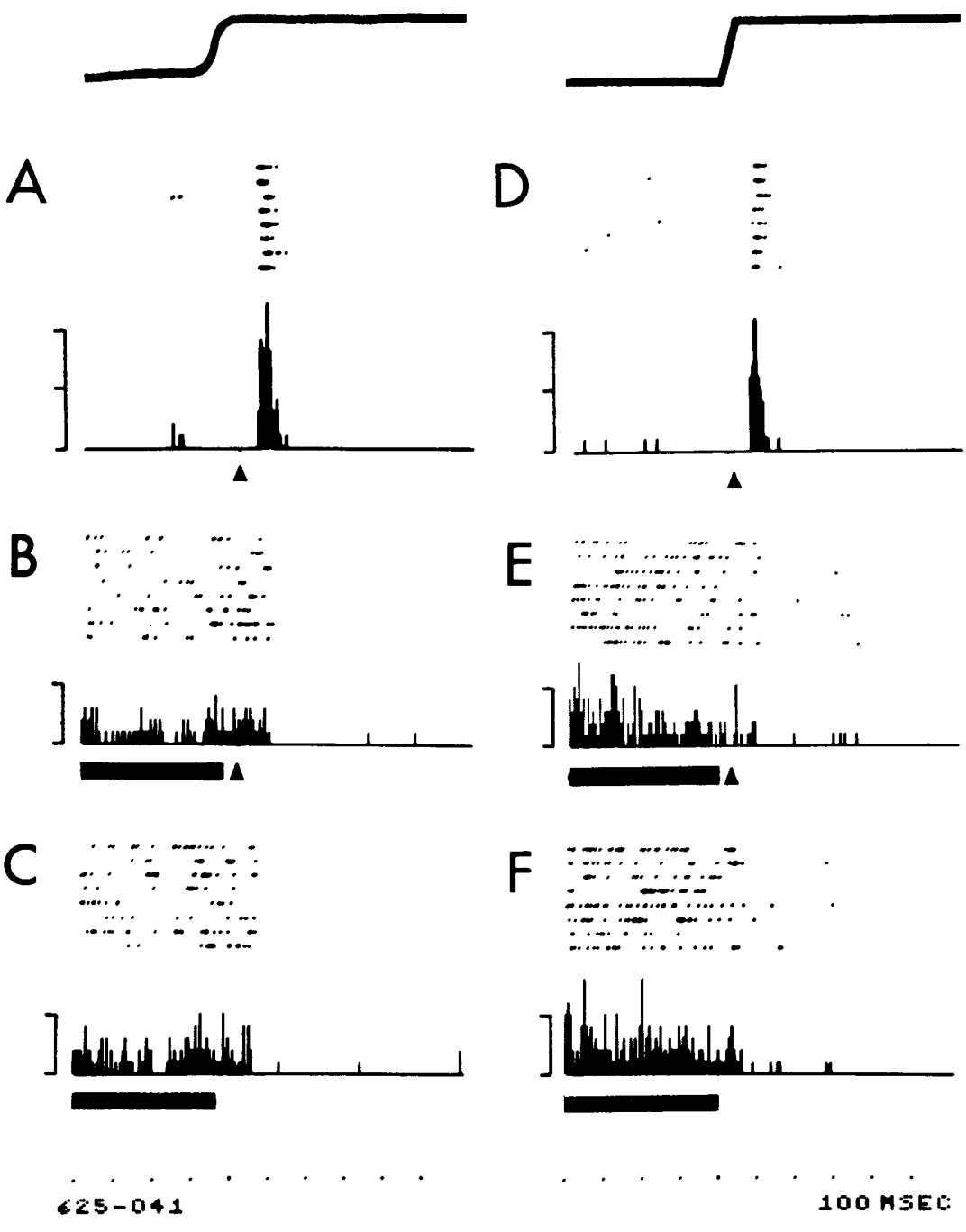


FIG. 6. Similarity of response attenuation as the eye sweeps across a stationary stimulus (A–C) or a stimulus sweeps across a stationary receptive field (D–F). The presence of either a presaccade stimulus (B) or a presweep stimulus (E) eliminates the response to the saccadic stimulus (A) or the sweep stimulus (D). Responses to the presaccade stimulus alone (C) or the presweep stimulus alone (F) are indistinguishable to the responses when either the presaccade stimulus (B) or presweep stimulus (E) is present. The eye movement is indicated by the schematic EOG trace, the stimulus movement by the ramp producing the movement. The attenuation of response is equally effective both with and without eye movement, showing that the attenuation is a purely visual phenomenon. The receptive field of the cell was nonoriented, and the cell was in the supragranular layers. The saccadic and sweep stimuli were 3.5° x 1.5°.

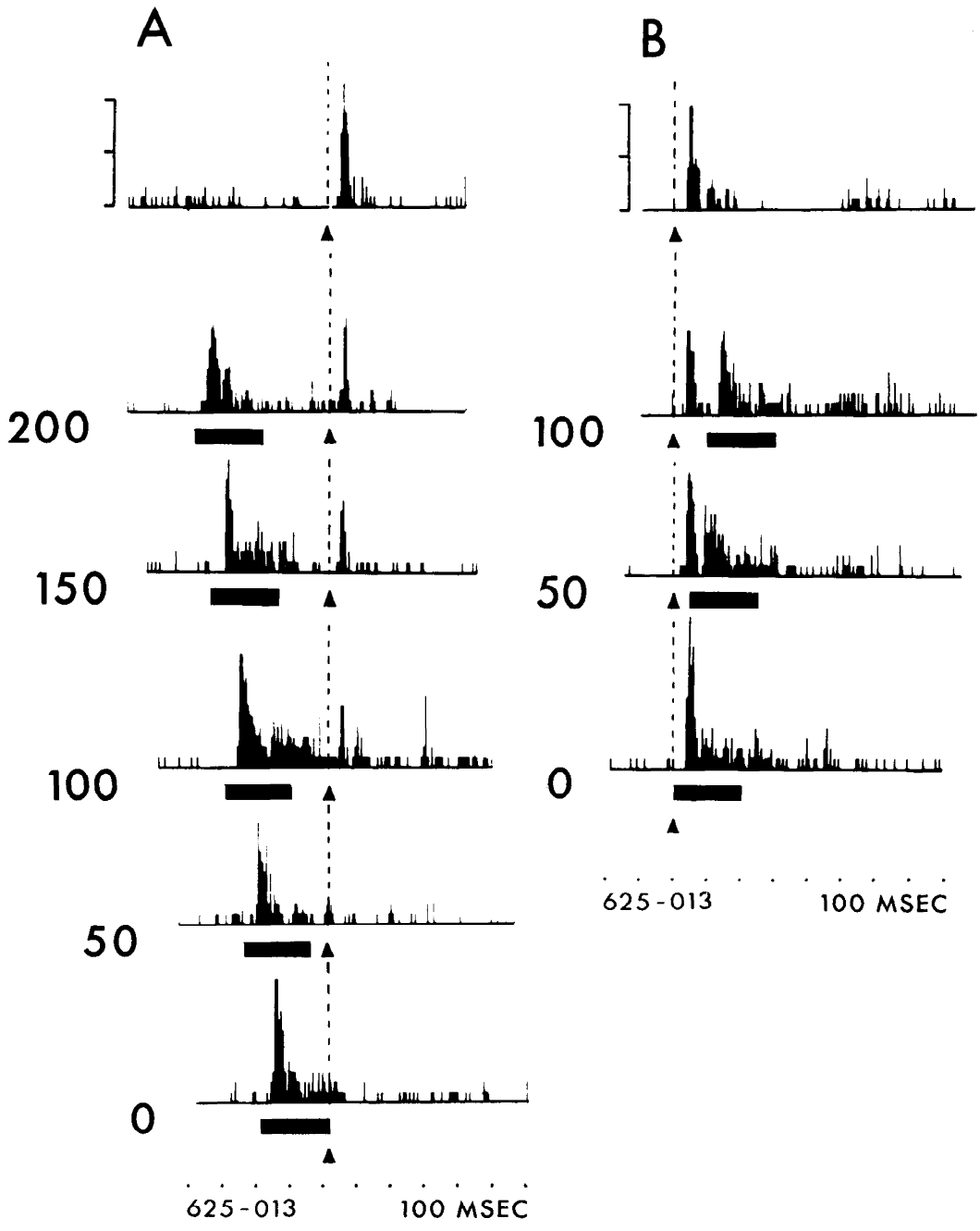


FIG. 7. Time course of forward (*A*) and backward (*B*) stimulus-interaction effects. The upper histogram in each column shows the response to the sweep stimulus alone while the monkey fixated. Subsequent lines show the effect of the presweep stimulus (*A* column) or postsweep stimulus (*B* column). Time interval (in milliseconds) between presweep stimulus and sweep (*A* column) and sweep and postsweep stimulus onset (*B* column) is indicated by numbers to the left of each column. In *A*, the response to the sweep stimulus decreases progressively as the interval between the stimuli is reduced from 200 to 100 ms, and with an interval of 50 ms the sweep response is eliminated. In *B*, the sweep response is unaffected at intervals of 100 and 50 ms and even when the interval between sweep stimulus and the onset of the postsweep stimulus is 0, the response is greater than to the postsweep stimulus alone. A 1.5° x 0.5° slit of light swept over the receptive field, which was a nonoriented type. The cell was located in the supragranular layers.

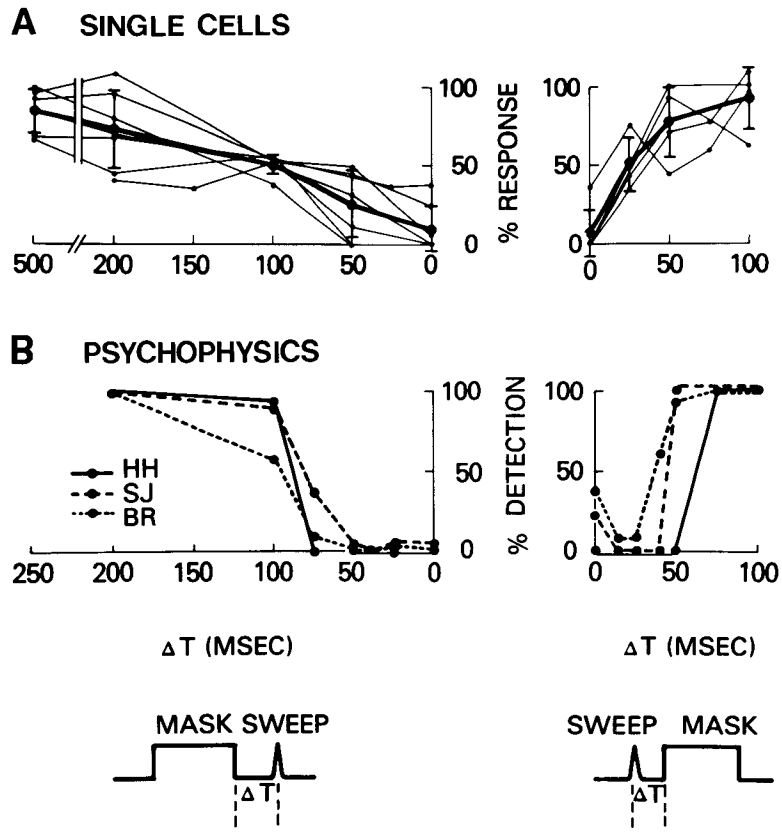


FIG. 8. Time course of forward and backward effects in physiological experiments on cells in the supragranular layers of the cortex (*A*) and in psychophysical experiments (*B*). In both *A* and *B* the abscissa, ΔT, is the interval between the presweep or postsweep stimulus and the sweep stimulus as illustrated by the schematic timing diagram at the bottom of the figure. In the physiological case (*A*), the ordinate is the difference between the response to the pre- or postsweep stimulus alone and the response to the pre- or postsweep stimulus when accompanied by the sweep stimulus. In the graph on the left (showing forward effects), the attenuation of the response to the saccadic stimulus is not quite recovered even with an interval of 500 ms between presweep and sweep stimuli. In the graph on the right (showing backward effects), it is essential to realize that the reduced response when the sweep stimulus is followed within 50 ms or less by a postsweep stimulus does not imply that the response to the sweep stimulus itself is attenuated, but only that responses to the sweep and postsweep stimuli interact nonlinearly. In fact, it is probably the postsweep response that is attenuated (see text). The data were calculated as follows: The number, R, of additional spikes generated by presenting the sweep in addition to the presweep or postsweep stimulus was expressed as a ratio of the mean number of spikes generated by sweep alone, i.e., $R = (M + SW - M)/(SW - S)$ where $M + SW$ is the number of spikes generated by both stimuli presented together, M the number generated by the mask alone, SW the mean number generated by the sweep alone, and S the spontaneous count. These numbers were obtained by programming the computer to count and display the number of spikes in a time window (50 or 100 ms wide) set to bracket the interval of the sweep response resulting from eight stimulus presentations. The dark line shows mean response with standard deviation for seven cells studied. The light lines are results for the individual cells. The duration of the pre- and postsweep stimuli was either 200 or 500 ms (for different cells). In *B*, the ordinate is the percentage of sweeps detected (corrected for false positive responses) by three subjects. The standard deviations (calculated according to the binomial probability formula) were never more than $\pm 10\%$. The duration of the pre- and postsweep stimuli was 500 ms.

responses to the two stimuli were merged, and it is a moot point whether the nervous system can distinguish the presence of the sweep stimulus under these conditions (see below under PSYCHOPHYSICAL MASKING).

The time course of the backward interaction is much shorter than the time course of the attenuation of response seen in the forward condition (Fig. 8*A*, left). We will use the term visual interaction to include both the attenuation effect seen in the forward condition and the nonlinear interaction seen in the backward condition.

In these experiments we used a rapid sweep

of the stimulus across the receptive field of cells to imitate the movement that is produced by an eye movement. The brief time that the moving stimulus was on the receptive field suggested to us that the sweep stimulus would act like a slit of light flashed briefly onto the receptive field. We used a flash duration of 4 ms since 4 ms would be about the total time that a typical slit of light (4° long) moving at 900°/s would be on a receptive field. The responses of the cells to flashed stimuli were attenuated just as they were to sweep stimuli, confirming the view that the stimulus interaction effect we observed is not specific to moving stimuli.

PSYCHOPHYSICAL MASKING. Since we found such a striking difference in the time course of the physiological stimulus interaction effects in the forward and backward cases, we investigated whether perceptual masking would also show similar differences. In the psychophysical experiments, each of the three subjects fixated a small spot of light on the screen, and the task was to detect the occurrence of a peripheral sweep stimulus when it was preceded or followed (at a randomly varied interval) by a stationary stimulus of 500 ms duration. As in the experiments on striate cortex cells, the sweep stimulus moved axially across the screen (as in Fig. 2*C* and *D*) at a velocity of 900°/s. Both the sweep stimulus and the stationary stimulus were 0.5° × 3° bars with the path of the sweep stimulus superimposed on the stationary stimulus. The stimuli were centered 7° to the right of the vertical meridian and 7° below the horizontal meridian, i.e., 10° eccentric to the fovea (an eccentricity similar to that of the receptive fields in the physiological experiments). Only the central 3° of the sweep was visible, the rest of the trajectory being masked by an aperture behind the screen that was invisible to the subjects. The purpose of this arrangement was to limit the stimuli in the psychophysical experiments to the same part of the visual field as the visual receptive field of striate cortex cells we had studied in the physiological experiments.

Figure 8*B* compares the detectability of the sweep stimulus for three human observers for forward masking (left graph) with backward masking (right graph). Clearly, the forward masking has a longer time course than does the backward masking. In this respect, the psychophysical data resemble the physiological data shown in Fig. 8*A*. The observers were unable to detect the sweep stimulus for short intervals between it and the postsweep stimulus. The intervals were approximately the same as those in which the physiological responses to the sweep and postsweep stimuli were merged and interacted nonlinearly.

Stimulus interaction: visual noise

In a normal visual environment only a limited number of striate cortex cells would be stimulated by such an effective stimulus before or after rapid eye movements as the discrete stimuli used in the experiments described so far. For most cells some less effective stimulus would more likely fall on the receptive field. In an attempt to determine whether such a suboptimal stimulus would still attenuate the response to temporally contiguous stimuli, we did the physiological and psychophysical experiments using a static visual noise pattern (29) as a pre- and postsweep stimulus. We should emphasize that while the pre- and postsweep stimuli are less than optimal ones, the sweep stimulus was still selected for maximal response.

PSEUDOSACCADIC STIMULATION. In experiments on 50 cells, we found that a presweep noise pattern was effective in attenuating the response to a sweep stimulus, as shown for two cells in Fig. 9*A* and *C*. We continued to use elongated stimuli, which were the most effective stimuli when moved rapidly across the receptive field of a cell. When the noise pattern was present on the receptive field up until 50 ms before the sweep stimulus, the response to the sweep stimulus was eliminated.

The noise pattern attenuated the response to the sweep stimulus whether or not there was a sustained discharge of the cell to the noise pattern alone. Figure 9*A* shows response attenuation caused by the noise pattern, which by itself produced a discharge (Fig. 9*B*, upper histogram) for that cell nearly as vigorous as that to the appropriately oriented stationary stimulus (Fig. 9*B*, lower histogram). For another cell (shown in Fig. 9*C*), the noise pattern also attenuates the response to the sweep but the discharge of this cell to the noise mask (Fig. 9*D*, upper

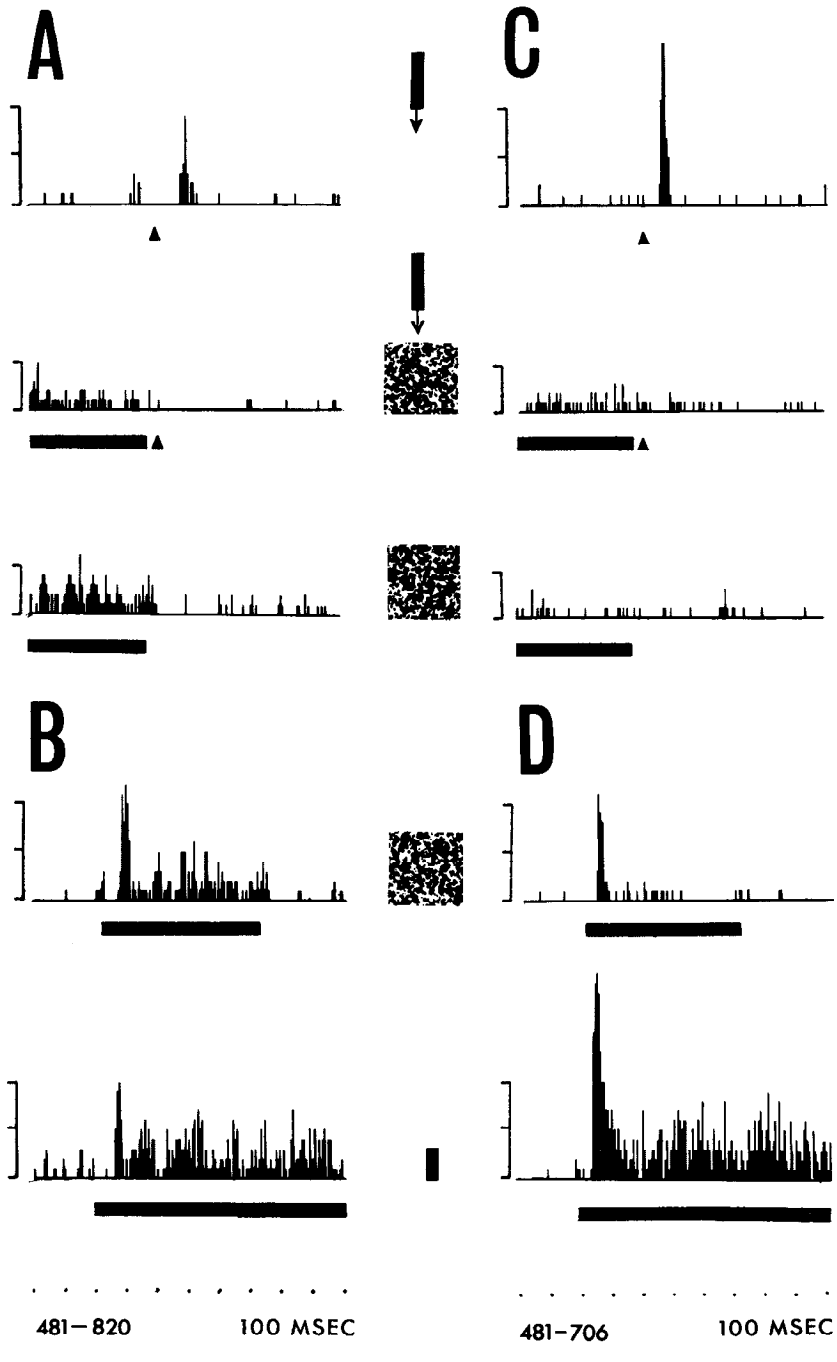


FIG. 9. Effectiveness of a visual noise pattern as a presweep stimulus. *A* shows the response of one cell to the sweep alone (upper record), to the presweep and sweep stimulus together (middle record), and to the presweep stimulus alone (lower record). The three traces in *C* show the same sequences as in *A* for a second cell. The presweep stimuli came on before the start of the histogram so no on-response is visible. The interval between the end of the noise mask and the sweep was 50 ms. This interval was chosen to be long enough to permit easy separation between any off-response to the presweep stimulus and the response to the sweep stimulus, but short enough to still produce attenuation of the sweep response. In both cells the response to the sweep stimulus is eliminated by the noise pattern. We should emphasize that the noise pattern was stationary at all times. *B* and *D* show that the effectiveness of the visual noise pattern was independent of the response of the cell to the noise

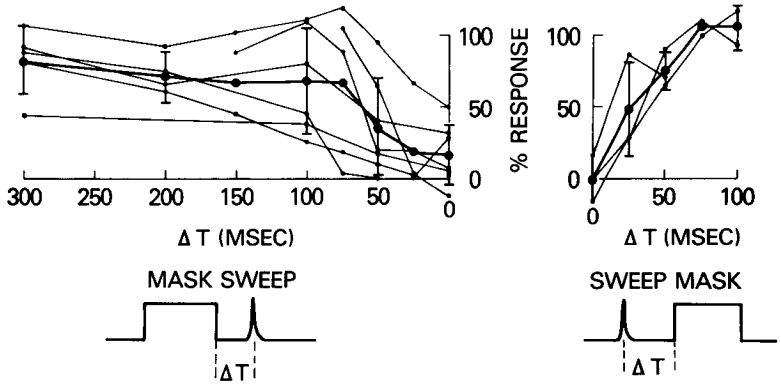


FIG. 10. Time course of the physiological forward and backward interaction effects in cells in the supragranular layers with a visual noise pattern as the pre- or postsweep stimulus. The forward effect is more protracted than the backward effect. See legend of Fig. 8 for further explanation.

histogram) was less vigorous and more transient than was the discharge to the most effective stimulus (Fig. 9*D*, lower histogram).

To see how important a particular position of the noise pattern was in attenuating the response to the sweep stimulus, we moved the noise pattern about 5° in an arbitrary direction and compared the masking effect of the noise in the two positions. The difference in the response attenuation at the two positions was 10% or less in nearly all cases (the maximum difference among the 11 cells tested was 25%).

What did produce a change in the strength of the attenuation associated with the noise pattern was altering the sweep stimulus. If the sweep stimulus was reduced in length, the response attenuation was more striking. The more striking attenuation of the shorter stimulus probably reflects the smaller energy falling on the receptive field; the shorter the stimulus, the less its total energy, and the greater the relative strength of the noise pattern.

The time course for both forward and backward effects of the noise pattern is shown in the graphs in Fig. 10. As was the case with the optimal stimulus (cf. Fig 8*A*), the visual interaction effect has a longer time course in the forward direction (Fig. 10, left) than in the backward direction (Fig. 10, right).

The forward and backward effects observed using a noise pattern were present in cells with all receptive-field types and in both supragranular and infragranular cells. The exception to this generalization was that infragranular complex cells showed only slight forward visual interaction effects.

PSYCHOPHYSICAL MASKING. The results of psychophysical experiments using a sweep stimulus of two different lengths (1 and 3°) and a pre- or postsweep noise pattern (10° x 10°) are shown in Fig. 11. The duration of the forward masking effect is clearly very sensitive to the length of the sweep stimulus and also varies between the two subjects.

DISCUSSION

We have studied the responses of neurons in the striate cortex of monkeys to stimulation produced by saccadic eye movements across stationary stimuli. There are three salient points. First, cells require the stimuli to be precisely aligned if they are to respond to these stimuli during saccades, and fewer supragranular cells than infragranular cells respond. Second, the brief response to a

pattern. The upper record in *B* (same cell as in *A*) shows that the response to the noise pattern was sustained, while in *D* (same cell as in *C*) it was transient. The lower record in *B* shows a sustained response to a discrete slit stimulus, and in *D* that cell also shows a sustained response to a discrete slit stimulus. Drawings show the type of sweep stimuli used in experiments on both cells; the slit was 2.0° x 1.0° for the cell on the left and 3° x 1.0° for the cell on the right. The noise pattern covered an area 15° x 15°. The cell on the left had a complex receptive field and was located in the supragranular layers and that on the right, a simple receptive field but layer was not determined.

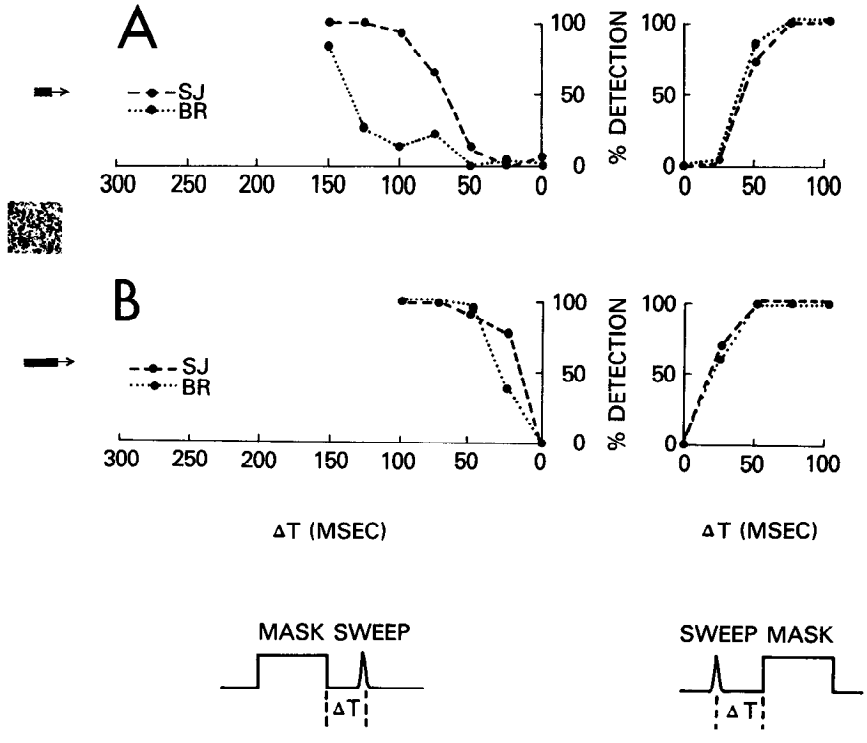


FIG. 11. Time course of the psychophysical detectability of sweep stimuli 1° (*A*) or 3° (*B*) long, with a visual noise pattern as the pre- or postsweep stimulus. The time course of the forward masking effect depends greatly on the sweep stimulus length and varies somewhat between subjects.

rapidly moving stimulus is attenuated by a preceding stimulus falling on the receptive field of the cell, and a forward masking effect is also observed psychophysically using the same stimuli. Third, a stationary stimulus falling on the receptive field after the moving stimulus usually does not change the amplitude of the response to the moving stimulus, but the responses of the two stimuli are confounded. We will discuss these three findings and then compare these visual factors to other possible sources of modulation of visual cortical neurons during saccadic eye movements.

Response of cells to rapid stimulus movement

We found that the conditions for activating neurons in striate cortex during rapid stimulus movements were very stringent indeed. Not only did the stimuli have to be oriented appropriately, but the movement had to be in a direction parallel to the orientation of the receptive field of the cell. Even for nonoriented fields, the direction of movement still needed to be parallel to the long axis of the stimulus. Furthermore, in the supragranular layers of the cortex, nearly 50% of the cells could not be driven at all by stimuli moving at saccadic velocities, at least with stimuli whose length was no more than 2 or 3 times that of the receptive field. These supragranular cells are also more persnickety in their stimulus requirements than infragranular cells, even to stationary stimuli. The lack of response of these cells to rapid stimulus motion may be due to inhibition from the surrounding area (as is the case in the superior colliculus—50), although we did not often see stopped-end effects when the receptive fields of these cells were studied with stationary stimuli. This lack of response to rapid stimulus movement is an important point since it is the cells in these layers that (28) project to prestriate areas of cerebral cortex, while the cells in the infragranular layers project primarily to subcortical nuclei. On the assumption that activity in higher cortical areas is closely related to perception, the cell population of

most interest is in the supragranular layers. The first point we wish to make is that during saccades made under the conditions of our experiment, a much smaller proportion of cells in the supragranular layers of striate cortex is responding than would respond to the same stimuli delivered to the stationary retina.

Attenuation of response by presaccade stimuli

Our second finding was that the response to stimuli during saccades was eliminated or greatly attenuated by stationary stimuli present on the receptive field of the cell before the saccade. The responses were attenuated not only by stationary stimuli chosen to vigorously activate the cell, but also by stationary stimuli, which were noise patterns often producing only transient responses from the cells. With the noise patterns the attenuation was usually quantitatively less dramatic but was by no means slight. When these same discrete and noise pattern stimuli were used in psychophysical experiments, we found a pronounced forward-masking effect. Both the physiological and the psychophysical experiments point to a forward visual-masking effect as a potent factor in eliminating vision during saccadic eye movements.

We have only a few clues about the mechanism of the forward visual interaction in the striate cortex. The effectiveness of a visual noise pattern as a presaccadic stimulus indicates that stimulation of the center of the receptive field alone is not necessary to produce a forward visual interaction. Nor is a vigorous discharge of the cell to the presaccade stimulus necessary since cells that had little prolonged discharge to a noise pattern still produced pronounced attenuation of the response to subsequent stimuli. While we have studied the visual interaction effects in the striate cortex, the interaction could originate at an earlier point in the visual pathway, particularly since visual interactions have been observed in the retina (14). What physiological mechanism underlies the visual interaction effect would be better studied after determining where in the visual pathway the effect first occurs.

We did our experiments using a very limited set of experimental conditions, but we do not think that our results are the product of a fortuitous choice of experimental parameters. Certainly we did not select our parameters in order to optimize the visual interactions, but rather were constrained by the following practical consideration. In order to simplify our experiments we concentrated on cells with one size of receptive field (center 1–3° in length), saccadic stimuli several times the length of the receptive field, and saccades of only one size (20°). We chose the receptive-field size so that small eye movements would not affect analysis of the receptive field and so that small deviations from linear saccade trajectories would not be critical. The cells we studied closer to fovea or more peripherally showed the same forward visual interaction effects. We did not use longer stimuli because longer stimuli require very precise alignment of the stimulus axis with the saccade direction. The saccade size was chosen so that the saccadic stimulus would be well away from the receptive-field center before and after the saccade. Altering either of these factors is unlikely to weaken the visual-interaction effects.[1]

We see no reason to believe the visual interactions would not also occur under more natural conditions. These visual interactions are consistent with the suggestion by Dodge (10) that saccadic stimuli are weak and that they are undetectable because they are overwhelmed by the stronger stimulation by stationary stimuli before or after the saccade.

Confounding of responses by postsaccade stimuli

A very different type of stimulus interaction occurs when a stimulus falls on the receptive field of a cortical cell after a saccade. We have little evidence for retroactive de-

[1] If one can assume that stimuli moving at saccadic velocities effectively act synchronously on all parts of a cell's receptive field, then one can measure the strength of a stimulus by the time taken for it to traverse the receptive field. Thus, in theory there would be two ways to increase stimulus strength: increasing the length of the stimulus or decreasing the size (and velocity) of the saccade. Increasing the length of the stimulus requires a correspondingly more precise alignment of the stimulus axis with the saccade direction (or the stimulus will sweep over the suppressive flanks of the field as well as the excitatory center). Decreasing the size of the saccade would increase the stimulus duration somewhat, but would also decrease the interval between the presaccadic and saccadic stimuli, which would presumably increase the strength of the stimulus interaction.

pression of sensitivity to stimuli during saccades in that the initial response to the saccadic stimulus is usually unaltered. The response to the saccadic and postsaccade stimuli overlap in time, and where the responses are overlapped there is a nonlinear interaction between the stimuli. It seems unlikely that the saccadic stimulus can be detected in subsequent cortical processing under such circumstances unless one is willing to postulate a complex mechanism with exact information about the timing of the saccade. Such a mechanism would need to know the time of the saccade to compute the estimated latency of the visual response to the postsaccadic stimulus (which is dependent on the luminance) and to see if there was a response prior to this, which would then have to be due to an intrasaccadic stimulus.

Assuming that no such mechanism exists, the responses to intrasaccadic stimuli and postsaccadic stimuli would be confounded. During the time when the responses to the intrasaccadic and postsaccade stimuli are merged (a period of less than 50 ms—see Fig. 7*B*), cells subsequent in the chain of processing would have only one on-response as an input, and in many this on-response would be coupled with the continuing discharge of the cell resulting from the postsaccade stimulus. The presence or absence of a saccadic stimulus would not be detectable.

That such a confounding occurs is suggested by the psychophysical experiments we did using the same stimulus conditions on man as in the physiological experiments on monkeys. Sweep stimuli were not detectable when followed by postsweep stimuli after an interval of less than 50 ms.

The psychophysical data also show that the degree of asymmetry in the masking effect depends on the stimulus conditions used. This dependence on the stimulus conditions is one possible reason why a more symmetrical forward and backward effect was seen in some previous psychophysical experiments (8).

This confounding of responses is a very different kind of mechanism for backward masking during saccades than that postulated by most recent workers (5) who have concentrated their attention on interactions between sustained and transient neurons eliminating the responses of sustained channel signals. Such sustained and transient mechanisms may not be needed if the confounding effect is of general relevance as a mechanism of backward masking. Of course, we are not addressing ourselves to the question of the origin of a metacontrast type of backward masking, which is maximal for 50- to 100-ms separation of stimuli and requires contoured stimuli whose margins are separated.

In light of the usual emphasis on backward masking in relation to saccadic eye movements, particularly in saccadic suppression (1, 5, 33, 34), it is striking that we see prominent forward effects and that the backward effects we see are not operating by suppressing the responses to the first stimulus. Previous single-cell experiments in the lateral geniculate nucleus of the cat (42) have also failed to find significant retroactive attenuation effects. Recent experiments in the somatosensory system also have shown minimum backward attenuation effects; cells in primary somatosensory cortex show a forward effect lasting about 70 ms, while any backward effect required interstimulus intervals of less than 10 ms (27).

Comparison of stimulus interaction and central inhibition

The traditional view has been that extraretinal factors modulate the visual sensitivity of visual cortical neurons during saccadic eye movements. One such factor is central inhibition or what has come to be known as a corollary discharge (18, 19, 43, 44): a centrally generated signal locked to the occurrence of a saccadic eye movement. Such extraretinal signals might act on neurons of striate cortex to reduce visual sensitivity during saccades. Since cells that responded to rapid stimulus movement also responded during saccades, it is immediately obvious that an extraretinal signal associated with saccades is not powerful enough to eliminate stimuli 1 log unit of intensity above background under our experimental conditions. Any central inhibition on striate cortex cells is certainly small in comparison to that acting on many colliculus cells (40); the response of colliculus cells to a stimulus 1 log unit above background is always eliminated or greatly attenuated (41).

Another factor acting during saccadic eye

movements is the periphery or shift effect (2, 26, 31, 32) in which stimuli moving in the periphery of the visual field alter the response of cells to stimuli falling in the central part of the visual field. While we had a large homogenous area around the receptive field in our experiments (60° on either side of the fixation point and 30° above and below it), the far periphery of the visual field could still have been stimulated by patterns during saccades. But since cortical cells responded both when the monkey made a saccade across a stimulus (and a periphery effect could have been present) and when we moved the stimulus across a stationary receptive field (and no periphery effect was present), any contribution of a shift effect is minimal.[2]

There was a tendency for cells to discharge less vigorously to stimuli during a saccade than to the same stimulus swept across the receptive field, although in some cells exactly the opposite occurred (see Fig. 6). The meaning of this fact is a matter of conjecture because we cannot be sure that the cells were stimulated in exactly the same way under the two conditions. This is because saccades, except in a strictly horizontal direction, are often curved, and this would result in less effective stimulation during saccades. While this may be the explanation for the difference between saccadic responses and sweep responses, we certainly cannot exclude the possibility of a slight central inhibition effect, such as that observed by Bartlett et al. (3) and Duffy and Burchfiel (13) in the monkey and Noda, Freeman, and Creutzfeldt (36) in the cat.

The masking effects we observed are certainly larger than any central inhibition or periphery effect under the conditions of our experiment. While the presence of the presweep stimulus eliminates the response to the sweep stimulus (Fig. 6*E* and *F*), central and periphery effects have little if any effect on the response to the same stimulus (Fig. 6*B* and *C*). We should emphasize that we have not quantified the magnitude of this difference between visual interaction effects and other factors. We conclude, however, that the stimulus interaction effect at the single-cell level is the primary factor affecting the sensitivity of striate cortex cells to stimuli during saccadic eye movements under our simplified experimental conditions.

[2] We have subsequently tested 20 striate cortical cells to examine whether they exhibited a periphery or shift effect. The monkey viewed a screen on which was projected a large-grain visual noise pattern. The central 40 x 40° of this pattern was of uniform intensity. The pattern was displaced 5° with a 25 ms duration ramp waveform. Such peripheral image shifts could occur alone or in synchrony with a flashed receptive-field center stimulus. The response of cells to a receptive-field stimulus alone and to a receptive-field stimulus accompanied by peripheral image shift were recorded for several receptive-field stimulus intensities close to threshold, enabling us to determine whether the sensitivity of the cells to a receptive-field stimulus was altered by the occurrence of a peripheral image shift. In 18 cells the differences of sensitivity were less than 0.1 log units. In two cells the sensitivity to the receptive-field stimulus was decreased about 0.3 log units when a peripheral image shift occurred. The shift stimulus when presented alone did not alter the spontaneous activity of the cells. While we cannot exclude the possibility that there is a small population of striate cortex cells whose sensitivity is altered by peripheral-shift stimuli, we are able to be reasonably sure that such cells would have been rare in the sample on which this paper is based.

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