

Visual Cortex Neurons: Response to Stimuli during Rapid Eye Movements

Abstract. *While awake, unanesthetized monkeys held their eyes stationary, a motionless or slowly moving stimulus falling on the receptive field of striate cortex neurons produced an excitatory response. When a rapid eye movement was made across the same stimulus, many of these neurons continued to give an excitatory response. But the discharge of other neurons was unchanged or was suppressed during the eye movement.*

With each movement of the eye, the visual world sweeps across the retina. The maximum rate of such movement during the rapid (saccadic) eye movements is about 700 degrees of arc per second for man, 900 degrees per second for monkeys (1). A stimulus moving in front of the stationary eye at this speed appears only as a blur. Yet during these eye movements there is an apparent blanking out of vision.

During the phase of sleep characterized by rapid eye movements (2), there is a decrease in the visual evoked response in the lateral geniculate nucleus of cats with each rapid eye movement. This effect apparently results from a presynaptic inhibition of the optic tract fibers terminating in the lateral geniculate nucleus. Since it occurs in total darkness as well as in light, it would seem to be caused by the same neural apparatus causing the eye movements. This presynaptic inhibition could provide a mechanism for a blanking of visual information during an eye movement.

My purpose was to determine whether any blanking out occurs by the time visual afferent information reaches cerebral cortical neurons. With the eye stationary, responses of single neurons in the visual cortex were studied in awake, unanesthetized monkeys and the size, shape, orientation, and location of the stationary or slowly moving visual stimulus necessary to activate the neuron (the receptive field characteristics) were determined. Then, the effect of this stimulus on the cell was tested during an eye movement.

First, rhesus monkeys were presented with a tangent screen 58 cm in front of them. Each time the monkey pressed a bar, a slit of light 0.5 degree of arc long (the fixation light) appeared at the center of the tangent screen and remained on for 1 to 3 seconds. After this variable interval, the fixation light dimmed for 400 msec; if during that time the monkey released the bar, it was rewarded with a drop of fruit juice or water. That the monkey was actually

fixating during the experiment was determined by measuring the eye movements with an electrooculogram derived from the electrodes pasted on the skin.

Next, responses of spontaneously active single cells were recorded from the striate area of visual cortex by means of a movable microelectrode positioner and glass-insulated platinum microelectrodes (3). During recording, the monkey sat in a primate chair with its head held rigid (4). When single-cell activity was recorded, a search was made for its receptive field by projecting a second light (in addition to the fixation light) onto the screen. The receptive field stimulus was a white light with an intensity of 1.0 to 1.5 log units above that of the background illumination (1 cd/m²). Each time the monkey began the fixation period of several seconds, a search for the receptive field was made by moving the stimulus in the visual field and by changing its size and shape.

Finally, when the receptive field of a cell had been at least approximately determined, a horizontal, saccadic eye movement through 20 degrees of arc was elicited. The fixation light was turned off and a second fixation light came on at a point 20 degrees of arc away from the first light. Since both the first and the second light could dim, the monkey fixated the second light when it came on, making the 20-degree movement in order to change fixation points. During these saccadic eye movements, the effective stimulus was projected about halfway between the two fixation points, at a vertical position where the receptive field of the cell was sure to cross as the eye movement was made.

The receptive fields of the cells considered here all had excitatory centers at a distance of at least 3 degrees from the fixation point. With the eyes stationary (5), the most effective stimuli for these field centers were stationary or slowly moving slits of light several degrees long and less than a degree wide (6). If these cells responded during an

eye movement as they did to a stationary stimulus, there should be a burst of cell discharges following the stimulus. Such a response was observed for many cells in the visual cortex (Fig. 1A). The regularity of this response is indicated for the same neuron in Fig. 1B. Here each cell discharge is represented by a dot; successive eye movements are indicated on successive lines. The eye movement occurred at about the middle of each line. The burst of cell responses followed the eye movement with a regular latency of about 20 msec from the time the receptive field crossed the stimulus. The range of latencies for all cells was between 20 and 50 msec.

The burst of cell discharges followed both the stimulus event and the eye movement, and the cell response could be related to either or both of these events. The same eye movements were repeated with the same cell without a stimulus present (Fig. 1C) and there

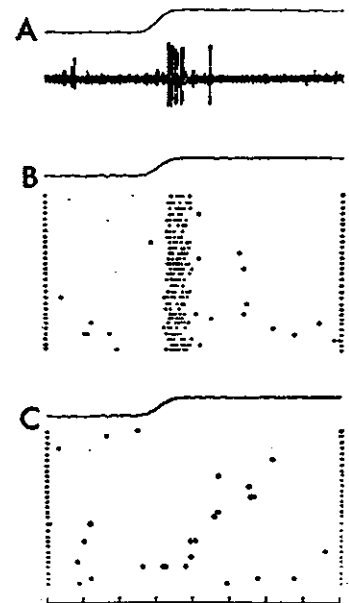


Fig. 1. Excitatory response of a single neuron during a rapid eye movement. In (A) the upper trace indicates a 20-degree eye movement across a stationary stimulus; lower trace shows a burst of cell discharges following the eye movement. In (B) stimulus is present during an eye movement; in (C) it is not. In both (B) and (C), each cell discharge is indicated by a dot produced by intensifying the beam of the oscilloscope. The beginning and end of each line is also indicated by a dot. Each row of dots represents the cell discharges preceding and following successive 20-degree eye movements in the right and left direction. Above the discharge patterns is a sample record of eye movement. Divisions on time scale are 50 msec and 400 msec for the entire line.

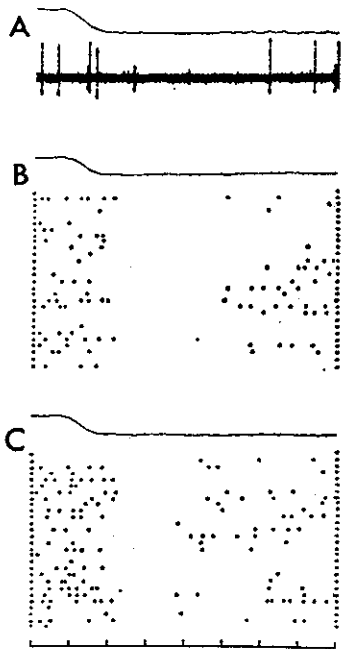


Fig. 2. Suppression of discharge rate of a single neuron during an eye movement. In (A) and (B), stimulus is present during the eye movement, in (C) it is not. Each cell discharge in (B) and (C) is indicated by a dot as in Fig. 1, (B) and (C). Occurrence of eye movement is indicated above the discharge patterns. Divisions on time scale are 50 msec.

was no burst of cell discharges following the eye movement. The cell responses are therefore not related to eye movement, but are instead related to the presence of the stimulus as the eye passes over it. Similar results have been obtained in 29 of the 65 cells studied in two monkeys.

The majority of these cells (36 cells) did not show an excitatory response to the stimulus during an eye movement; instead, many of them (18 cells) paused. In these cells (Fig. 2, A and B), when the eye moved across the stimulus, there was a suppression of the background activity even for a cell that was excited by the same stimulus when the eyes were stationary. Suppression occurred with eye movements in either horizontal direction.

The suppression also occurred when the effective stimulus was not present (Fig. 2C), but this need not imply that visual input is not a factor, because the background was not homogeneous. There were dark areas of several degrees surrounding the fixation lights and the white screen was not perfectly uniform. These irregularities in the visual field may have caused the suppression effect. Suppression of the discharge rate following an eye movement with no stimulus

present was also observed in some of those cells which gave an excitatory response when the stimulus was present during an eye movement. But the most striking suppression occurred in those cells which did not show any excitatory response to the stimulus during an eye movement.

To determine whether the suppression was due to visual input, eye movements were elicited in total darkness by noises made in the experimental room. No suppression was observed in darkness, but spontaneous eye movements in the light continued to produce the suppression effect as did the controlled 20-degree movements of the eye. Since the suppression occurred during an eye movement only in the light, it is suggested that the suppression is related to a sensory event at the retina.

The neurons studied represent only a small sample of those in the striate cortex of a primate, and even then a biased sample, since they are only those cells with readily identifiable receptive fields. Within this sample, at least three types of neuron response during an eye movement are distinguishable—one showing excitation, one showing no response, and one showing suppression.

The first type of neuron bursts vigorously to an appropriate stimulus during a rapid eye movement. There can therefore be no complete blanking out of visual information during an eye movement either at this or a more peripheral level of the visual system. Any blanking due to presynaptic inhibition at the lateral geniculate nucleus must be far from complete in the monkey. This lack of block in transmission is consistent with behavioral experiments that indicate that a stationary stimulus may still be detected during a rapid eye movement. There is only a rise in threshold (a saccadic suppression) usually of about 0.5 log unit with a maximum of 1.5 to 2.0 log units (7). At light intensity levels well above threshold, there is apparently no suppression for stationary objects (8).

A second type of neuron gives an excitatory response to a stationary stimulus but fails to respond during an eye movement. These cells can provide information about the stimulus when the eyes are stationary but not when the eyes are moving. Over a quarter of the cells studied were of this type. Because of these cells, the total number of cortical cells responding to a stimulus is smaller when the eyes are moving than when the eyes are stationary and this is consistent with the rise in threshold for

a stimulus during an eye movement. The mechanism responsible for the failure of these cells to respond during rapid eye movements might be either that they are insensitive to rapid stimulus movements or that there is some active blanking process associated with eye movement which prevents a response. Resolution of this problem would require a comparison of rapid stimulus movements in front of a stationary eye with rapid eye movements across a stationary stimulus.

The discharge rate of a third type of neuron is suppressed during a rapid eye movement. This is true even though the most effective stimulus when stationary on the receptive field center produces an excitatory response. The suppression response requires visual input and is not produced by the eye movement alone (or a "corollary discharge" of the eye movement) since there is no suppression with eye movements made in total darkness. This type of cell therefore does provide information about the stimulus when the eyes are moving, but information different from that provided when the eyes are stationary. This suppression might be a specific indicator within the visual system that an eye movement has occurred. Such information on eye movement might in turn be used at some later stage in the nervous system to produce the perceptual blanking during rapid eye movement.

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