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SELECTION OF VISUAL TARGETS FOR THE INITIATION OF SACCADIC EYE MOVEMENTS

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SUMMARY

When a monkey uses a visual stimulus falling in the receptive field of a cell in one of the superficial layers of the superior colliculus as the target for a saccade, the response of the cell to that stimulus is frequently enhanced. The effect is selective; eye movements to other parts of the visual field are not associated with the enhancement. The selective enhancement is related to the superior colliculus and is not found in striate cortex. The selective enhancement is therefore a property of the superior colliculus branch of the visual system and is not simply a reflection of activity in the geniculo-cortical system. The enhancement in the colliculus is clear when the monkey responds to the stimulus with an eye movement to the stimulus but not when it responds with a hand movement. The enhancement is therefore dependent on the type of response made to the stimulus and is possibly specifically related to eye movements.

RÉSUMÉ

Lorsque le singe utilise comme cible pour une saccade, un stimulus visuel localisé dans le champ récepteur d'une cellule située dans l'une des couches superficielles du tubercule quadrijumeau supérieur, la réponse de la cellule à ce stimulus est fréquemment renforcée. L'effet est sélectif: des mouvements oculaires dirigés vers d'autres parties du champ visuel ne s'accompagnent pas de renforcements semblables. Le renforcement se manifeste de manière spécifique au niveau du tubercule quadri-

jumeau supérieur et ne s'observe pas dans le cortex strié. Le renforcement sélectif est dès lors la propriété de la partie colliculaire du système visuel et n'est pas simplement le reflet de l'activité du système géniculo-strié. Le renforcement colliculaire se manifeste clairement lorsque le singe répond au stimulus par un mouvement des yeux, mais ne s'observe pas lorsqu'il répond par un mouvement de la main. Le renforcement est donc dépendant du type de réponse au stimulus et pourrait être lié de manière spécifique aux mouvements des yeux.

The visual guidance of saccadic eye movements is usually thought of as a sequence of steps starting with computation of the retinal error between the fixation point and the target point. But the brain does not respond to the target point alone; the target point must be selected from a matrix of retinal activity. The selection of the target point precedes calculation of retinal error and is an essential step in making an eye movement. This paper considers this process of selection and its relation to eye movement.

Stimulus selection in the superior colliculus

The superior colliculus seemed a likely structure to be involved in target selection because it receives the matrix of retinal outputs directly from the retina and indirectly from the striate area of visual cortex[8]. In the upper collicular layers (superficial gray and optic) the cells respond with a burst of cell discharge within 40–50 msec to spots of light but do not show any such burst of activity preceding eye movements[3]. Cells in the intermediate layers (intermediate gray and white) frequently show a slight response to visual stimuli and discharge vigorously before eye movements[7,10]. The cells we studied for evidence of the selection process were those with visual responses in the upper layers of superior colliculus.

We trained monkeys to fixate their gaze so that it was possible to stimulate the same point on the retina repeatedly. The trained monkeys pressed a bar to turn on a small spot of light on the screen in front of them, fixed their eyes on the spot until it dimmed, and released the bar in order to obtain a reward[9].

We then recorded single cell discharges while the monkey performed this task. During the fixation period we projected a second spot of light, the receptive field stimulus, onto the screen and used it to map the visual receptive field of the cell under study. At one point within the visual receptive field of a single cell in the superficial layers of superior colliculus, we recorded the response of that cell during successive fixations (Fig. 1A). We then required the monkey to make a saccadic eye movement to the receptive field stimulus by turning the fixation point off as the receptive field stimulus came on. In the reaction time of 200–300 msec required to make this saccade, the stimulus still fell on the visual receptive field of the cell — only the significance of the stimulus to the monkey had changed. Fig. 1B shows that the response of the cell to the stimulus was enhanced during the time the monkey used that stimulus for a saccade as described previously[4]. Fig. 1C shows that when the monkey was returned to the original condition (as in 1A) and was no longer required

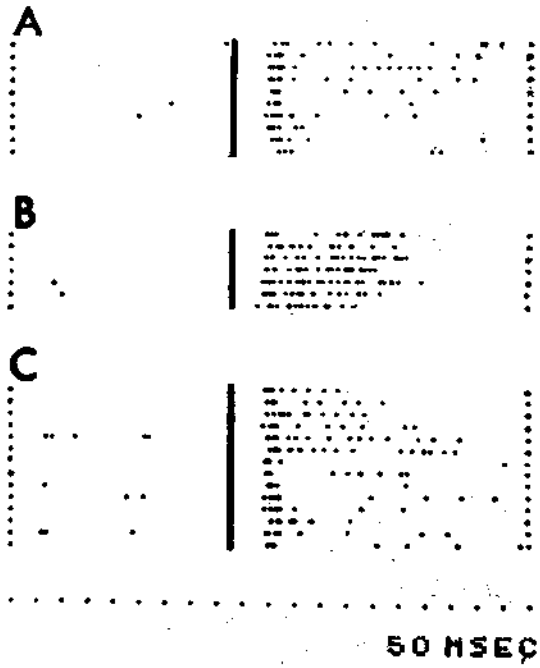

Fig. 1. Response enhancement in a superior colliculus cell during saccadic eye movements. The vertical line indicates when a 0.5° × 0.5° spot of light came on in the receptive field; it remained on during the rest of the trial. Each dot represents a cell discharge or the beginning or end of a line. Successive rows of dots represent consecutive trials. In A the monkey was looking at a fixation point of light. In B the monkey was making a saccadic eye movement from the fixation point to the 0.5° × 0.5° spot of light and the response of the cell is enhanced. In C the monkey was fixating as in A and the response returns to its original level. Time scale is for the interval between the dots.

to make saccadic eye movements to a visual stimulus, the response of the cell to that stimulus declined to its original level. About half of the cells studied in the superficial layers of the superior colliculus showed this enhanced response[4].

To control for factors unrelated to target selection, we had the monkey make saccadic eye movements not only to the receptive field stimulus but also to another stimulus outside of the receptive field. In these experiments the response of the cell to the receptive field stimulus was enhanced when the monkey used that stimulus as the target for his saccade, but not when the saccade was to some other stimulus distant from the receptive field of the cell. Therefore the response of the cell was enhanced when a stimulus in the receptive field of that cell was selected to be the eye movement target and was not a generalized effect associated with all eye movements.

Comparison of superior colliculus with striate cortex

Since superior colliculus receives inputs from the striate cortex[8], it is logically possible that the enhancement we see in the superior colliculus is simply a reflection of an earlier selection process at striate cortex. To test this, we repeated the type of experiment described for the superior colliculus on striate cortex neurons. We first

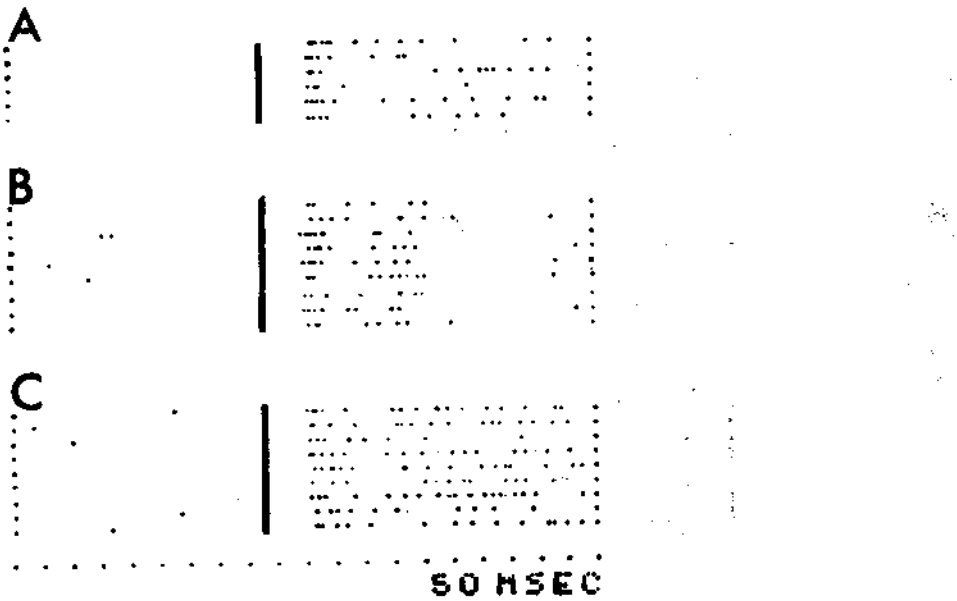

Fig. 2. Lack of response enhancement in a striate cortex cell during saccadic eye movements. The vertical line indicates onset of a 0.25° × 0.25° spot of light which remained on for the rest of the trial. In A, the monkey was looking at a fixation point of light. In B the monkey was making saccadic eye movements from the fixation point to the 0.25° × 0.25° spot of light, but no response enhancement is apparent. In C the monkey was fixating as in A.

found the receptive field of a striate cortex cell and categorized it as non-oriented, simple, complex, and hypercomplex using criteria similar to those of Hubel and Wiesel[5]. Of the 91 cells studied in striate cortex 80 showed no clear enhancement. The remaining 11 cells showed only slight enhancement as in Fig. 2. Unlike the enhancement seen in the superior colliculus, this enhancement frequently faded during an extended series of saccades. In addition, this enhancement was also present with saccades to other parts of the visual field and therefore was not selectively related to saccades to the visual stimulus. No change in background activity of the cell occurred during the period preceding stimulus onset. The selective enhancement of response to a stimulus seen so clearly in the superior colliculus is therefore absent in striate cortex.

Relation of enhancement to eye movement

Since this enhancement effect seemed to be related specifically to the cells in the superficial layers of the superior colliculus, and since cells just below these cells discharge in relation to eye movements, we next investigated how closely the enhancement effect was associated with eye movements. We therefore devised an experiment which again kept the stimulus on the receptive field and required the monkey to respond to it — but the response was now with his hand rather than his eye. In this task, the monkey again looked at the fixation point and released the bar when the fixation point dimmed. During this fixation period the response of a cell to a receptive

field stimulus was determined. Then the task was changed, and on half the trials the receptive field stimulus rather than the fixation point dimmed, and on these trials the monkey was required to release the bar following the dimming of the receptive field stimulus in order to obtain a reward. The monkey was still required to look at the fixation point since any eye movement larger than 2° terminated the trial. Of a total of 37 cells in the superior colliculus of one monkey, we would have expected to see about half shown enhancement; we saw none. A second monkey was trained to do both tasks — saccade to the receptive field stimulus in some series of trials or release the bar when the stimulus dimmed in another series. We studied 18 cells in this monkey which demonstrated an enhanced response when the monkey used the visual field stimulus as the target for a saccade. None of these 18 cells showed any enhanced response when the monkey then used the stimulus in the hand movement task. From this it seems probable that the response enhancement is not related to any response to the stimulus but only to certain types of responses such as eye movements.

The superior colliculus and target selection

Cells in the superficial layers of the superior colliculus demonstrate two useful properties for a target selection system: the response of a cell to the stimulus is enhanced when the stimulus becomes the target for a saccade, and the enhancement is selective for stimuli in one part of the visual field. The central mechanism which generates this selective response enhancement is tonic in nature: it takes several saccade trials to build up, it enhances the stimulus on-response on subsequent saccade trials, and it persists for several trials after the monkey is no longer making the saccades. In addition, these cells do not discharge with eye movements in total darkness so that the enhancement must be related to a readiness to make eye movements and not to the eye movement itself.

In the present experiments we have shown that the selective enhancement does not occur in striate cortex so that the enhancement in the colliculus is not a reflection of activity in the striate cortex. In addition there were no changes in the background activity of cells in the striate cortex during the series of saccades; the striate cortex is therefore not providing a tonic facilitation which could produce a response enhancement in the colliculus. The selection process therefore appears earliest in the superior colliculus branch of the visual system, and this supports the previous suggestion that the colliculus might be particularly related to the selection of visual stimuli, that is, to a shift of visual attention[4].

Our failure to find enhancement when the monkey responded to the stimulus with a hand movement rather than eye movement does not show that the enhancement is related only to eye movement. But it does show that the enhancement process is dependent on the type of subsequent response made to the stimulus. The association of the enhancement with eye movement coupled with the close relationship of other cells in the colliculus to the generation of eye movements suggests that the stimulus selection or attention effects seen in the colliculus are specifically related to eye movements.

The eye movement that is effective in producing the enhanced response in

superior colliculus is a natural behavioral response to a visual stimulus. Such stimulus selection and response enhancement might also be revealed in other sensory modalities if a behavioral response required use of the sensory stimulus. In sensori-motor cortex such selection seems to be occurring. Asanuma and Rosén[1,6] first showed that cells related to finger movement respond to stimulation of the muscles, skin, and joints activated by the movement. Evarts[2] has subsequently demonstrated that the sensory response of these cells is enhanced when the monkey is required to use the somatosensory information from the hand to make a hand movement. If this system is similar to the superior colliculus branch of the visual system, one would also expect to see selective enhancement at earlier stages in the somatosensory system.

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