FUNCTIONAL PROPERTIES OF NEURONS IN THE MONKEY SUPERIOR COLLICULUS: COUPLING OF NEURONAL ACTIVITY AND SACCade ONSET

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SUMMARY

One class of superior colliculus neuron was isolated which meets two criteria for participation in the initiation of visually elicited saccades. First, the pulse of spike activity recorded from these neurons was tightly coupled to saccade onset, preceding the onset of eye movements by approximately 20 msec. Secondly, if a visual stimulus sometimes elicited a saccade and sometimes failed to elicit a saccade, the occurrence of the spike pulse was highly correlated with saccade occurrence. For these neurons, there was a clear distinction between the most vigorous neuronal activity occurring in the absence of a saccade and the least vigorous activity accompanying appropriate saccades.

These findings are consistent with views which attribute to the superior colliculus a role in the initiation of visually elicited saccades.

INTRODUCTION

Converging lines of evidence from anatomical, electrical stimulation and electrophysiological studies suggest that the superior colliculus (SC) is an important structure in the control of saccadic eye movements (see refs. 6, 20 and 22 for recent reviews of this literature). Indeed, the SC is thought to play a major role in the computation of retinal error (the distance of the retinal image of a target from the fovea) and in the initiation of saccades which acquire visual targets for foveal viewing.9,13-16,19

If the SC participates in the initiation of saccades, then it should be possible to isolate a subpopulation of SC neurons in which the onset of neuronal activity is tightly coupled to saccade onset. Furthermore, in a situation in which a visual stimulus
sometimes elicits a saccade and sometimes fails to elicit a saccade, the occurrence of the neuronal activity should be highly correlated with saccade occurrence. The experiment described below was designed to test these predictions.

Recently, Mohler and Wurtz\textsuperscript{10} reported results from experiments designed to test these and similar hypotheses. In their experiments, SC neurons with saccade-related activity were observed to discharge in the absence of eye movements and, under certain conditions, the interval between the neural discharge and the eye movement could be altered. In contrast to the Mohler and Wurtz\textsuperscript{10} report, the present paper describes SC neurons with discharges tightly coupled to the onset of appropriate eye movements. The occurrence of the discharge was highly correlated with the occurrence of appropriate eye movements. Possible explanations for the discrepancy between the results reported in this paper and those of Mohler and Wurtz\textsuperscript{10} are offered.

METHODS

\textit{Subjects and surgical procedures}

Four rhesus monkeys (\textit{Macaca mulatta}) weighing from 2.5 to 4.0 kg were used. Each animal underwent 3 aseptic surgical procedures. First, 4 stainless steel bolts were implanted into the skull to permit immobilization of the animal's head during subsequent training and recording sessions. Approximately one month later, a coil of fine wire was surgically implanted beneath the bulbar conjunctiva and recti insertions. The ends of the coil were led, subcutaneously, to a connector mounted on the skull. After 4–6 weeks of behavioral training, a stainless steel receptacle for a microdrive was secured to the skull. The receptacle was placed at stereotaxic zero (anterior–posterior) and centered at the midline above a 15 mm diameter opening in the skull. The dura was left intact. During all training and recording sessions, monkeys were seated in a modified Foringer primate chair located in an electrostatically shielded and sound-resistant room. During experimental sessions, the head of the monkey was immobilized using a modification of the method described by Evarts\textsuperscript{2}.

\textit{Eye movement recording}

Horizontal and vertical eye position signals were obtained (with a sensitivity of 0.25\degree) using the method described by Fuchs and Robinson\textsuperscript{3}. With the head restrained, exposure of the animal to two alternating magnetic fields in spatial and phase quadrature generated signals in the implanted eye coil. These signals were phase-detected to produce two voltages — one proportional to horizontal eye position and one proportional to vertical eye position. The alternating magnetic fields were driven by an 18 kHz signal.

\textit{Microelectrode recording techniques}

Tungsten microelectrodes insulated with Teflon tubing and glass were advanced through a sterile 16-gauge stainless steel cannula by means of a remotely operated
hydraulic microdrive (Kopf). The cannula tip usually extended 3–4 mm below the dura.

Extracellular unit potentials were coupled through a high impedance probe to a WP Instrument DAM-5A amplifier and to a low-pass filter. The filter provided steep attenuation of frequencies above 5 kHz and reduced the contamination of the neural recordings by the 18 kHz signals of the magnetic fields. Spike potentials and trigger levels of a window discriminator were displayed on a Tektronix 502 oscilloscope. Spike potentials were also transcribed on a direct channel of an Ampex FR1300 7-channel tape recorder. The remaining FM channels of the tape recorder were used to record digital codes representing trial type, stimulus and response events, and horizontal and vertical eye positions.

Recording sites within the SC were confirmed histologically.

Behavioral training

Monkeys were trained to track a visual target presented on a Hewlett-Packard 1310A oscilloscope (CRT viewing area of 27 by 37 cm). The horizontal and vertical positions of the target, a dot subtending a visual angle of less than 0.1°, were controlled by a PDP-8/I computer via two 12-bit digital-to-analog converters. The oscilloscope was placed in front of the monkey at a distance of 35 cm. At this distance, the maximum horizontal excursion of the target was ± 25°, the maximum vertical excursion, ± 20°. In addition to controlling target position, appropriate programs allowed the computer to: (a) generate a serial pulse code of target parameters which was recorded on analog tape; (b) sample horizontal and vertical eye position every 2 msec; (c) compare horizontal and vertical eye position with target position; (d) deliver reinforcement for appropriate tracking of the visual target; (e) provide an on-line display of eye and target positions and of instantaneous spike frequency; and (f) permit modification of target parameters based upon the response properties of each neuron studied.

On training and recording days, animals were water-deprived for 23 h. Water reinforcement consisted of 0.1 ml of water delivered through a tube mounted on the primate chair and resting near the animal’s mouth.

During initial training, the animal’s eye movements were observed by the experimenter. Intermittently, the target was presented at the center of the oscilloscope screen. If the animal appeared to ‘look at’ the target, a reinforcement was delivered. This procedure continued until the animal reliably oriented to the onset of the target with short latencies and tracked the target as it was moved to other positions. During subsequent training and recording sessions, these tracking movements were used to calibrate the eye movement recording system at the beginning of each session. Thereafter, target presentations and reinforcements were under computer control.

Data collection and analysis

During data collection the receptive and movement fields of SC neurons were plotted by requiring animals to track target displacements which varied systematically in radius and angle from an initial fixation point. Then, 4 types of trials were presented
Fig. 1. Two types of eye movement responses observed during O-A-B trials. O-A-B trials required an initial fixation of point O. Then the target was moved to A for a chosen interval. At the end of the interval, the target was moved to B and remained there until acquired by the animal. I: at particular durations of A, a saccade was made to A and then a second saccade was made to B. II: on other trials, with the same duration of A, the saccade to A did not occur, and the monkey made a single saccade to B.

During O-A trials, monkeys were required to fixate a dot at the center of the oscilloscope screen (O) and after a variable interval the target was moved to a position near the center of the receptive or movement field of the neuron being studied (A). If the animal acquired the target within 400 msec and maintained fixation for 2 sec, a water reinforcement was given. During O-B trials, after fixation of point O for a variable period, the target was moved to position B. Target B was not in the receptive or movement field of the neuron being investigated. O-A-B trials required fixation of point O for a variable period. Then the target was moved to point A and remained there for a chosen interval. At the end of the interval, the target was moved to point B and remained there until acquired by the animal. As illustrated in Fig. 1 (I), for some duration of A, the monkey would sometimes make a saccade to position A and then a second saccade to position B. On other trials, with the same duration of target A, only a single saccade to target B was observed (see Fig. 1 (II)). Similarly, on some O-A-O trials, with a given duration of target A, a saccade to acquire A would occur followed by a saccade back to O. On other trials, with the same duration of A, the monkey maintained fixation of point O.

From recordings taken during O-A-O and O-A-B trials, the relationship between the occurrence of neuronal activity and saccade occurrence could be determined. The latency of the behavioral response and the latency of the neuronal response were measured from recordings taken during O-A trials.

For most animals, the probability of a saccade to target A during O-A-O and O-A-B trials could be controlled by varying the duration of A. However, after repeated exposure to this task, two animals adopted the strategy of postponing a saccade until they could determine whether or not the target would move or remain in position A. This strategy was discarded when O-A-O and O-A-B trials were intermixed with a large proportion of O-A trials in which reward was contingent upon acquisition of target A within 300 msec.
Computer-generated plots of instantaneous spike frequency (accurate to the nearest 100 μsec) and horizontal and vertical eye position were used to determine the temporal relationship between spike activity and changes in eye position.

RESULTS

The response properties of 78 SC neurons were examined in detail. Six of these neurons had only visual receptive fields. The remaining units had saccade-related discharges clearly isolated from background noise. SC neurons were grouped into one of 3 major functional classes according to their responses on the task used for plotting receptive and movement fields.

Saccade-related burst neurons

Saccade-related burst neurons are characterized by low levels of spontaneous activity and a discrete burst of activity tightly coupled to saccade onset. Fig. 2 illustrates the discharge pattern of two of the 20 saccade-related burst neurons studied in this experiment. The presaccadic discharge is composed of an initial low frequency component followed by a pulse of activity beginning approximately 20 msec before saccade onset. For the 20 neurons studied, the average interval between the onset of the pulse of spike activity and saccade onset was 19.9 msec. The range was from 16.0 to 24.8 msec.

![Diagram](image)

Fig. 2. Discharge patterns recorded from two saccade-related neurons in the superior colliculus. H, horizontal eye position; V, vertical eye position. Middle tracing: spike activity. Bottom graph: instantaneous spike frequency. The dotted line represents the onset of the eye movement. Examination of the instantaneous frequency records reveals that there is a discrete pulse of spike activity occurring approximately 20 msec prior to saccade onset.
Fig. 3. Relationship between spike-burst latency and saccade latency for 4 neurons. The abscissa represents the interval between target onset and the onset of the spike pulse. The ordinate represents saccade latency.

For this class of SC neuron, the pulse of spike activity is tightly coupled to saccade onset. On each O-A trial the interval between the onset of target A and the onset of the spike pulse was compared to the interval between target A onset and saccade onset. Fig. 3 plots the relationship between these measures for 4 typical SC neurons. There is a high degree of association between the onset of the spike pulse and saccade onset.

For saccade-related burst neurons, the probability of occurrence of the spike pulse is highly correlated with the probability of saccade occurrence. Fig. 4 (top left) illustrates a O-A-B trial in which the monkey made a saccade to acquire the target at position A and a second saccade to acquire the target at position B. The instantaneous frequency record of this trial shows a typical response — some prepulse activity followed by a discrete pulse of spike activity before the saccade to A. Also illustrated (top right) is a trial, with the same duration of target A, in which a single saccade to acquire target B was observed. Some build-up of spike activity was observed, but the high frequency pulse of activity was not present. Fig. 4 (bottom left) also illustrates a O-A-O trial in which a saccade to acquire target A and a second saccade back to target O occurred. The saccade to acquire target A was preceded by a high frequency pulse of spike activity. On O-A-O trials, with the same duration of target A, when no saccade occurred some build-up of spike activity was observed but a discrete high-frequency pulse of activity was not present (Fig. 4, bottom right).
Fig. 4. Top left: O-A-B trial with a saccade to A and a second saccade to acquire B. In the instantaneous frequency record, there is some prepulse activity followed by a discrete pulse of activity. Top right: O-A-B trial with a single saccade to acquire B. Some build-up of spike activity is seen, but a pulse of activity was not present. Bottom left: O-A-O trial with a saccade to A and a saccade to reacquire O. A discrete pulse of spike activity occurred. Bottom right: O-A-O trial in which the monkey maintained fixation of O. Some build-up of spike activity was observed, but a discrete pulse of activity was not present.

Fig. 5 represents the activity of a single SC neuron during 20 trials. The left column illustrates 5 O-A-O trials in which a saccade to acquire A and a second saccade back to O occurred. In each case, a pulse of spike activity preceded the saccade to acquire target A. The second column illustrates 5 O-A-O trials in which no saccade occurred. Although some build-up of spike activity was observed, a discrete pulse of activity did not occur on any of these trials. The third column shows that, on O-A-B trials in which a movement to A occurred, a discrete pulse of spike activity preceded each saccade. The last column represents O-A-B trials in which a single saccade to acquire target B occurred. On these trials the high frequency pulse of spike activity was absent.

To further examine the relationship between saccade occurrence and neuronal activity of saccade-related burst neurons, the magnitude and configuration of the discharges occurring on O-A-B and O-A-O trials in which no saccade to A occurred were
Fig. 5. Discharge pattern of a superior colliculus neuron during 20 trials. Left column: 5 O-A-O trials in which a saccade to A and a second saccade to O occurred. Second column: 5 O-A-O trials, with the same duration of target A, in which a saccade to acquire A did not occur. Third column: 5 O-A-B trials in which a saccade to A and a second saccade to B occurred. Right column: 5 O-A-B trials, with the same duration of target A, in which a single saccade to acquire target B occurred. Note that saccades to acquire target A are preceded by a high frequency pulse of spike activity, whereas on trials in which a saccade to A does not occur, some low frequency spike activity is observed, but the high frequency pulse of activity does not occur.
Fig. 6. Instantaneous frequency records for two saccade-related burst neurons. A: typical instantaneous frequency profiles for movements to the center of the movement field. B: selected instantaneous frequency profiles showing the least vigorous discharges associated with a movement to the center of the movement field. C: selected instantaneous frequency profiles illustrating the most vigorous discharges observed on O-A-O trials in which a saccade to A failed to occur.
compared with the discharges on trials with saccades to A. Fig. 6A illustrates, for two neurons examined for over 250 trials, the typical instantaneous frequency profiles observed for movements to the center of the neuron’s movement field. The profiles for the least vigorous discharges associated with a movement to the center of the movement field are shown in Fig. 6B. Fig. 6C displays the most vigorous discharges occurring on trials in which a saccade failed to occur. Although, as this figure illustrates, a vigorous discharge of spike activity may sometimes be observed in the absence of an appropriate saccade, the magnitude of this discharge is less than the least vigorous discharge which precedes saccades to the center of the movement field — i.e., the distribution of activity occurring in the absence of an appropriate saccade does not overlap the distribution of activity occurring prior to saccades to the central region of the movement field.

The activity of the 20 saccade-related burst neurons was observed for more than 2500 trials. For 19 of these neurons, the coupling between the spike burst and saccade onset was extremely reliable. Each saccade to the movement field of the neuron was preceded by a discrete burst of spike activity. Furthermore, a burst of spike activity comparable in number of spikes or peak instantaneous frequency never occurred unless a saccade to the movement field followed. In one neuron, two failures to generate a spike burst were observed when a saccade was made to the center of the movement field. For this neuron the distinction between the vigor of the discharge associated with saccades to the movement field and the discharge occurring in the absence of saccades to the movement field was less clear than the examples shown above.
Fig. 8. Left: discharge patterns recorded from a visual neuron in the superficial layers of the superior colliculus. A phasic discharge was observed following presentation of a target in the neuron's receptive field whether or not a saccade to acquire the target occurred. Right: discharge patterns recorded from a visual-motor neuron in the superior colliculus. Both a target-related and a saccade-related discharge were observed on trials in which a target in the receptive field elicited a saccade (top). Only the target-related discharge occurred in the absence of a saccade to acquire the target (bottom).

Saccade-related burst neurons were found throughout the rostral-caudal extent of the SC sampled in this study, and were located within collicular laminae ventral to the stratum opticum (See Fig. 7).

**Cells with visual receptive fields**

Six SC neurons with visual receptive fields but not saccade-related discharges were studied. These neurons, located in the superficial layers, were characterized by low levels of spontaneous activity and a phasic increase in spike frequency following the onset of a stationary spot of light in the receptive field. Fig. 8 (left) illustrates the discharge pattern of a typical visual neuron. The onset of target A in the receptive field was followed by a phasic discharge whether or not a saccade to acquire the target occurred.

**Cells with visual receptive fields and movement fields**

The activity of 52 neurons having both receptive and movement fields was studied. The usual pattern of spike activity observed in this experiment is shown in Fig. 8 (right). On trials in which a saccade was made to acquire a target in the receptive field, an initial target-related discharge was followed by a second saccade-related discharge. On O-A-O or O-A-B trials in which a saccade was not made to acquire target A, only the target-related discharge was observed.

A different pattern of activity was sometimes observed on O-A-O or O-A-B trials
with unusually long saccade latencies. Instead of a single target-related and a single saccade-related discharge, repetitive discharges were observed in the interval between target onset and saccade onset (Fig. 9). On those trials in which a delayed saccade to target A occurred, the burst of activity which preceded the saccade to A was usually the most vigorous burst in the series.

Neurons with visual receptive fields and movement fields were usually isolated in close proximity, but immediately above, saccade-related burst neurons.

**DISCUSSION**

One class of SC neuron, the saccade-related burst neuron, has been isolated which meets two criteria for participation in the initiation of visually elicited saccades. First, the pulse of spike activity recorded from saccade-related burst neurons is tightly coupled to saccade onset, preceding the onset of eye movements by approximately 20 msec. Secondly, if a visual stimulus sometimes elicits a saccade and sometimes fails to elicit a saccade, the occurrence of the spike pulse is highly correlated with saccade occurrence. Although neuronal discharges may be recorded from saccade-related burst neurons in the absence of a saccade, there is a clear distinction between the most vigorous activity occurring in the absence of a saccade and the least vigorous activity accompanying appropriate saccades.
It is important to note that SC neurons with activity tightly coupled to saccade onset represent a homogeneous category of cells — neurons with a discrete high frequency burst of activity preceding saccade onset. Other SC neurons display different patterns of saccade-related activity characterized by a looser linkage between neuronal activity and saccade onset. This is particularly true of some SC neurons with both visual receptive fields and movement fields, in which dissociations between neuronal activity and saccade occurrence may be observed (see Fig. 9).

Mohler and Wurtz\textsuperscript{10} also examined the coupling between the activity of SC neurons and saccade occurrence. They studied 15 neurons for evidence of coupling and reported a dissociation between the neuronal activity of SC neurons and saccade occurrence. Discharges were observed in the absence of eye movements, or, when instead of making a single saccade to a visual target, the target was acquired with two successive smaller saccades. Furthermore, in a situation in which the position of a target could be anticipated, the temporal relation between unit activity and eye movement onset was observed to shift, with the onset of unit activity sometimes actually preceding target onset. It is not clear from their report whether or not all of the 15 neurons examined showed such a dissociation.

There are two likely explanations for the discrepancy between the findings of Mohler and Wurtz\textsuperscript{10} and the results of the present experiment. First, since saccade-related burst neurons comprise a small percentage of SC neurons with saccade-related activity, the small sample of neurons studied by Mohler and Wurtz\textsuperscript{10} may not have included neurons displaying a tight coupling between unit activity and saccade onset. It is not possible to tell from the rasters shown in their paper whether or not any of the cells showed the high frequency burst which is characteristic of those neurons displaying the property of tight coupling. Moreover, since their total sample of saccade-related neurons included neurons with both visual and saccade-related discharges, the subpopulation of neurons examined for coupling properties may have consisted, primarily, of visual-motor neurons which may not be characterized by tight coupling. Secondly, Mohler and Wurtz\textsuperscript{10} did not compare the magnitude or configuration of the discharge occurring in the absence of a saccade with that of discharges preceding appropriate saccades. In the present study, discharges of saccade-related burst neurons were observed in the absence of a saccade. Indeed, low frequency preburst activity commonly occurred in the absence of a saccade. This preburst activity is often indistinguishable from a more vigorous burst of activity when displayed as rasters with the resolution used by Mohler and Wurtz\textsuperscript{10}. However, when the configuration of the discharge is viewed with greater resolution, there is a clear distinction between the most vigorous responses occurring in the absence of a saccade and the least vigorous responses occurring prior to an appropriate saccade.

Mohler and Wurtz\textsuperscript{10} do not claim that the activity of all SC neurons with discharges related to eye movement is loosely coupled to saccade onset. Nevertheless, their general conclusion that the saccade-related discharge of SC neurons is more related to the readiness to respond than to the metrics of saccades is clearly based upon the properties of loosely coupled cells. Their general conclusion is not supported by the results of the present experiment. There is at least one category of SC neurons with activity tightly coupled to the actual onset of saccadic eye movements.
The axons of the saccade-related burst neurons probably comprise a major efferent pathway from SC to subsequent oculomotor premotor neurons. This suggestion is supported by several observations. First, saccade-related burst neurons are located in the regions of the SC which give rise to the major descending projections of the SC. In the monkey, the majority of descending tectofugal axons arise from collicular laminae which lie ventral to the stratum opticum. Lesions made at the recording site of saccade-related burst neurons are located in these layers. Secondly, for saccade-related burst neurons, the interval between spike burst onset and saccade onset is comparable to the latency of saccadic movements following stimulation of the deeper layers of the SC. Thirdly, the pattern of spike activity recorded from SC saccade-related burst neurons resembles the patterns of activity recorded from the long-lead burst units of the paramedian pontine reticular formation (PPRF), an important oculomotor structure critically involved in the generation of saccadic eye movements. A direct comparison of the functional properties of saccade-related burst units of the SC and the long-lead burst units of the PPRF is not possible, since the movement fields of the long-lead burst units have not been carefully examined. However, anatomical data show that in the monkey, SC neurons in the intermediate and deeper layers project to the PPRF. Furthermore, the long-lead burst neurons of the PPRF receive short latency excitatory input from the SC, with approximately one-third of the responses being in the monosynaptic range.

Results of the present experiment show that visual neurons in the superficial layers of the SC discharge when a stimulus is presented in the neuron’s receptive field whether or not a subsequent saccade is made to acquire the stimulus. Similarly, the visual component of the discharge of visual-motor neurons is present whether or not a saccade to acquire the stimulus in the receptive field is made. These results indicate that the activity of visual and visual-motor SC neurons reflects the occurrence of a visual stimulus whether or not the stimulus is selected as a target for foveal viewing. The response of these neurons may be enhanced if the stimulus becomes a target for a saccade, but vigorous activity may occur in the superficial layers which does not become translated into saccade-related discharges in corresponding regions of the deeper layer cells. This result is compatible with other recent findings from this laboratory suggesting that activity in the superficial layers of the SC is neither necessary nor sufficient to produce activation of saccade-related neurons in deeper layers of the underlying SC. Although the anatomical and functional interaction between the superficial and deeper layers of the monkey SC is poorly understood, one may speculate upon the significance of these findings. One interpretation is that, while activity of superficial layer neurons may modulate the excitability of deeper neurons, either the superficial layer input is insufficient to directly drive neurons with saccade-related activity, or the input can be negated by other inputs. An alternative interpretation is that visual activity in the superficial layers is more related to perceptual processes mediated by ascending projections of the SC, and may have only indirect effects upon neurons with saccade-related discharges located in deeper layers of the SC.
In summary, results of the present experiment are consistent with views which attribute to the SC a role in the initiation of visually elicited saccades. One class of SC neurons has been isolated which generates a high frequency pulse of spike activity tightly coupled to saccade onset. When the probability of a saccade being elicited by a visual target is varied, saccades to acquire the target are always preceded by a pulse of spike activity. Comparable spike pulses are not observed in the absence of saccades to the neuron's movement field. Indirect evidence suggests that the saccade-related pulse of activity travels over descending efferent pathways of the SC to reach other premotor oculomotor structures.

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