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MOVEMENT FIELDS OF SACCADE-RELATED BURST NEURONS IN THE MONKEY SUPERIOR COLLICULUS

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SUMMARY

The presaccadic burst of superior colliculus (SC) neurons was examined in detail to determine whether or not information concerning the vector components (amplitude and direction) of a saccade is contained within the burst. Results indicate that the pattern of spike activity originating from a single saccade-related burst neuron in the SC does not encode saccade direction or amplitude. Identical discharges may precede a wide range of saccades. Neither the magnitude, configuration nor timing of the discharge are related in any unique way to the duration of the saccade alone or the amplitude of the saccade alone. Furthermore, it is unlikely that information concerning saccade amplitude or direction is encoded by different types of signals originating from different SC neurons. For different neurons, there is no consistent relationship between the parameters of the burst and the optimal saccade amplitude or direction.

It is suggested that the discharge of saccade-related burst neurons of the SC serves as a trigger input to pontine circuitry generating the required saccadic burst signals. Information concerning saccade direction and amplitude is not contained within this trigger signal, but must be extracted from the spatial distribution of SC activity.

INTRODUCTION

Repeated microstimulation of a discrete point of the monkey superior colliculus (SC) reliably produces a saccade with the same direction and amplitude[18,21,28]. The vector of the evoked saccade is dependent upon the site of stimulation within the SC, not the parameters of stimulation. Thus, excitation of discrete regions of the SC initiates a sequence of neural events controlling both the direction and amplitude of

the ensuing saccade. The question of how information concerning saccade amplitude and direction, contained as a spatial code in the SC, is transmitted to subsequent oculomotor brain regions is unresolved.

Many neurons in the intermediate and deeper layers of the SC discharge before saccades with particular directions and amplitudes[15,20–23,30]. The major purpose of the present experiment was to examine, in detail, the presaccadic burst of SC neurons and to determine whether or not information concerning the vector components (amplitude and direction) of a saccade is contained within the burst. This was thought to be necessary because of recent studies[1,2,8] showing that the discharge of pontine and rostral midbrain neurons, if carefully analyzed, contains information about either the direction or the amplitude of saccadic eye movements. Results confirm earlier suggestions[14,19,24,27,30] that the information necessary to generate signals concerning saccade amplitude or direction is not contained within the spike discharge of individual SC neurons but must be extracted from the spatial distribution of activity within the SC.

METHODS

The methods used have been previously described[23,27]. Briefly, 4 rhesus monkeys *(Macaca mulatta)* weighing from 2.5 to 5.0 kg underwent three aseptic surgical procedures. First, 4 stainless steel bolts were implanted into the skull to permit immobilization of the head[6] during subsequent training and recording sessions. Approximately one month later, 3 turns of fine wire were surgically implanted beneath the insertions of the 4 recti muscles to be used as a search coil for eye movement recordings[7]. Finally, after 4–6 weeks of behavioral training, a stainless steel receptacle for a microdrive was secured to the skull.

Extracellular unit potentials were recorded using tungsten microelectrodes and a remotely operated hydraulic microdrive. Recording sites were histologically confirmed.

During all training and recording sessions, monkeys were seated in a primate chair located in an electrostatically shielded and sound-resistant room. During experimental sessions, the head of the monkey was immobilized. 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.

Monkeys were trained to track a visual target presented on a Hewlett-Packard 1310A oscilloscope. A small laboratory computer was used to control the horizontal and vertical positions of the target, to deliver reinforcement for appropriate tracking of the target and to provide an on-line display of eye and target positions and instantaneous spike frequency. 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 (R) and angle (θ) from an initial fixation point.

On-line, computer-generated plots of instantaneous spike frequency (the reciprocal of interspike interval) and horizontal and vertical eye position were used to

determine the temporal relationship between spike activity and changes in eye position. Additionally, selected trials were played back on analog tape and a 400 msec period following target displacement was converted to a digital format. Horizontal and vertical eye position signals were sampled each msec and interspike intervals were measured with a resolution of 100 μsec. Saccade onset and offset were automatically defined by appropriate subroutines and the time of occurrence recorded. A listing of the duration of each interspike interval, the time of occurrence, and the instantaneous spike frequency for each interspike interval was obtained. These values were used to define burst onset, burst offset, burst duration, peak instantaneous frequency, and average instantaneous frequency. Burst onset was defined as the time when instantaneous spike frequency exceeded 300 spikes/sec; burst offset as the time when instantaneous spike frequency returned to less than 300 spikes/sec.

RESULTS

This report is restricted to a description of the response properties of 58 neurons: 30 saccade-related burst neurons and 28 neurons with other response properties, described below.

Saccade-related burst neurons

Saccade-related burst neurons[23] are characterized by a discrete, high frequency burst of activity beginning approximately 20 msec before the onset of a particular saccade.

Variations in the configuration and timing of saccade-related bursts. We observed systematic changes in the timing and configuration of the saccade-related discharge as a function of the position of the saccade in the movement field. Fig. 1 illustrates, for one neuron, the instantaneous frequency records which accompanied 14 different saccades in the movement field. Fig. 1 (I) shows 7 records for saccades of the optimal amplitude (9°) but which differed in direction. Examination of the profiles of these records indicates that the most intense discharge occurred prior to a 9° saccade with a direction of 60° (up and right). Deviations from this direction were accompanied by reductions in peak instantaneous frequency and average instantaneous frequency, by shorter burst durations, and by alterations in the timing between saccade onset and the neural discharge. For movements at the fringe of the movement field, the neural discharge may follow rather than precede saccade onset.

Similar changes in burst profile were seen when saccade direction remained constant and saccade amplitude was varied. Fig. 1 (II) shows the instantaneous frequency records for 7 saccades of the optimal direction but which varied in amplitude from 2 to 25°. The peak instantaneous frequency, average instantaneous frequency, pulse duration and timing varied as a function of saccade amplitude.

Burst magnitude is poorly correlated with saccade direction alone. Saccades of a particular direction may be accompanied by either vigorous or weak discharges depending upon saccade amplitude. Similarly, there is not a systematic relationship between burst magnitude and saccade amplitude alone since saccades of a particular

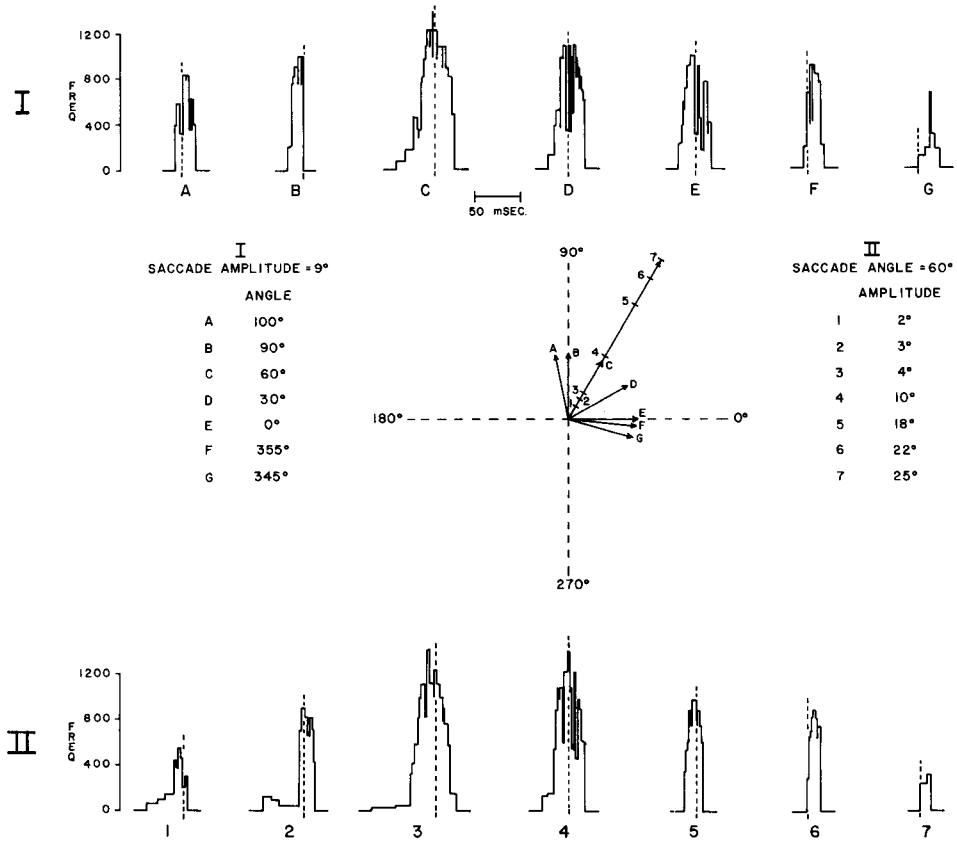

Fig. 1. Variations in the configuration and timing of the discharge of a typical saccade-related burst neuron. I: instantaneous spike frequency records for 7 saccades of the optimal amplitude (9°) but differing in direction. The dotted line represents saccade onset. II: instantaneous spike frequency records for 7 saccades of the optimal direction ($\theta = 60°$) but differing in amplitude. Note that for saccades on the fringe of the movement field, the neural discharge may follow, rather than precede, saccade onset.

amplitude may be accompanied by weak or vigorous discharges depending upon saccade direction. As previously reported, the maximal discharge of a SC neuron occurs prior to a saccade with a particular direction *and* a particular amplitude[15,20–23, 27,30].

Except for the maximal discharge which precedes saccades to the center of the movement field, the discharge of SC neurons is ambiguous with respect to saccade direction or amplitude. Identical discharges may precede many saccades with different directions and amplitudes. Burst profiles B, F, 2, and 5 (see Fig. 1) are almost identical. But one accompanied a purely vertical saccade of 9°; one a down and right saccade of 9°; one an up and right saccade of 3°; and the other an up and right saccade of 18°.

Another illustration of the finding that identical spike bursts may precede different saccades is given in Fig. 2. The maximal burst accompanying saccades to the center of the movement field is shown in Fig. 2A. Two spike bursts accompanying a

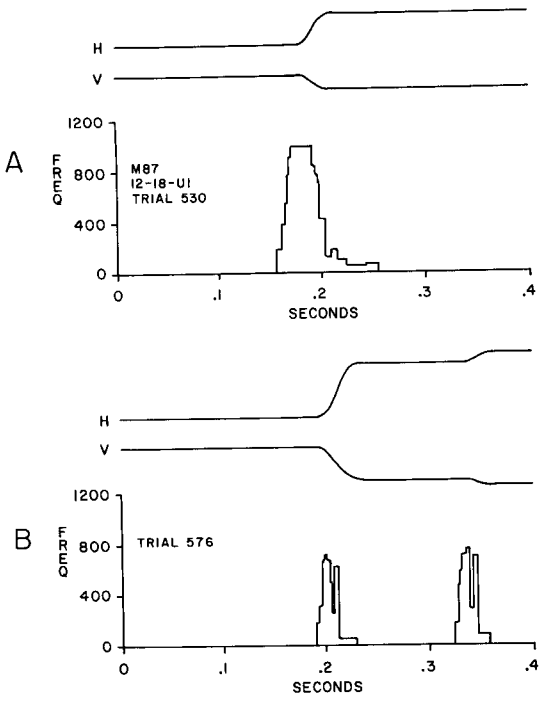

Fig. 2. A: maximal discharge occurring prior to a saccade to the center of the movement field. B: identical spike bursts occurring before a large primary saccade and a small corrective saccade.

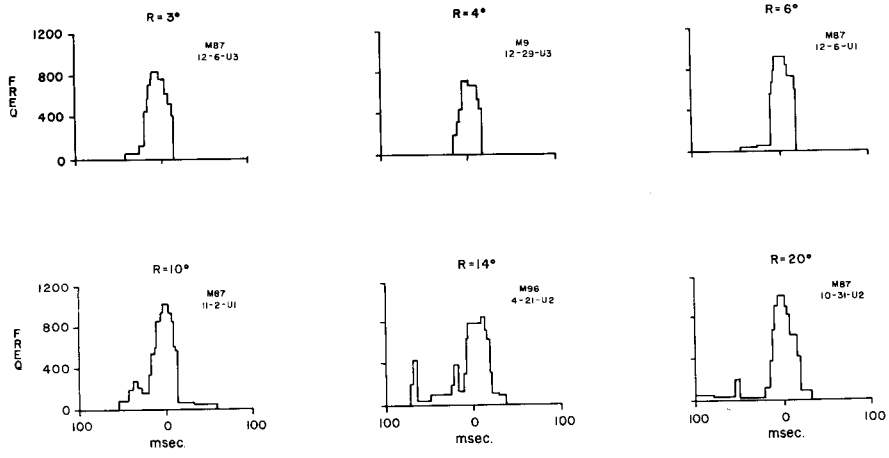

Fig. 3. Instantaneous spike frequency profiles of the maximal discharge recorded from 6 SC neurons. Saccade onset occurs at time 0. In general, the discharge of different saccade-related burst units, some discharging maximally to small saccades and some discharging maximally to larger saccades, are indistinguishable.

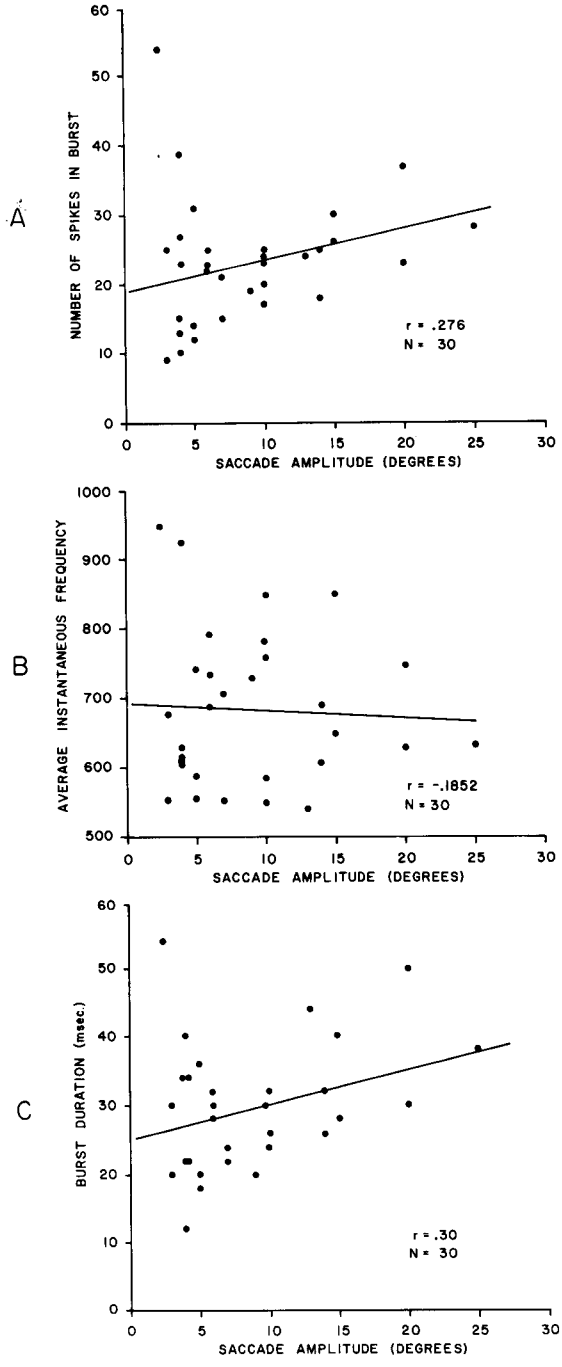

Fig. 4. Comparison of the discharge of 30 saccade-related burst neurons. A: number of spikes in a saccade-related burst as a function of the optimal saccade amplitude. B: average instantaneous spike frequency of the burst as a function of saccade amplitude. C: burst duration as a function of optimal saccade amplitude.

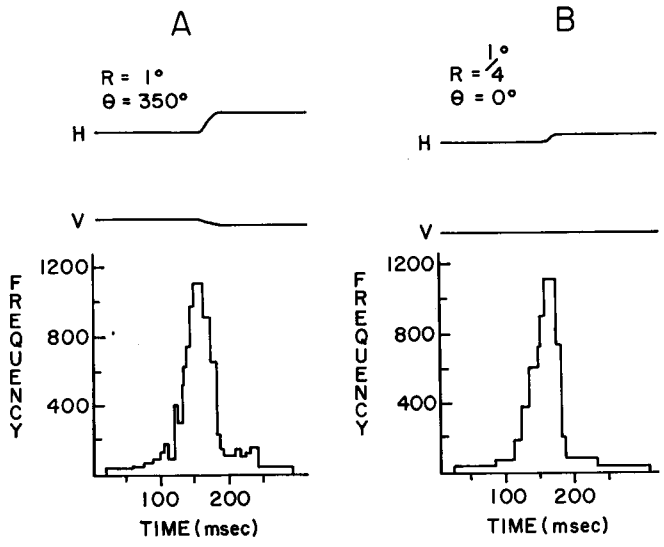

Fig. 5. Instantaneous spike frequency records of bursts accompanying small saccades. A: the frequency profile of a burst accompanying a 1° saccade. B: the instantaneous spike frequency profile of the same neuron discharging before a 0.25° saccade.

primary saccade 15° in amplitude and a 3° corrective saccade are shown in Fig. 2B. Although the saccade amplitudes are different, the spike bursts are almost identical, each containing 14 spikes.

Comparison of bursts originating from different SC neurons. The discharge of different saccade-related burst units, some which discharge maximally to small saccades and some which discharge maximally to large saccades, are indistinguishable. Fig. 3 illustrates the instantaneous frequency records of the maximal discharge observed from 6 different SC neurons. These neurons discharged maximally prior to saccades of 3, 4, 6, 10, 14 and 20°. There are no obvious distinguishing features of bursts accompanying saccades of particular amplitudes.

In an attempt to quantify this observation, we selected bursts accompanying saccades to the center of the movement field for 30 SC neurons and measured a number of characteristics of the burst. Fig. 4A plots the number of spikes in the saccade-related burst as a function of the amplitude of the optimal eye movement for the different neurons. Average instantaneous frequency during the saccade-related burst is plotted as a function of the amplitude of the optimal eye movement in Fig. 4B. Fig. 4C plots burst duration as a function of optimal saccade amplitude. The relationship between these measures of neural discharge and saccade amplitude is either very weak or nonexistent.

Burst accompanying small saccades. In the course of this study we observed neurons located in the rostral SC which discharged prior to small refixation saccades of 0.25° or less. The instantaneous spike frequency plots of the spike burst accompanying saccades of 1° and 0.25° in amplitude are shown in Fig. 5. In typical experiments with the oscilloscope screen placed at 35 cm, eye position gain was insufficient to systema-

tically study the discharge of rostral SC neurons discharging to small refixation saccades. In a few experiments, the oscilloscope screen was moved to 70 or 140 cm, the gain of the eye position signals increased, and the movement fields of rostral SC neurons plotted. We plotted the movement fields of 7 SC neurons which produced vigorous spike bursts prior to saccades with amplitudes of 0.25° or less. However, in each case, the maximal discharge preceded a saccade of 1–2°. More systematic explorations of the rostral SC are needed to determine whether or not some SC neurons produce their maximal discharge prior to saccades with amplitudes of less than 1°.

SC activity which may reflect arousal states. Neuronal activity is often encountered in the SC which may reflect arousal or attentive states of the monkey. We observed one type of neuron (n = 20) which is characterized by relatively high spontaneous levels of activity and a cessation of activity during the entire trial period (See Fig. 6A). Spontaneous activity gradually returns during intertrial intervals. The cessation of activity is not dependent upon the location of the visual targets. The

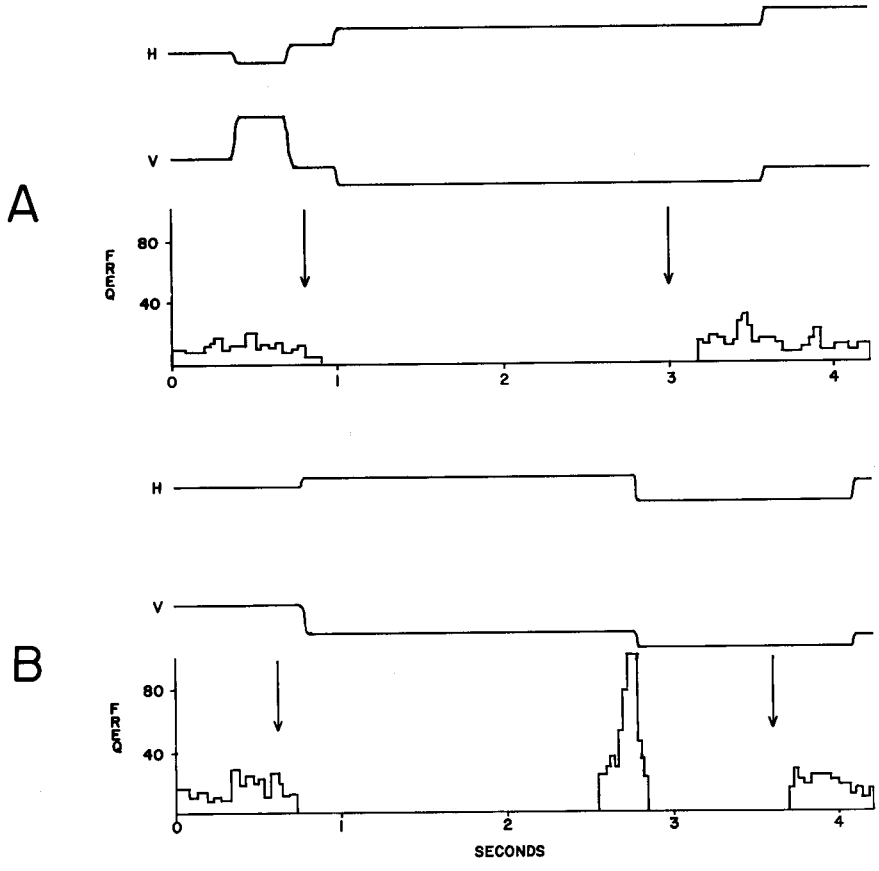

Fig. 6. A: cessation of firing of a SC neuron during an entire fixation trial. Arrows indicate trial onset and end of the trial. B: cessation of firing of the same neuron during a saccade trial except for the burst of spike activity accompanying a saccade in the neuron's movement field.

spontaneous discharge rate is also observed to decrease in response to extraneous noises and to either the auditory click signalling reinforcement or to the actual delivery of the reinforcement. During periods of low arousal, characterized by slow drifting eye movements, we observed an increase in the level of spontaneous activity. Many of these neurons have a weak movement field (Fig. 6B) and one neuron was observed which displayed a visual receptive field and a movement field. Other SC neurons, with low levels of spontaneous activity, were observed (n = 8) which showed an opposite type of response — a dramatic increase in discharge frequency during fixation or saccadic trials. Neurons displaying increases or decreases in spike activity during behavioral trials were isolated, in many cases, adjacent to neurons whose activity was clearly related to saccadic movements. These neurons were found throughout the region of the SC examined, although the majority of the 28 neurons were found in regions of the SC which discharged prior to 12–18° saccades.

DISCUSSION

Three major findings emerged from the present study: (1) neurons in the rostral SC discharge before small saccades of 0.25° or less; (2) the neuronal discharge of some SC neurons appears to reflect attentional or arousal states of the organism; and (3) careful examination of the presaccadic burst of SC neurons failed to reveal any component of the discharge which was capable of coding the vector components of a saccade. In the following sections, the implications of these findings for SC function are discussed.

Discharge of SC neurons before small saccades

Van Gisbergen and Robinson[29] demonstrated that microsaccades are accompanied by an appropriate burst or pause in motoneuron activity. They conclude that the miniature overshoots and oscillations accompanying small refixation saccades are not mechanical in nature, but are generated by the same control signals which produce large saccades. Results of the present experiment suggest that the SC may participate in the generation of the control signals for miniature saccades, but further investigation of this question is needed.

Attentional or arousal states

We observed unit activity in the SC seemingly related to the attentional or arousal state of the monkey. The discharge of these neurons is characterized by a cessation of activity during the entire tracking trial, by reduced firing rates following extraneous noises and the auditory click signalling reinforcement, and by an increase in spontaneous activity during periods of low arousal. We encountered similar units in previous studies[22,27] but were unable to verify the recording sites histologically. Neurons with similar properties have been previously observed in the pontine reticular formation[17,25]. Furthermore, most of the attentional-type units isolated in the pons are activated by stimulation of the SC[17]. The state of alertness has been shown to be an important factor influencing the velocity of saccades[3,4]. Perhaps the discharge of these

neurons contributes to the general level of excitation of subsequent premotor neurons, thereby influencing the velocity of saccadic eye movements.

Coding of saccade direction and amplitude

Results of the present experiment indicate that the pattern of spike activity originating from a single saccade-related burst neuron in the SC does not encode saccade direction or amplitude. Identical discharges may precede a wide range of saccades. Neither the magnitude, configuration or timing of the discharge are related in any unique way to the direction of the saccade alone or the amplitude of the saccade alone. This is in contrast to neurons in the paramedian pontine reticular formation (PPRF) or rostral midbrain in which burst duration and the number of spikes in the burst increases linearly as a function of the amplitude of the horizontal or vertical component of the saccade[9,13,26,29]. Also, this differs from the discharge of other neurons in the PPRF and rostral midbrain in which the number of spikes in a burst is related to the overall amplitude of eye movements, regardless of saccade direction[1,2,8,16]. It is also unlikely that information concerning saccade amplitude and direction is encoded by different types of signals originating from different SC neurons. The discharges of different SC neurons, some which discharge maximally to large saccades, some which discharge maximally to small saccades, are indistinguishable. For different neurons, there is no consistent relationship between burst duration, number of spikes in a burst, average instantaneous frequency, or any other obvious characteristics of the burst and the optimal saccade amplitude or direction.

The axons of the saccade-related burst neurons are thought to comprise a major efferent pathway from SC to subsequent oculomotor premotor neurons[23], particularly the paramedian pontine reticular formation (PPRF). The PPRF is thought to contain the immediate supranuclear neuronal networks for the control of all types of conjugate horizontal eye movements[8,9,16]. Three major types of neurons with activity related to eye movement are found in this structure: long-lead burst neurons, medium-lead burst neurons, and pause neurons. Long-lead burst units display a relatively long interval of irregular low-frequency activity followed by an intense burst of firing preceding saccade onset[9,13,26]. Medium-lead burst neurons produce a discrete high-frequency burst of activity which precedes saccade onset[9,13]. For these neurons, the duration of the spike burst is highly correlated with saccade duration. Pause neurons stop firing before and during saccades in all directions for an interval equal to saccade duration[9,13,26]. Microstimulation of the pontine region containing pause neurons exerts a powerful and selective inhibitory effect upon the saccadic system[5,11,12]. Rapid eye movements are totally inhibited during stimulation of the pause cell pool although the slow phase movements of optokinetic and vestibular nystagmus are unaltered.

Robinson developed a model of the PPRF circuitry which generates the required saccadic burst signal[19]. According to this model, the duration of the medium-lead burst neuron discharge is controlled by the pause cells. The tonic discharge of pause cells during fixation is assumed to inhibit burst cells and thereby prevent saccadic movements. When a decision to produce a saccade is reached, a trigger input briefly disables the pause cell, allowing the burst neuron to begin discharging. The discharge

continues until an efference copy of actual eye position matches the desired eye position. The trigger input signal must be tightly coupled to saccade onset and need not convey information concerning saccade direction and amplitude.

The discharge of saccade-related burst neurons of the SC may serve as a trigger input to a circuit similar to the one described by Robinson[19]. The onset of the high frequency burst is tightly linked to saccade onset[23] and precedes the onset of the eye movement by an appropriate time — approximately 20 msec. Consistent with the features of the trigger signal, saccade-related burst neurons signal saccade onset, not saccade direction, amplitude or duration. The suggestion that the SC provides a trigger input to the PPRF is supported by recent observations of Keller[10] that 10 of 10 saccade-related burst units recorded in the SC were antidromically activated by stimulation of the region of the PPRF containing pause units. Only 1 of 11 other SC neurons with saccade-related discharges, but lacking the high frequency burst, were antidromically activated by PPRF stimulation.

The question of how information concerning saccade direction and amplitude is extracted from the spatial distribution of SC activity remains unresolved.

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