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# Brain stem unit activity related to horizontal eye movements occurring during visual tracking

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There is considerable evidence that neurons in the pontine reticular formation are intimately involved in the initiation of eye movements. Electrical stimulation of the pontine reticular formation (PRF) induces short latency horizontal eye movements[2,8,9]. Clinically, bilateral lesions of the PRF at the level of the abducens nuclei produce a paralysis of all horizontal versions: saccadic or pursuit, reflexive or voluntary[10]. In animal studies, lesions of the PRF abolish ipsilateral saccades and the quick phases of nystagmus but slow movements may not be permanently affected[3,7]. Gross potential changes in the region of the PRF precede each rapid eye movement by 10–20 msec (see ref. 4) and unit activity in the pons related to the quick phases of nystagmus has been observed in acute microelectrode experiments[10].

More recently, chronic microelectrode recording experiments have described neuronal activity in midbrain and PRF related to saccadic eye movements and to the quick phases of nystagmus[5,12,15]. However, these studies did not systematically examine the response of PRF neurons to slow, visually guided pursuit movements. Since it has been suggested[6] that both slow and rapid horizontal eye movements may be generated in the PRF, a primary purpose of the present experiment was to determine whether or not changes in PRF unit activity occur during smooth pursuit as well as saccadic eye movements.

Three monkeys (*Macaca mulatta*) were trained to track a visual target presented on a modified TV monitor. On discrete tracking trials the animal was required to fixate the center target for a variable time (1–4 sec) and then the target was moved, randomly, to one of 6 other horizontal locations (4, 8, or 12° to the left or right of center). If the animal acquired the new target position within 500 msec and maintained fixation for an additional 1.5 sec, a liquid reinforcement was given on a 2:1 variable ratio schedule. During pursuit tracking trials, the target was moved with a sinusoidal forcing function. Target excursion was 12° to either side of the center position and a velocity of 8°/sec was most commonly used. To ensure that movement related discharges were not the result of retinal image displacements, the activity of each unit was also observed during spontaneous eye movements occurring in total darkness. A PDP-8/I computer was used to control target position and to compare horizontal eye position with target position every 4 msec.

During recording sessions, animals were seated in a chair with head restrained[11]. A movable microelectrode positioner and glass-insulated platinum microelectrodes were used to record, extracellularly, the activity of neurons in the brain stem. Horizontal eye position was measured with an infrared system described by Barmack[1]. Lesions were placed at the maximum depth of tracks in which responsive units were encountered and, at the termination of the experiment, 50 $\mu$m frozen sections were mounted and stained with thionin. Reconstructions of the electrode path were made based upon lesion sites and measurements of electrode position taken during recording sessions.

Programs were written for the PDP-8/I computer to aid in describing the rela tion between spike frequency and changes in eye position. Displays provided by these programs and photographs of unit activity, eye position, and target position taken on moving film were used to determine the responsiveness of each unit.

The firing patterns of 582 brain stem neurons were analyzed during eye movements. The activity of 90 units from this sample was clearly related to horizontal eye movements and an additional 27 units were responsive to aspects of the visual tracking task other than eye movements. Six functional types of units responsive to eye movements were isolated. Although most of these cell types have been described[5,12,15], the activity of these units during pursuit tracking movements has not been reported previously.

*Burst-tonic units ($n$ = 36).* Units categorized as burst-tonic displayed a burst of activity prior to or during saccadic movements in one horizontal direction, a

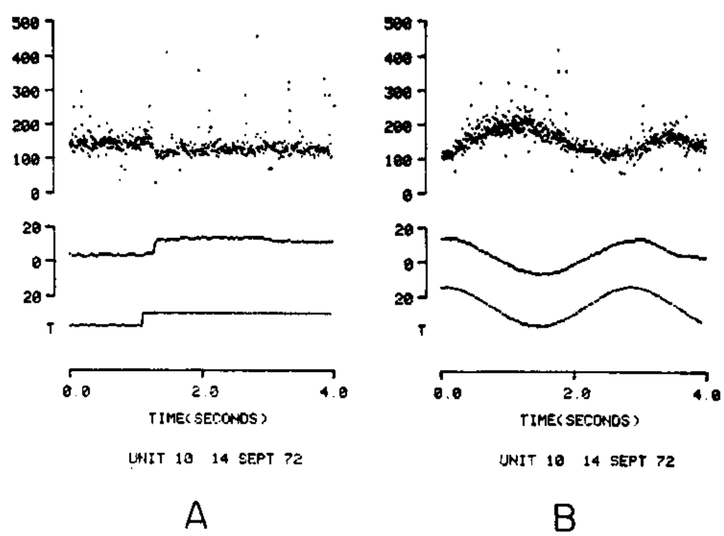


Fig. 1. Discharge of a PRF unit during saccadic (A) and pursuit (B) tracking. Top trace — each dot represents an interspike interval and is plotted as instantaneous frequency, calibrated in spikes/sec. Middle trace — horizontal eye position calibrated in degrees. Bottom trace — target position. Up is right, down is left for target and eye position records.

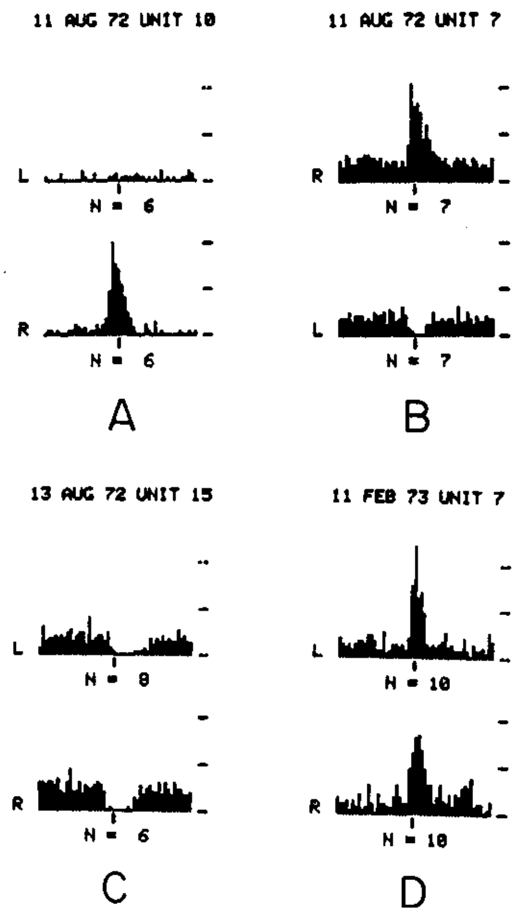


Fig. 2. Histograms of activity of 4 types of units encountered in the PRF. Each histogram represents the cumulative number of spikes occurring 125 msec prior to the saccade onset (indicated by the vertical line below each baseline) and 125 msec after saccade onset for the number of saccades (N) indicated. Since each bar represents the cumulative number of spikes in consecutive 5 msec intervals, the time relationship between changes in spike activity and saccade onset can be described for each unit. R = right saccades, L = left saccades, N = number of saccades included in each histogram. Calibration: each vertical division represents a cumulative total of 25 spikes.

decrease in rate during saccades in the opposite direction, and maintained a steady discharge rate proportional to horizontal eye positions within their movement fields during periods of nonmovement (Fig. 1A). During pursuit movements, their response was characterized by a burst or pause associated with the saccade to acquire the target and then a discharge rate proportional to horizontal eye position during slow pursuit movements (Fig. 1B). The histogram analyses indicated that for neurons in the PRF a burst of spike activity usually preceded the saccade onset by approximately 10 msec with a range of 0–15 msec. Thirty-two burst-tonic units were located in the PRF in the vicinity of the abducens nucleus and 4 in the midbrain reticular formation.

*Burst units (n = 25).* Burst units in the PRF were characterized by very low

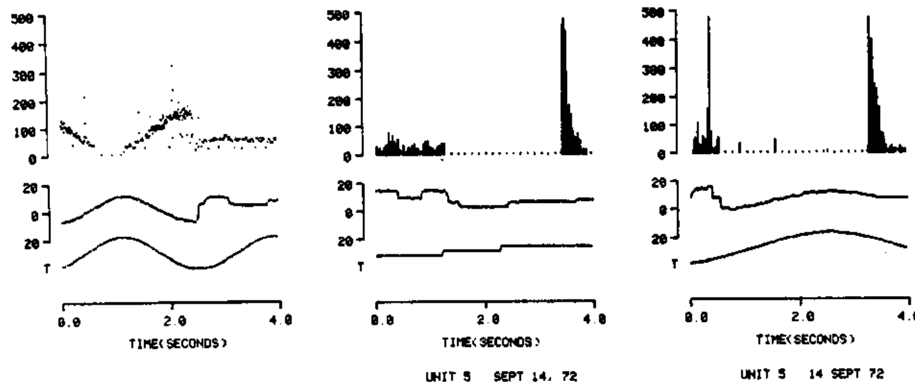


Fig. 3. A: discharge of a tonic unit during pursuit tracking and during spontaneous saccadic movements. (For legend, see Fig. 1.) B and C: cessation of firing of PRF unit during both discrete (B) and pursuit (C) tracking. Top trace — instantaneous spike frequency calibrated in spikes/sec. Middle trace — horizontal eye position. Bottom trace — target position. Note that the unit represented in B and C also responds with a high frequency burst when reinforcement is delivered at the end of each tracking trial.

levels of tonic activity during steady eye positions and by a high frequency burst occurring approximately 10–15 msec prior to saccades in a particular direction (Fig. 2A). Noticeable changes in spike activity of burst units were not observed during smooth pursuit movements. Ten burst units were isolated in the paramedian PRF, 4 in the PRF near the abducens nucleus, 4 in the midbrain reticular formation, and 7 in the superior colliculus.

*Burst-pause units ($n = 8$).* Burst-pause units exhibited a burst of spike activity approximately 10 msec prior to saccades in a particular horizontal direction, a decrease or cessation in activity asociated with saccades in the opposite direction, and a tonic rate that was unrelated to horizontal eye position (Fig. 2B). The activity of these units was not altered during smooth pursuit movements. Four burst-pause units were located in the PRF (2 in the paramedian PRF and 2 near the abducens nucleus) and 4 in the midbrain reticular formation.

*Pausing units ($n = 3$).* Units characterized as pausing units had a tonic spike frequency unrelated to eye position and a decrease in spike rate related to the onset and duration of saccades in either horizontal direction (Fig. 2C). The tonic rate was unrelated to eye position during smooth pursuit movements.

*Bidirectional burst units ($n = 11$).* Bidirectional burst units displayed a burst of activity related to the onset and duration of eye movements in either horizontal direction (Fig. 2D). Burst onsets ranged from 0 to 20 msec prior to the beginning of a saccade but generally, the burst–saccade interval was greater for ipsilateral saccades than for contralateral saccades. Six bidirectional burst units were isolated in the PRF (3 in the vicinity of the abducens nucleus and 3 in the paramedian PRF), 3 in the midbrain reticular formation and 2 in the superior colliculus.

*Tonic units ($n = 7$).* Tonic units displayed a discharge frequency proportional to horizontal eye position during periods of non-movement but discharge rate was not altered during saccades in either direction. During pursuit tracking trials, the activity of tonic units was not altered during the acquisition saccade but the proportionate discharge rate changed continuously during the sinuisoidal eye movements (Fig. 3A). Six of these units were isolated in the PRF in the vicinity of the abducens nucleus and 1 in the midbrain reticular formation near the trochlear nucleus.

*Other unit types.* Unit activity seemingly related to the attentional or arousal properties of the visual tracking task was observed in the paramedian region of the PRF. Fig. 3B, C illustrates the response of a unit displaying a cessation of spike activity for the duration of either discrete or pursuit tracking trials. Fifteen units which responded with a cessation of activity or with an equally dramatic increase in firing during the entire tracking task (either discrete or pursuit trials) have been isolated. These units were, in many cases, adjacent to neurons whose activity was clearly related to saccadic eye movements. This suggestion that the activity of these units may be related to the arousal properties of the target is strengthened by the observation that several units of this type also responded to the presentation of the reinforcement and to loud, sudden noises.

In summary, 6 types of unit activity related to horizontal eye movements have been isolated in the PRF and midbrain reticular formation. The activity of 2 types was altered during smooth pursuit tracking movements. Burst-tonic units (isolated in the PRF near the abducens nucleus) displayed a burst of spike activity prior to the onset of a saccade in a particular direction, a gradual increase in firing rate as the eye moved in one direction and a gradual decrease as the eye moved in the opposite direction. The activity of tonic units was not altered during saccades but changes in spike frequency did accompany smooth pursuit movements.

Apparently, the region of the brain stem in the immediate vicinity of the abducens nucleus represents a point of convergence for the phasic and tonic inputs to abducens motor neurons. The findings of the present study confirm the previous report[12] of at least 3 types of units in this area with spike activity related to eye movements. Units displaying a spike burst prior to saccadic but not smooth pursuit movements, units with discharge frequencies associated with eye position during fixation and smooth pursuit movements but not with saccadic movements, and units with changes in spike frequency related to both rapid and smooth movements have been observed. The question of the origin of the inputs to this region is an important, but unanswered one.

It has been suggested[13,14] that neurons in the paramedian region of the PRF serve as pulse generators for rapid eye movements — saccades and the quick phases of nystagmus. Results of chronic microelectrode recording studies from this brain area are consistent with this hypothesis. Cohen and Henn[5] reported that neuronal activity in this region is primarily related to saccadic movements and to the quick phases of vestibular or optokinetic nystagmus. Our results confirm this finding. The tonic rate of units in this region is low and if present is unrelated to eye position during periods of fixation or changes in eye position during smooth pursuit movements. The burst of activity associated with saccades and with the quick phases of nystagmus may be generated by neurons in this brain region. Furthermore, the isolation of units in the paramedian region of the PRF whose activity appears to be related to the attentional properties of visual stimuli suggests that neurons in this area may be involved in the selection of which visual targets are to be tracked — an important aspect of oculomotor control which has received little neurophysiological investigation.

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