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## Presaccadic burst discharges of tecto-reticulo-spinal neurons in the alert head-free and -fixed cat

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Tecto-reticulo-spinal neurons (TRSNs) discharge high frequency bursts of action potentials prior to visually triggered gaze shifts made in the head-fixed (eye only moves) or head-free (eye and head move together) conditions. These high-frequency presaccadic bursts are weak or absent when the cat generates gaze shifts to non-visible remembered targets. TRSNs remain silent during spontaneously generated gaze shifts. The visually triggered gaze shifts, that are preceded by TRSN bursts are faster than gaze shifts directed at non-visible targets.

A major descending efferent pathway from the cat superior colliculus (SC) is the tecto-reticulo-spinal tract. Axons that compose this tract cross the midline within the mesencephalon and descend to the upper cervical spinal cord terminating predominantly in lamina VII<sup>7</sup>. Throughout their descent, these axons send out a multitude of axon collaterals that terminate within mesencephalic, pontine and medullary reticular centers involved in the control of eye and head movements<sup>3</sup>. About two-thirds of the axons project all the way to the upper cervical spinal cord<sup>3,15</sup>. Grantyn and Grantyn<sup>3</sup> found no differences in 'soma-dendritic and axonal architecture' between cells projecting to both the brainstem and cervical spinal cord and cells terminating within the brainstem only.

We have been studying the discharge characteristics of tecto-reticulo-spinal neurons (TRSNs) in the alert, behaving cat<sup>10–13</sup>. A most interesting feature of TRSN activity, previously reported<sup>10</sup>, was a sustained discharge that depended on the magnitude and direction of the vector between a desired food target and the current position of the visual axis. We defined this as a TRSN's gaze position error (GPE) signal<sup>10</sup>. This discharge reflects the increased excitability of a group of cells at a specific site in the SC

that may then participate in the generation of the required gaze shift. In our previously published examples of TRSN discharges coding GPE we emphasized the sustained discharge and did not consider high frequency presaccadic bursts. In this short communication we describe the presaccadic *burst* activity of TRSNs that occurred when cats generated gaze shifts in two different conditions: (1) to a visible food target that suddenly appeared in the peripheral visual field; or (2) to a location where the cat *predicted* a food target would appear. In the former condition, the gaze shift was directed at a sensory event while in the latter condition the cat was required to generate a gaze shift of the same amplitude and direction in the *absence* of a sensory event but based on knowledge gained from previous trials.

TRSNs, located in the intermediate and deep layers of the cat SC, were identified antidromically by their responses following stimulation of either: (1) the ventromedial funiculus of the spinal cord at C1 with implanted stainless steel microwires; or (2) the predorsal bundle, immediately rostral to abducens nucleus using a bipolar concentric stainless steel microelectrode (Kopf, SNEX 100). In the animals from which data were obtained, only one of these two sites had functional stimulation. For the 35 cells described

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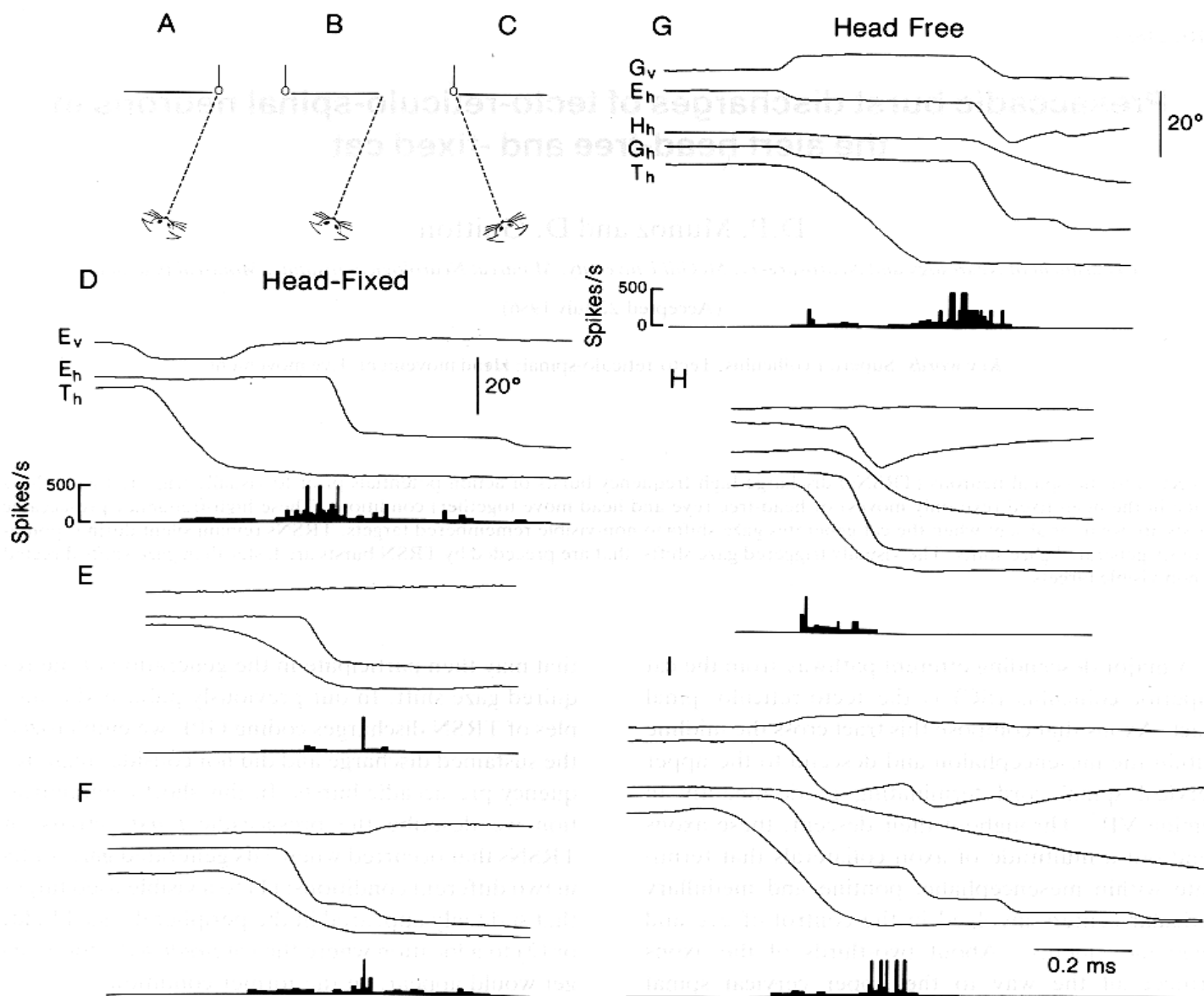


Fig. 1. Paradigm used in this study and discharges of a TRSN, located in the right SC. A: cat looked at food target visible to the right of a barrier. B: the target was moved from the right to the left side of the barrier, into the TRSN's visual receptive field. C: the cat oriented to the target, visible to the left side of the barrier. D–I: actual data records of the head-fixed (D–F) and head-free (G–I) cat orienting to visible (D, G), and predicted (E, F, H, I) targets. F and I also show corrective movements triggered by the visible target. E, H, G and T are eye, head, gaze and target position traces, respectively. Subscripts h and v correspond to horizontal and vertical components of eye, head and gaze position traces. Up-going and down-going horizontal eye, head, gaze and target position traces indicate movements to the right and left, respectively. Similarly directed vertical traces indicate upward and downward movements respectively. TRSN activity expressed as instantaneous firing frequency. Action potentials were collected in 2 ms bins.

here the behaviorally related discharges were independent of whether the cells were antidromically identified from the spinal cord or brainstem. Eye, head and target movements were measured with the search-coil-in-magnetic-field technique<sup>14</sup>. Procedures for surgical preparation of cats, calibration of eye and head movements, and antidromic identification (including collision testing) of TRSNs have been previously reported<sup>5,10</sup>.

In our experimental paradigm, the animal could be rapidly trained to make gaze shifts to both visual and predicted targets. Initially, the cat fixated the food target that was visible to the right side of the barrier (Fig. 1A). The target then disappeared behind the barrier and reappeared to the left side (Fig. 1B). Following the reappearance of the target, the cat quickly oriented to the *visible* target (Fig. 1C) and was rewarded. The animal quickly learned the above task

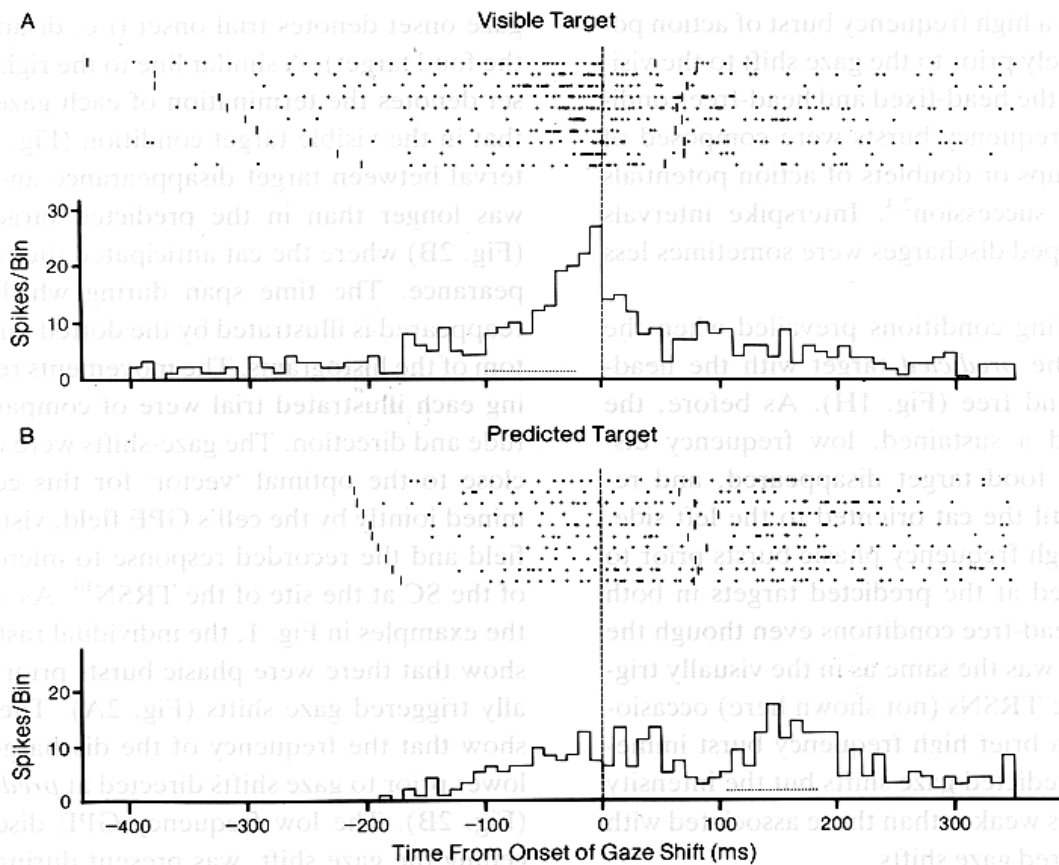


Fig. 2. Rasters and histograms summarizing a TRSN's (same cell in Fig. 1) activity during gaze shifts to visible (A) and predicted (B) targets in the head-fixed condition. Each dot corresponds to a single action potential. The rasters are aligned on the onset of the gaze shift. The disappearance of the target is denoted by a small vertical line to the left of gaze onset on each raster. Target reappearance is denoted by the dotted line at the bottom of the histograms. The small vertical line on each raster to the right of gaze onset corresponds to termination of the saccade. The histograms (10 ms bin width) summarize the activity of the ten trials displayed in each condition.

and began predicting that the disappearance of the food target from one side of the barrier meant future reappearance of the target on the other side. On some trials the cat oriented from one side of the barrier to the other before the target reappeared, thereby orienting to a *predicted* target. The barrier width and orientation were adjusted to have the cat generate gaze shifts of various amplitudes and directions. The movement vector that was associated with the best response from the cell could then be determined.

Before describing TRSN discharges we reemphasize that these neurons *were never observed to discharge, either tonically or phasically, during spontaneous gaze shifts made in the light or dark*<sup>2,10</sup>. Thus cats could make saccadic gaze shifts even though their TRSN pathway remained silent. Note also that TRSNs had visual receptive fields whose boundaries were difficult to delineate in the alert behaving cat

but which appeared to be coextensive with their GPE field<sup>10</sup>.

The discharge of a TRSN, located in the right SC, is illustrated in Figs. 1 and 2 as the cat oriented to visible and predicted targets. The most intense presaccadic bursts occurred when the cat oriented to the *visible* food target. In both the head-fixed (Fig. 1D) and head-free (Fig. 1G) conditions the neuron began to discharge action potentials when the target disappeared from the right side and continued to discharge until the cat oriented to the target, visible on the left, and situated in the cell's visual receptive field. The sustained, low frequency discharge began before the target reappeared on the left side of the barrier. It was not dependent on the target being present and corresponded to the previously described GPE signal carried by these neurons whenever the vector error between current and desired gaze positions was optimal for the cell<sup>10</sup>. In addition to the sustained dis-

charge, there was a high frequency burst of action potentials immediately prior to the gaze shift to the visible target in both the head-fixed and head-free conditions. The high frequency bursts were composed of several small groups or doublets of action potentials that occurred in succession<sup>2,4</sup>. Interspike intervals within these grouped discharges were sometimes less than 0.002 s.

The same starting conditions prevailed when the cat oriented to the *predicted* target with the head-fixed (Fig. 1E) and free (Fig. 1H). As before, the neuron generated a sustained, low frequency discharge when the food target disappeared, and remained active until the cat oriented to the left side. There were no high frequency phasic bursts prior to gaze shifts directed at the predicted targets in both head-fixed and head-free conditions even though the movement vector was the same as in the visually triggered trials. Some TRSNs (not shown here) occasionally discharged a brief high frequency burst immediately prior to predicted gaze shifts but the intensity of these bursts was weaker than those associated with the visually triggered gaze shifts.

On some trials the cat oriented to the left side of the barrier with more than one gaze shift. The first gaze shift occurred before the target reappeared while subsequent corrective gaze shifts were visually triggered. Such orienting movements are illustrated in the head-fixed (Fig. 1F) and head-free (Fig. 1I) conditions. Once again, the low frequency sustained activity began when the food target disappeared and continued until the cat oriented to the left side of the barrier. Notice that there was no high frequency burst before the predictive gaze shifts but the visually triggered gaze shifts were preceded by a burst, provided the neuron was still active with a gaze position error signal. When the error was small, as in the head-free condition (Fig. 1G, I), the neuron ceased to be tonically active and no phasic bursts preceded small visually triggered corrective gaze shifts since the target was now outside the cell's visual receptive and GPE fields.

Fig. 2 shows, in raster form, the discharges of the TRSN illustrated in Fig. 1 during several trials in which the cat made gaze shifts to both visible (Fig. 2A) and predicted (Fig. 2B) targets in the head-fixed condition. The rasters are aligned on the onset of each saccade. The small vertical line to the left of

gaze onset denotes trial onset (i.e. disappearance of the food target). A similar line to the right of gaze onset denotes the termination of each gaze shift. Note that in the visible target condition (Fig. 2A), the interval between target disappearance and gaze onset was longer than in the predicted target condition (Fig. 2B) where the cat anticipated the target's reappearance. The time span during which the target reappeared is illustrated by the dotted line at the bottom of the histograms. The movements recorded during each illustrated trial were of comparable amplitude and direction. The gaze-shifts were chosen to be close to the optimal 'vector' for this cell as determined jointly by the cell's GPE field, visual receptive field and the recorded response to microstimulation of the SC at the site of the TRSN<sup>10</sup>. As suggested by the examples in Fig. 1, the individual rasters in Fig. 2 show that there were phasic bursts prior to the visually triggered gaze shifts (Fig. 2A). The histograms show that the frequency of the discharge was much lower prior to gaze shifts directed at *predicted* targets (Fig. 2B). The low frequency GPE discharge, preceding the gaze shift, was present during both types of trials. Notice that, on some trials, low frequency discharge persisted after the termination of the gaze shift. This was because the gaze axis was still not on target and hence a GPE signal persisted. A brief decrease in discharge rate was observed at the termination of saccades directed at both types of targets. In the predicted target condition there was an increase in activity 100–200 ms after the onset of the gaze shift. This corresponded to the reappearance of the target, on the left side of the barrier, in the cell's visual receptive field indicated by the horizontal dotted line.

The high frequency bursts shown in Fig. 1D, F, G, I and Fig. 2A occurred immediately prior to gaze shifts of the appropriate amplitude and direction. These bursts were *visually* evoked; that is, the reappearance of the food target in the neurons visual receptive field triggered the burst. The neuron was, however, already at an elevated level of excitability as demonstrated by the presence of the low frequency GPE signal prior to the reappearance of the food target. This low frequency sustained discharge reflected increased neuronal excitability within a specific zone of the right SC indicating that this zone has been prepared for the eventual generation of a gaze

shift<sup>10</sup>. The visual response generated by the sudden reappearance of the target in the neuron's visual receptive field was added to the low frequency sustained discharge and may have been the immediate trigger to generate the gaze shift. Indeed, once the food target reappeared on the left side of the barrier, the cat *always* oriented to the left *immediately* after the burst. No example was ever observed of the food target reappearing and the cat not orienting immediately. Grantyn and Berthoz<sup>2</sup> also reported that TRSNs had high frequency phasic bursts prior to visually triggered saccades and that these bursts were absent prior to spontaneous saccades of comparable amplitude and direction.

Can any distinction be made between the trajectories of gaze shifts that are associated with TRSN phasic bursts and those that are not? Our data suggest that, for a given amplitude, the former are *faster*. The maximum gaze velocity attained during visually triggered gaze shifts (head-free, leftward, 20–25° in amplitude) was  $389 \pm 29$  degrees/s ( $n = 22$ ) while the maximum gaze velocity recorded during gaze shifts of comparable amplitude and direction directed at predicted targets was  $298 \pm 47$  degrees/s ( $n = 41$ ) which was significantly slower ( $P < 0.001$ ). Hikosaka and Wurtz<sup>6</sup> found that application of lidocaine to the SC of an alert monkey led to a decrease in saccade velocity. Thus, the SC output converging, with other saccade command signals, on downstream premotor circuits can influence saccade velocity.

TRSN high frequency presaccadic bursts were observed prior to visually triggered gaze shifts in both the head-fixed and head-free conditions. These presaccadic bursts were also well correlated to bursts of

EMG activity recorded from contralateral splenius and biventer cervicus neck muscles. Thus, TRSN presaccadic bursts appear well correlated to parameters of eye and head movements, or the sum of these: gaze. Further analysis is still required to determine if the TRSN burst signal is better matched to eye, head or gaze.

Many neurons in the deeper layers of the monkey SC generate high frequency bursts of action potentials immediately prior to saccadic eye movements of the appropriate amplitude and direction, made in the light or dark<sup>16–18</sup>. These SC burst neurons have always been assumed, but not proven to be, the collicular output cells projecting to the paramedian pontine reticular formation (PPRF) where saccadic eye movements are generated (see ref. 1 for review). Only a small subpopulation of monkey SC burst neurons, 'visuo-motor' cells, have their presaccadic bursts contingent on the saccade being triggered by a visual target<sup>8,9</sup>. All cat TRSNs we have recorded appear to be similar to the monkey visuomotor cells. However, in the predicted target condition we occasionally recorded small phasic bursts in some TRSNs (not shown in this paper). This suggests that a motor signal, independent of a visual trigger is present on cat TRSNs but that its efficacy is low. In the monkey the gain of this motor signal could simply be greater thereby yielding many output cells that discharge before spontaneous and non-visually triggered gaze shifts.

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