

Short Communications

Tectospinal neurons in the cat have discharges coding gaze position error

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Tectospinal neurons (TSNs) in the caudal superior colliculus of the alert behaving cat have a sustained discharge that depends on the magnitude and direction of the vector between a food target and the visual axis. Each TSN has its 'optimal' vector for which it will be activated at a maximum discharge rate independent of whether the animal's head is free or fixed. The discharge is not due to prolonged stimulation of a TSN's receptive field since the discharge persists even when the target is not visible.

The cat has a restricted ocular motility (oculomotor range, OMR) permitting eye movements with maximum amplitude of only about $\pm 25^\circ$ from center⁵. These limits to ocular motility require that head and eye movements be used together to attain targets outside the OMR. The deeper layers of the caudal superior colliculus (SC) are thought to play a role in controlling such movements since microstimulation of this region evokes coordinated eye-head movements^{5,18}. Tectospinal neurons (TSNs) in the cat project to levels C1–C5 of the contralateral spinal cord, terminating predominantly in lamina VII (ref. 7), which is known to contain interneurons that may be implicated in neck and forelimb motor control^{8,16}. TSNs also project to brainstem areas implicated in eye and head motor control^{3,4,14,17}. To determine what signals are carried by this major tectal efferent projection and its role in the control of gaze we have recorded from TSNs in the alert head-fixed and/or head-free cat. A preliminary report of these data has appeared previously¹³.

Eye and head movements were measured by the search coil in magnetic field technique. Procedures and calibrations have been previously reported⁶.

Three cats were trained to perform visuomotor tasks while remaining quiet in a simple restraining apparatus consisting of a bag and box. The trained cats were prepared in two surgical sessions, performed under Nembutal anaesthesia. First, an eye coil was sutured to the sclera of one eye. A craniotomy was performed to permit access to both colliculi through a stainless steel recording chamber fitted to hold a hydraulic microdrive. The recording chamber, a clamp for holding the cat's head, an attachment for a head coil, and all of the electrical sockets were part of a dental acrylic explant that was anchored to the skull with stainless steel screws.

Two weeks later, the dorsal surface of the spinal cord was exposed at the level of the first cervical vertebra (C1). A bundle of four 75 μm diameter stainless steel wires (teflon-insulated) were lowered to an optimal location in the ventromedial funiculus of the spinal cord. This position was obtained by recording a field potential in the SC while stimulating the cord with pulses of low current (20–100 μA). To maintain the position of the stimulating wires, a small pedestal was constructed on the first cervical vertebra with dental acrylic and anchored by a small stainless steel

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screw. Electromyographic (EMG) electrodes were inserted into the splenius and biventer cervicus neck muscles before the muscles were resutured along the midline.

Single TSNs were recorded when the animal's head was either held fixed or totally unrestrained. Conventional amplifying, display and recording techniques were employed. Recording of TSNs in alert cats began about 4 days after the second surgical session. TSNs were identified by stimulating at C1. The antidromic nature of the response was verified using a number of criteria that included collision testing⁹. Following the last recording session, a DC current was passed through an electrode to create lesions at selected electrode positions where TSN activity had been recorded. The brain was fixed and examined histologically.

A total of 36 TSNs were identified in the caudal SC. Of these, 13 were held long enough head-free and head-fixed to obtain the data described below. TSNs were characterized by a total absence of spontaneous discharge. They were located by slowly advancing the recording electrode through the SC while at the same time repeatedly stimulating, at 0.5 Hz with a single pulse (20–300 μ A), the spinal cord. Of the identified TSNs, 70% were located in the intermediate grey layer. The remaining 30%, found in the deep grey layer, had similar discharge characteristics. The latency of the recorded antidromic response ranged from 0.5 ms to 2.8 ms with a mean of 1.0 ms. A collision test of a TSN is shown in Fig. 1A. Orthodromic action potentials were used to trigger both the oscilloscope traces and the stimulus pulses applied to the spinal cord. Decreasing the interval between the orthodromic action potential and the stimulus pulse caused collision of the orthodromic and antidromic action potentials.

The recorded TSNs, all located in the caudal SC, had very large visual receptive fields which, though difficult to delineate in the alert behaving animal, appeared to encompass most of the contralateral visual field. Like many other cells in the cat SC^{1,2,10,15,19}, TSNs discharged a burst of spikes when a visual stimulus (e.g. a dark tongue projected on a screen) was moved through their receptive field. Moving natural stimuli (e.g. a hand, a spoonful of food) evoked more vigorous bursts. The responses to moving stimuli were directionally selective. Movement of a stimulus

away from the area centralis evoked the largest responses.

We recorded TSN activity while the cat made spontaneous eye and head movements as it looked about the laboratory in either the light or the dark. Neither saccade nor neck EMG-related discharges

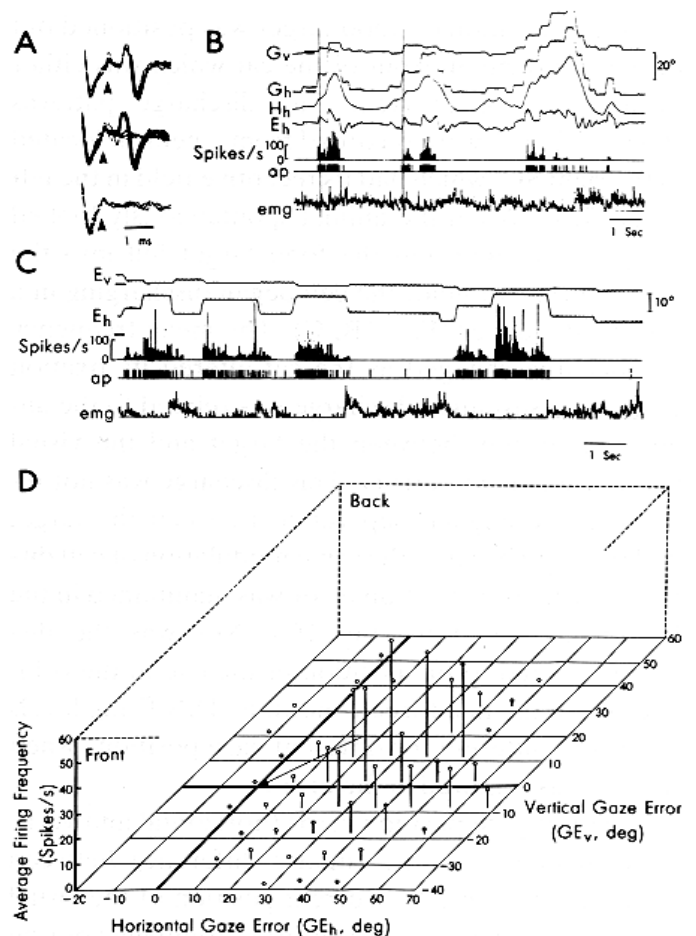


Fig. 1. TSN in the right SC coding gaze position error relative to a stationary food target. A: collision test of this TSN. Traces were triggered by orthodromic action potentials. Arrowheads represent stimulation of the spinal cord at C1. B: head-free example of sustained TSN discharge as the cat looked away from the food target, placing the target in the cell's receptive field. The target position is represented by the black bars on the horizontal and vertical gaze position traces (G_h and G_v , respectively). Other traces shown are horizontal head and eye positions (H_h and E_h , respectively), instantaneous firing frequency of the TSN, the individual action potentials, and EMG activity recorded from the left biventer cervicus neck muscle. Up-going and down-going horizontal gaze, head and eye position traces indicate movements to the right and left respectively. Similarly directed vertical traces indicate upward and downward movements respectively. C: same paradigm but with the head fixed. D: plot of gaze position error (head free) versus the average frequency of discharge for this same TSN, illustrating its gaze position error field. Dashed arrow represents the average gaze shift evoked by stimulating the SC at the recording site while the head was free.

were observed in this behavioral condition. The cat was rotated in the horizontal plane to produce vestibular nystagmus. TSNs did not discharge in relation to either the slow or quick phases of vestibular nystagmus.

TSN discharges were also studied during different visually guided orienting movements. In the simplest paradigm a stationary food target was positioned out of reach directly in front of the cat which was either head-free or head-fixed. The discharge patterns shown in Fig. 1 were recorded from a neuron located in the right SC, which had its receptive field in the left visual field. When the animal spontaneously looked away to the right and the food target fell into the TSN's receptive field, the cell began discharging in a sustained manner (Fig. 1B, C). The mean frequency of discharge changed as the cat altered its fixation point. The sustained discharge was related to the angular separation between the target and the visual axis (gaze position error). This discharge was not related to the angular separation between the target and the head because the same modulation of cell discharge with gaze position error was maintained in the head-fixed condition (Fig. 1C). Nor was the discharge related to the position of the eye in the orbit because in the head-free condition, TSN firing levels were very different for different gaze positions when the eye was centered in the orbit.

A plot of gaze position error (horizontal and vertical components of the angular difference between the food target and the current position of the visual axis in space) versus average firing frequency during the corresponding fixation period was generated from 20 head-free trials, consisting of 568 fixation points (Fig. 1D). Different target positions in space were used. The gaze position error and the average firing frequency were calculated at each fixation point, and the data were grouped into 10° horizontal by 10° vertical bins. TSNs discharged in a sustained manner for a family of gaze position error vectors that defined a gaze position error field (GPEF). There was an optimal vector (direction and magnitude) between the visual axis and the target that was associated with the maximum average firing frequency. As the visual axis departed from this position, the unit's activity decreased. The cell's preferred gaze position error vector (i.e. that which generated the highest average frequency of discharge) was located

at the center of the bell-shaped GPEF. The TSN illustrated in Fig. 1 responded best when the food target was located 30° to the left and 10° down of the cat's current fixation point. The same GPEF was observed in both head-free and head-fixed conditions.

The SC was stimulated (150 ms trains, $10\text{--}30\ \mu\text{A}$ intensity, pulses 0.5 ms in duration at 300 Hz) at the site where the unit in Fig. 1 was recorded. In the head-free condition (with gaze starting at center), stimulation of the SC drove the gaze along a particular vector (dashed line in Fig. 1D) that was very

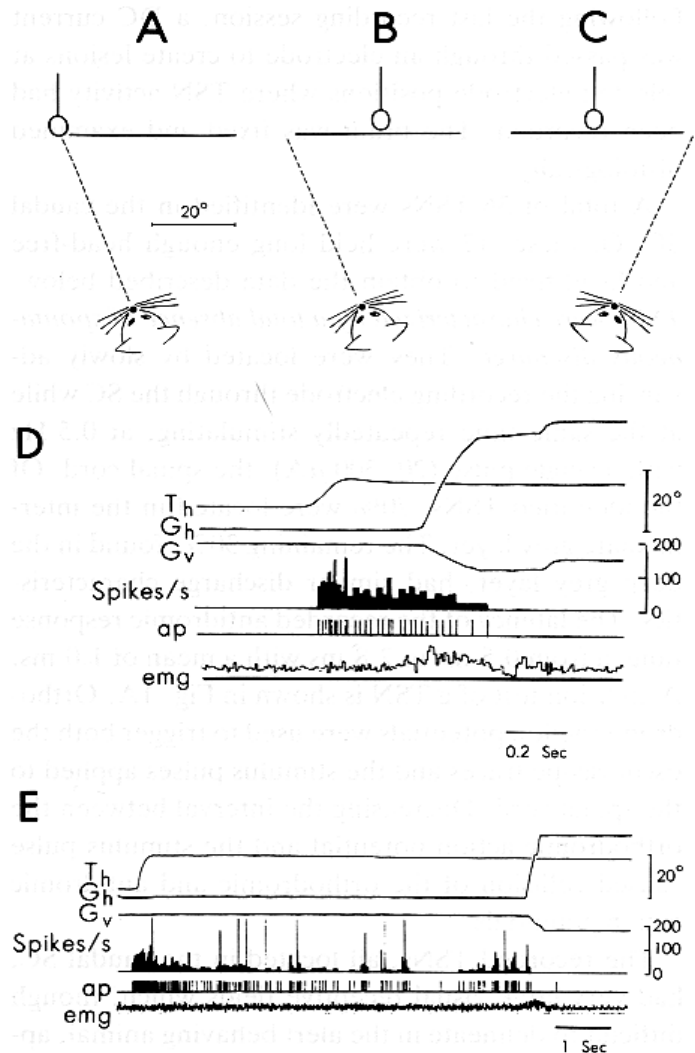


Fig. 2. Example of the cat orienting to an imagined target in the TSN's (located in the left SC) gaze position error field. A: cat looked at the food target to the left of a barrier. B: the target disappeared behind the barrier. C: the cat predicted the reappearance of the target and oriented to the right of the barrier. D, E: actual data records. A search coil was placed on the food target to give horizontal target position (T_h). G_h and G_v are the horizontal and vertical gaze position traces. Below is the instantaneous firing frequency, action potentials of the TSN, and EMG activity recorded from the right splenius neck muscle.

similar to the gaze position error vector for that cell.

It might be argued that the sustained discharge pattern, described above, was visually evoked, being caused by the presence of the target in the cell's receptive field. This seems unlikely since these neurons never discharged during spontaneous movements of the eyes made in the lit, visually rich laboratory where stationary targets were frequently present in the cell's large receptive field. Furthermore, TSNs when tested for visual responses showed only phasic discharge patterns. However, to definitely rule out this hypothesis, the following paradigm was used. A barrier of variable width was placed in front of the cat and food was randomly protruded either to the cat's left or right. In this 'cat and mouse' game, the aroused animal frequently looked to and fro, to each side of the barrier, in anticipation of the food's appearance. Fig. 2 illustrates the response of a TSN (located in the left SC) when food was first held to the left of the barrier (Fig. 2A) and then moved behind (Fig. 2B) without reappearing to the right. The animal, however, predicted the appearance of the target and oriented to the right (Fig. 2C). The neuron began discharging (Fig. 2D, E) soon after the target disappeared and continued to do so until the cat had oriented to the location of the imagined target. In one example (Fig. 2E) the cat took over 7 s before orienting to the right side of the barrier and the cell continued to discharge, albeit sporadically, during the entire period.

In addition to the sustained discharge characteristics reported here, phasic discharges could be evoked from a TSN when the animal rapidly oriented to a visual stimulus moving through the receptive field in the appropriate direction as described above^{3,13}. The visually evoked phasic bursts were also well correlated to the saccadic gaze shifts and accompanying bursts of EMG activity recorded from contralateral dorsal neck muscles. Most dorsal neck muscles have, in the head-fixed condition, a tonic level of EMG activity that is related to the position of the eye in the orbit²⁰. If the eye moves laterally to one side of the orbit,

then the neck muscles on the same side increase their tonic level of activity (see Fig. 1C). The sustained discharge pattern of a TSN in the head-fixed animal was observed when the cat's visual axis was directed away from the target towards the side ipsilateral to the cell. Thus, during such an ipsilateral gaze position, the TSN sustained discharges were of the wrong sign for activating contralateral neck muscles. Note, however, that the phasic TSN discharges that preceded a gaze shift to a moving visual target were of the correct sign and were well correlated to bursts of EMG activity in contralateral neck muscles.

The observation that a gaze position error signal was present in TSNs during visuomotor tasks but not when the animal looked spontaneously about the laboratory suggests that the two conditions use different output channels. Analogous findings in the monkey SC are cells that only discharge before visually triggered saccades^{11,12}.

The sustained discharge characteristics of TSNs in our particular experimental paradigm recall the 'quasi-visual' (QV) cells described in monkey SC by Mays and Sparks¹¹. A QV cell coded the vector error (magnitude and direction) between current and desired gaze positions and held this information in a 'spatial register' until the saccade to cancel the gaze error occurred. These authors postulated a use for this signal within the SC. TSNs, however, have no intracollicular axon collaterals⁴. Our results suggest, at least for our experimental paradigm, that one of the SC's output signals is gaze position error but a specific use for this signal in a TSN's highly branched axonal projection field⁴ remains unknown. Perhaps the sustained discharge acts to modulate the threshold of neurons within premotor circuits which will be called upon, imminently, to generate the signals that are responsible for driving a rapid gaze shift along the required vector.

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