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Research Note

Burst activity of identified tecto-reticulo-spinal neurons in the alert cat

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Summary. Activity of tecto-reticulo-spinal neurons (TRSN), identified electrophysiologically and/or by intra-axonal HRP injections, was studied in alert cats during presentation of moving visual stimuli. A majority of TRSNs showed complex visuomotor properties: directionally selective visual responses in the absence of motor counterparts of orienting, enhanced bursting when stimuli triggered saccades, and no activation for spontaneous saccades. Highest intraburst frequencies were observed during active orienting towards novel, "interesting" objects. The more vigorous bursts usually contained repetitive grouped discharges attaining instantaneous frequencies up to 700 imp/s but average firing rates remained in the range of 120–300 imp/s. Intra-axonal HRP injections confirmed terminations of TRSN collaterals in the premotor areas of the lower brain stem, including the abducens nucleus, but also disclosed differences in the details of collateralization between neurons showing different types of visuo-motor activity.

Key words: Visuo-motor behavior – Saccades – Tecto-reticulo-spinal neurons – Intracellular HRP – Repetitive firing – Burst neurons

Introduction

Studies in primates led to a general concept that the output projection neurons of the superior colliculus (SC) provide vectorial coding of impending saccades (Wurtz and Albano 1980; Sparks and Mays 1981). Keller (1979) performed a unique study which furnished direct evidence that SC neurons generating high frequency bursts (F max = 600–1100 Hz) with a rapid build-up of activity about 20 ms before saccades terminating in their movement fields do project to the pontine levels and probably establish the link between the SC and the "preoculomotor" circuits of the lower brain stem. In the cat, neurons with identified axonal projection have not been investigated. Reports based on extracellular recordings from randomly sampled neurons of the intermediate and deep SC layers indicate that "presaccadic" neurons of the cat have long and variable lead times, large and vaguely defined movement fields, and do not reach high discharge rates observed in monkeys. This discrepancy may reflect either the true species bound differences of the efferent function of the SC in primates, as compared to carnivores, or a lack of adequate behavioral paradigms in the cat to induce a higher level of the SC engagement in saccade generation, or, eventually, a lower probability of sampling from neurons with long distance projections in the available studies on the alert cats. To answer these questions, it is necessary to find out which type of correlations with motor and sensory events exists for different classes of collicular neurons. In the present study, we have combined electrophysiological and morphological techniques to identify tecto-reticular and tecto-reticulo-spinal neurons (TRSN) in the alert cats. These results have been presented earlier in a preliminary form (Grantyn and Berthoz 1983). We shall describe their discharge characteristics during visuo-motor reactions induced by a sudden appearance of moving visual targets.

Methods

The methods were similar to those described by Yoshida et al. (1982) and allowing for intracellular recording and HRP injections of axons in the fully alert cat with head fixed. Eye movements were recorded using the search coil technique. Electromyographic

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Offprint requests to: A. Grantyn (address see above) activity of mm. obliquus capitis anterior, longissimus capitis and splenius was monitored through chronically implanted flexible wire electrodes. Axons of TRSNs were impaled with capillary microelectrodes (3 M NaCl or 10% HRP in 0.5 M KCl, pH 7.6) in the region just rostral to the abducens nucleus. They were identified electrophysiologically by direct orthodromic responses (latency less 0.5 ms) to stimulation of the contralateral SC through chronically implanted needle microelectrodes (Fig. 1A and B). Projections to the spinal cord were verified by antidromic invasion from the anterior funiculus at C1 or C2 levels of the spinal cord.

For computer processing quasi-intracellular or intracellular TR(S)N activity was stored on analog tape together with horizontal and vertical eye position, bilateral neck EMG, and the position of visual target. As targets for visual stimulation and for eliciting orienting responses we used small objects (subtending 3–5°) bearing variable geometric patterns. These objects could be displaced by a mechanical device along any meridian of the visual field at a constant velocity of 50–250 deg/s. The maximal excursion of target movement was limited to 45°. To overcome habituation, informal stimuli (experimenter's hand, brushes, food) were also used to induce orienting. At the end of each experiment the locations of stimulating electrodes in the SC and in the spinal cord were verified basing on electrolytic lesions. Tissue blocks containing HRP-labeled axons were processed according to the method of Itoh et al. (1979).

Results

Activity during visuo-motor reactions

This communication is based on the observations of task related activity recorded from 23 TRSNs in 4 cats. A common feature was an absence of spontaneous discharge and of any significant periods of sustained firing during visuo-motor performance. Figure 1 illustrates the pattern of behavior, typical for a majority (n = 15) of the sample. Horizontal displacement of the visual target across the contralateral hemifield evoked bursts of activity as the target passed 5–15° eccentricity moving in centrifugal (but not in the opposite) direction (Fig. 1D). When the animal attempted to track the stimulus by saccades and, in some trials, also by head movements, as reflected in the unilateral activation of neck EMG (e.g. Fig. 1D1), bursts preceded saccades by 60–200 ms. However, this neuron responded to moving visual stimulus also in the absence of orienting saccades. Burst intensity, expressed as number of interspike intervals (N) in the frequency range above 50 imp/s (F min) varied from 4 to 10 in presaccadic bursts and from 0 to 3 in "purely visual" bursts. Presaccadic activity was associated with contraversive saccades only. They had variable amplitudes (2–12°) and directions which, in retinocentric coordinates, were distributed within a sector +70° (right/up) to -65° (right/down). Spontaneous saccades terminating in this movement field were not preceded by bursts, the physical presence of a visual stimulus being necessary for cell activation. The intensity of discharge was also influenced by factors related to attention towards novel stimuli and, hence, to the vigor of active orienting. Figure 1E shows a response to presentation of a new object (brush) which was introduced to the left of the vertical meridian and suddenly withdrawn to the right. Active following of the stimulus was manifested in a double saccade and an intended head movement (note EMG burst on the right side). TRSN burst preceding this motor sequence (Fig. 1G) was about twice as strong (N = 24 at F min $\geqq$ 50 Hz) as any of presaccadic bursts recorded during presentation of a conventional target.

Neurons whose behavior is qualitatively similar to that described above represent a group of TRSNs which can be called "visuo-motor". Their features can be summarized as follows: 1) Directionally selective responses to moving visual stimuli in the absence of eye movements or attempted head movements; 2) Enhanced discharges before saccades corresponding roughly to the preferred direction of visual response; 3) Absence of activation for spontaneous saccades with the same parameters; 4) Additional response enhancement in conjunction with active orienting towards attractive objects. While a majority of "visuo-motor" TRSNs fired mainly for horizontal target motion and, hence, for tracking saccades within 45° off-horizontal, about 27% (4/15) were related to orienting in oblique or vertical directions. Three out of 15 "visuo-motor" TRSNs lacked directional selectivity of visual responses and generated enhanced bursts before visually triggered saccades of any direction.

A second group of TRSNs (8/23) showed directionally selective visual responses but no saccade-related enhancement. They may be considered as a separate group of "visual" neurons, although the repertoire of behavioral tests may not have been adequate to disclose components of discharge clearly separable from visual responses. It should be mentioned that besides the two main types described above we encountered TRSNs which discharged single or double sporadic spikes but burst activity could be induced neither by sensory stimuli of different modalities, nor in relation to any observable motor events. The proportion of such "idle" TRSNs varied from 10 to 20% in different animals.

The intensity of burst activity varied considerably among individual "visuo-motor" and "visual" TRSNs and, for each neuron, as function of behavioral situation. Burst durations ranged from 30–1500 ms (50–400 ms for 80% of bursts). The weaker bursts contained 3–20 spikes with mean firing rate below 100 imp/s. In enhanced bursts the number of intervals

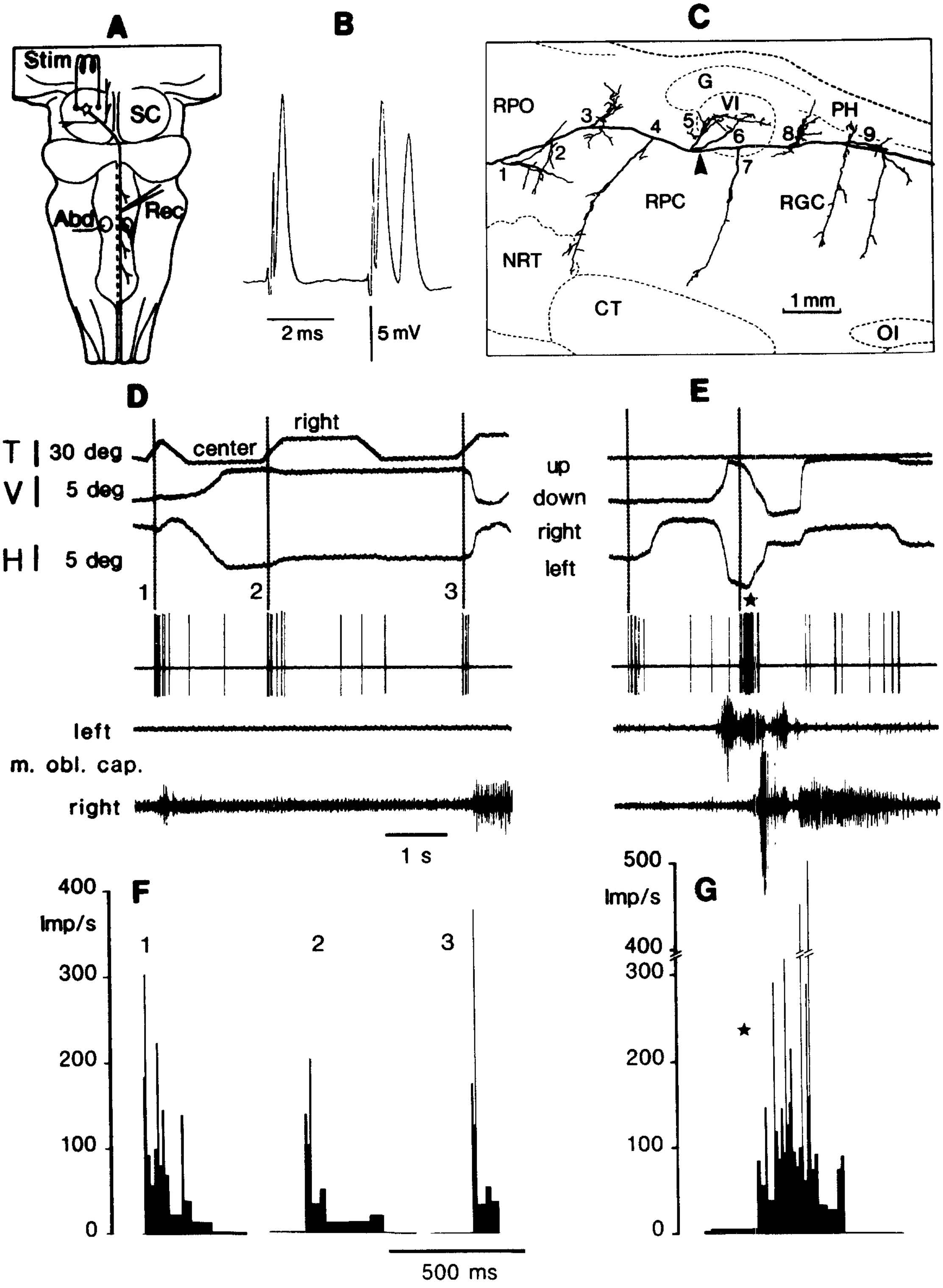

Fig. 1A–G. Morphology of ponto-bulbar collaterals and visuo-motor activity of an identified TRSN. **A** Dorsal view of brain stem illustrating locations of stimulating and recording electrodes. **B** Intracellularly recorded direct orthodromic responses to stimulation of contralateral SC. Note delayed, presumably, transsynaptic spike in response to second stimulus. **C** Reconstruction, in a parasagittal plane, of main axon and its collaterals in pontine and rostral bulbar tegmentum. Rostral is to left. Injection site indicated by arrowhead. Abbreviations: CT, trapezoid body; G, genu of the facial nerve; NRT, nucleus reticularis tegmenti pontis; OI, inferior olive; PH, nucleus prepositus hypoglossi; RGC, nucleus reticularis gigantocellularis; RPC, nucleus reticularis pontis caudalis; RPO, nucleus reticularis pontis oralis; VI, abducens nucleus. Injection site is 0.5 mm from the midline. Maximal lateral spread of colaterals is 1.8–2.1 mm. **D** Activity of same neuron as in **B**, **C** during horizontal displacement of visual target (trace T) recorded together with vertical (V) and horizontal (H) eye position and EMG of m. obliquus capitis anterior (two lower traces). Target was a striped disc subtending 5°. **E** Burst of same neuron during orienting to a novel object (brush) abruptly withdrawn from center to right. Same arrangement of records as in **D**. **F** Instantaneous frequency plots for bursts 1–3 of **D**. **G** Instantaneous frequency plot for burst marked by star in **E**

corresponding to F min ≧ 20 imp/s ranged from 4–50, with two neurons reaching 80 and 160. The mean intraburst frequencies were between 50 and 100 imp/s. The high frequency parts of these bursts, as delimited on the criterion F min ≧ 100 imp/s, contained 3–36 (exceptionally, up to 130) consecutive intervals, with a mean frequency of 120–300 imp/s. Bursts often contained grouped discharges, i.e. sequences of 2–5 spikes reaching instantaneous frequencies of 200–700 imp/s. This transition to regenerative firing mode (Calvin 1974; Grantyn et al. 1983) occurred when the mean intraburst frequency attained the levels above 40–50 imp/s.

Axonal branching in the ponto-bulbar tegmentum

Five intraaxonal HRP injections were of sufficient quality to follow the main axon from the site of injection near the abducens nucleus to the rostral tegmental decussation rostrally and to the bulbospinal junction caudally. All injected axons belonged thus to tecto-spinal neurons. Their diameters ranged from 6–8 μm. Full reconstruction of collaterals within 10–12 mm of axon length was possible for 4 neurons. Three of them were classified as "visuo-motor" on the basis of the behavioral tests performed before injection of HRP. The general pattern of their axonal ramifications in the ponto-bulbar tegmentum corresponded well to that established earlier in acute experiments (Grantyn and Grantyn 1982). An example is given in Fig. 1C: regularly spaced ventral collaterals ramify in the medial pontine and medullary reticular formation. Collateral no. 4 terminates in the caudal pole of the lateral division of the NRT. The dorsal collaterals (nos. 3, 5, 6, 8) are characterized by a more profuse branching and greater number of boutons per collateral. They terminate in the dorso-medial reticular formation anterior and posterior to the abducens nucleus, in the abducens nucleus itself and in the nucleus prepositus hypoglossi. One injected neuron classified as "visual" TRSN had a clear selectivity for vertical (downward) movement of visual stimuli. This neuron lacked collaterals terminating in the abducens or in the prepositus nuclei. Its second distinguishing feature was a profuse termination in the midline region of the caudal pons including the central division of NRT and the adjacent reticular formation.

Discussion

TRSN represent a morphologically homogenous class of projection neurons according to their somadendritic profiles, the course of the main axons, and the general plan of collateralization (Grantyn and Grantyn 1982). An important demonstration of the present study is that these neurons do differ with respect to their relationships to different aspects of visuo-motor behavior. At least three groups can be distinguished: "visuo-motor", "visual" and "idle". Further subdivisions could undoubtely be introduced basing on the differences of preferred directions and velocity tuning of visual responses, size and location of movement fields, and the degree of saccadic or attention-related enhancement.

The receptive properties of "visual" and "visuomotor" TRSNs are qualitatively similar and conform to the descriptions of unidentified deep SC neurons in paralysed (Straschill and Hoffmann 1969; Gordon 1973) and alert cats (Peck et al. 1980). The typical features are: poor responsiveness to stationary light flashes, directionally selective responses to moving stimuli and large receptive fields with a vaguely defined leading edge. Many TRSNs give stronger visual responses to attention-attracting three-dimensional objects, as compared to conventional stimuli.

"Visuo-motor" TRSNs resemble quite closely the "visual plus saccade" neurons of Peck et al. (1980). An important difference is, however, that TRSNs do not discharge for spontaneous saccades in light or in darkness even under the condition that these saccades have appropriate metrics. Qualitatively, "visuo-motor" TRSNs can be considered as a counterpart of "visually triggered eye movement cells" (VTEMC) described in the monkey by Mohler and Wurtz (1976). These cells discharge vigorously only before saccades to the physically present target but not before spontaneous saccades having same directions and amplitudes. Their visual responses are, as a rule, much weaker than presaccadic activation. Mohler and Wurtz (1976) proposed a convergence model of signal flow in the SC in which the role of output elements is ascribed to VTEMC. Our finding that about 2/3 of identified projection neurons of the cat SC share some properties with VTEMC renders support to the convergence model and suggests its applicability not only for the monkey but also for the cat.

It has been shown in acute experiments that TRSNs of the cat are able to generate high frequency spike trains when depolarized by intracellulaly injected currents (Grantyn et al. 1983). The present study shows that all TRSNs enter in the regenerative firing mode, in particular, during vigorous orienting towards novel stimuli. This, however, does not suffice to reach mean intraburst frequencies of presaccadic SC neurons of the monkey (Sparks et al. 1976). It appears that, in alert cats, TRSN firing is limited to the primary range (Grantyn et al. 1983).

The probability of extra-spike generation increases in the upper half of this range but repetition rate of grouped discharges remains low. As a result, instantaneous frequencies of 300–700 imp/s are well represented in strong bursts but the mean frequencies do not surpass 120–300 imp/s. It should be noted that maximal burst intensities observed in TRSNs are substantially higher than indicated by published records from unidentified neurons of the deeper SC layers (Straschil and Schick 1977; Harris 1980; Peck et al. 1980).

All TRSNs, with the exception of "idle" ones, generate bursts in response to visual stimuli in the absence of eye movements or other motor manifestations of orienting. HRP injections assure that this property is shared also by neurons establishing direct connections with the "preoculomotor" regions of the pontine and bulbar reticular formation, the sites of origin of reticulo-spinal projections, with the abducens nucleus and the spinal cord. Obviously, the synaptic efficacy of TRSNs in these regions is not sufficient to produce suprathreshold effects during "purely visual" activation. It may be supposed that only the stronger bursts, when TRSNs enter in the regenerative firing mode, contribute significantly to the driving of target neurons belonging to the input stages of the saccadic generator (Hepp and Henn 1983). Studies in progress indicate that selection of bursts according to their intensity is necessary to reveal closer correlations between the discharges of "visuo-motor" TRSNs and the parameters of saccades. It is important to note that some "visual" TRSNs generate bursts which are not followed by motor events but whose intensity is as high as that of presaccadic bursts observed in "visuo-motor" neurons. This fact suggests that the action of TRSNs may be gated at pontine levels or, alternatively, that "visual" TRSNs have different topography of ponto-bulbar collaterals which renders less efficient their coupling to premotor circuits.

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