

# Control of Orienting Gaze Shifts by the Tectoreticulospinal System in the Head-Free Cat. II. Sustained Discharges During Motor Preparation and Fixation

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## SUMMARY AND CONCLUSIONS

1. We recorded from electrophysiologically identified output neurons of the superior colliculus (SC)—tectoreticular and tectoreticulospinal neurons [together called TR(S)Ns]—in the alert cat with head either unrestrained or immobilized. A cat actively exploring its visual surrounds typically makes a series of coordinated eye-head orienting movements that rapidly shift the visual axis from one point to another. These single-step shifts in gaze position (gaze = eye-in-space = eye-in-head + head-in-space) are separated by periods in which the visual axis remains stationary with respect to surrounding space.

2. Eighty-seven percent (86/99) of the TR(S)Ns studied during periods when the visual axis was stationary presented a sustained discharge, the intensity of which depended on the magnitude and direction of the vector drawn between current gaze position and the gaze position required to fixate a target of interest (gaze position error or GPE). The maximum sustained discharge recorded from each TR(S)N corresponded to a specific GPE vector and was correlated with the cell's position on the SC's retinotopically coded motor map.

3. The 86 TR(S)Ns could be divided into two classes. "Fixation TR(S)Ns" [fTR(S)Ns,  $n = 12$ ] discharged maximally when the animal *attentively fixated* a target of interest, (i.e. GPE = 0°). These neurons were located in the rostral SC and had visual receptive fields that included a representation of the area centralis. "Orientation TR(S)Ns" [oTR(S)Ns,  $n = 62$ ] had visual receptive fields that excluded the area centralis and discharged for nonzero GPEs. The oTR(S)Ns were recorded more caudally on the SC's map.

4. For a given value of GPE, an ensemble of TR(S)Ns was active. When the cat changed its gaze position relative to a fixed target of interest, the zone of sustained activity shifted to a new collicular site. Thus, to maintain the maximum sustained discharge of a TR(S)N when target position was changed relative to the fixed body, it was necessary that gaze move to a new position that reestablished the preferred GPE.

5. The areal extent of GPEs for which a TR(S)N discharged defined a gaze position error field (GPEF) that was approximately coaligned with the cell's visual receptive field. The maximum sustained discharge occurred when GPE corresponded approximately to the center of the cell's GPEF.

6. The diameter of a TR(S)N's GPEF was related to the magnitude of that cell's optimal GPE. fTR(S)Ns had the smallest GPEFs, ~15–20°; GPEF diameter was larger for oTR(S)Ns. When imaged onto the retinotopically coded map of the colliculus, all GPEFs had an approximately constant diameter. These observations imply that, for any GPE including 0°, a relatively large but somewhat constant fraction of collicular tissue was being activated.

7. We interpreted the sustained discharge of oTR(S)Ns as a preparatory activity for an eventual gaze shift that they could trigger with a burst of discharge (described in the following paper). The occurrence of the sustained discharge was related to the animal's "set"; it was not necessary for the target of interest to be visible. In situations when the animal anticipated appearance of a food target, the expected target zone acquired significance, and sustained discharge was observed when gaze position was at the cell's preferred vector from that zone. This discharge existed even when ambient lighting was extinguished.

8. We postulate the existence of an attentional map in the collicular layer containing TR(S)Ns, in which mechanisms favoring fixation oppose those driving orientation such that 1) the sustained activity of cells lying outside the area centralis representation [i.e., oTR(S)Ns] reflects the animal's preparation and/or intent to eventually orient; and 2) the activation of cells lying within the area centralis representation [i.e., fTR(S)Ns] reflects the intent to maintain fixation.

## INTRODUCTION

Orienting movements, which direct the visual axis to the source of either a sensory stimulus or internally generated goal, are usually accomplished by the coordinated motion of the eyes and head (Bizzi 1981; Guitton 1988; Guitton et al. 1990). These movements produce a single-step, rapid shift in gaze position (gaze = eye-relative-to-space = eye-relative-to-head + head-relative-to-space) that orients the visual axis onto the target of interest. Whether they are performed with the animal's head restrained (head fixed) or unrestrained (head free), orienting gaze shifts are separated by periods in which the visual axis remains stationary with respect to surrounding space. Thus there are two basic behavioral states: 1) the target is attentively fixated or 2) a new orienting gaze shift is prepared and triggered.

A distinction between attentive fixation and motor preparation has been shown at the level of cortical neurons that show discharges specific to these behaviors. Some neurons in the frontal and parietal lobes discharge tonically when a monkey fixates a target (Bon and Luchetti 1990; Bruce and Goldberg 1985; Lynch et al. 1977; Mountcastle et al. 1975; Sakata et al. 1980; Segraves and Goldberg 1987). Other neurons in these structures discharge tonically, not when the animal is fixating a target of interest but rather during the period that precedes a gaze shift to a new target of interest that has appeared in peripheral vision (Bruce and Gold-

berg 1985; Funahashi et al. 1990; Gnadt and Andersen 1988; Segraves and Goldberg 1987).

In this paper we consider the role of the superior colliculus (SC) in controlling fixation and motor preparation. Fixation-related discharges have been recorded from collicular neurons in the SC of monkey (Goldberg and Wurtz 1971; Munoz et al. 1990; Sparks and Mays 1980) and cat (Peck 1989). Other SC cells, some known as quasivisual (QV) cells, discharge tonically whenever their location on the SC's motor map is the potential site for generating a saccadic eye movement (Mays and Sparks 1980; Waitzman et al. 1987). In the words of Mays and Sparks (1980): "The activity of these neurons appears to reflect eye position error (the differences between actual and desired eye positions) and to hold this information in spatial register until a saccade occurs or is cancelled." The discharge of these neurons, in our terminology, constitutes motor preparation.

We have recorded in the alert behaving cat the neural signals carried by a specific subpopulation of collicular neurons: electrophysiologically identified tectoreticular and tectoreticulospinal neurons, together called tectoreticulo(spinal) neurons or TR(S)Ns. These neurons constitute the major efferent projection from the SC to the contralateral brain stem and spinal cord premotor circuitry (Grantyn and Grantyn 1982; Moschovakis and Karabelas 1985). In the previous paper (Guitton and Munoz 1991) we considered the sensory responses of TR(S)Ns, and in the next paper (Munoz et al. 1991a) we show how these cells are involved in driving gaze shifts. Here we describe characteristics of TR(S)N discharges recorded during intermediate steps of neural processing: fixation and motor preparation. We devised a variety of behavioral tasks, performed by the cat in both head-fixed and head-free conditions, to study these discharges in isolation of sensory or motor responses.

TR(S)Ns located within the collicular map's area centralis representation discharged tonically whenever the animal attentively fixated a target of interest. By comparison, TR(S)Ns situated off the area centralis representation presented a tonic discharge with behaviorally related properties that are similar to monkey QV cells. Thus a preamble of activity, emanating from a specific collicular locus, could influence lower premotor circuits by promoting either fixation or orientation. Preliminary reports of these data have appeared elsewhere (Munoz et al. 1984; Munoz and Guitton 1985, 1988, 1989).

## METHODS

### General

General methods regarding details of animal preparation and recording of gaze, eye, head, and target positions are the same as those described previously (Guitton et al. 1984, 1990). Regarding the single-unit recording of TR(S)Ns, the first paper in this series (Guitton and Munoz 1991) describes the identification, recording, and analysis methods.

### Behavioral paradigms

Behavioral paradigms were designed to obtain rapidly and reliably a large number of coordinated eye-head displacements having a wide range of amplitudes and directions that the experimenter could control with minimal training of an alert animal behaving as naturally as possible. To conduct an experiment, we

placed a cat first in a loosely fitting cloth bag and then onto its belly in a box that gently restrained the body but permitted unrestricted horizontal head movements of up to 90° to the left or right. Upward head movements were unrestricted, whereas downward head movements were limited so that the "horizontal" stereotaxic plane could go no further than 60° below the earth's horizontal.

When there was no obvious target to solicit its attention, we observed that the cat usually assumed naturally a head posture with the horizontal stereotaxic plane roughly 10° below the earth's horizontal. For the purpose of defining target and barrier positions with respect to the cat's *body*, the "center line" is defined with the cat's head aligned with the body and is a line formed by the intersection of two orthogonal planes: one parallel to the earth's horizontal and passing through the center of each of the cat's pupils (when the head is in the natural position, with no angular torsion), the other vertical and passing through the center of the cat's body.

The behavioral paradigms used to study TR(S)N discharges were described previously (Guitton et al. 1990). A schematic representation of these different behavioral situations, as they apply to a hypothetical TR(S)N, are shown in Fig. 1. First, when the cat was looking straight ahead, the visual receptive field of the cell was located approximately by moving the food target throughout the visual field and noting areas of maximum discharge (see Guitton and Munoz 1991). Then, an opaque barrier was placed 40 cm in front of the animal. As shown in Fig. 1, barrier width and orientation were chosen so that one edge of the barrier bisected a cell's visual receptive field (RF, denoted by a dashed circle) when the cat looked to the opposite side. When the cat looked to the right side of the barrier (fixation point, FP; denoted by  $\times$ ), the left side was in the neuron's visual receptive field (Fig. 1A). When the visual axis was directed to the left side of the barrier, the cell's visual receptive field was displaced far to the left of the barrier (Fig. 1B). A food target, represented by the filled circle, was used to direct the animal's visual axis and attention to specific spatial loci, thereby creating several different behavioral situations. The food target could be absent from the experiment (Fig. 1, A and B), visible at the right (Fig. 1, C and D) or left (Fig. 1, E and F) edges of the barrier, or hidden behind it (Fig. 1, G and H). In the latter case the target is denoted as an empty circle. When the cat fixated the right side of the barrier (Fig. 1, A, C, E, and G), the left side was in the cell's visual receptive field and the position of the food target determined the behavioral situation. Placement of the food target on the right side of the barrier (Fig. 1C), where the animal's visual axis was directed, could result in the behavioral act of attentive fixation. If the target was located on the left side and the visual axis was directed toward the right side (Fig. 1E), then the target was in the cell's visual receptive field and an obvious target for a volitional orienting movement (visible-target condition). If the target was hidden behind the barrier (Fig. 1, G and H), then the trained animal could anticipate its reappearance on either side (hidden-target condition). When the target was absent from the experiment (Fig. 1, A and B), then the animal was left to make spontaneous movements (no-target condition).

In subsequent figures, schematics of the different behavioral situations will be presented below the discharge records. An uppercase letter occurring below each portion of the unit record will refer the reader to the appropriate behavioral condition.

In some experiments, ambient light was provided exclusively by a stroboscope flashing at 100 Hz. During some of the behavioral testing the stroboscope was turned off unexpectedly for 1–5 s to remove all visual input to the animal. (We used a stroboscope because the time constant of the light's decay is very short.) In the short period of darkness, the animal was not able to see the food target or to dark adapt and, therefore, oriented in complete darkness (Pélissier et al. 1989).

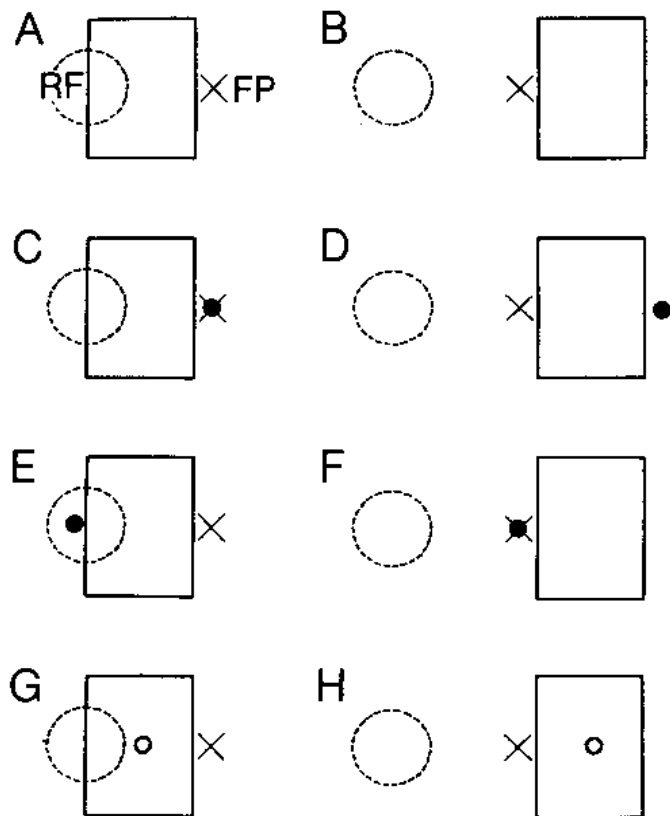


FIG. 1. Schematics illustrating the different behavioral situations used when studying a TR(S)N. An opaque barrier (represented by rectangle) was placed before the cat. Barrier width and orientation were chosen such that when the animal looked to one edge (fixation point denoted by X), the other edge was in the neuron's visual receptive field (dashed circle). A food target, represented by the small circle (filled, target visible; empty, target hidden behind the barrier), was used to direct the animal's visual axis and attention to different loci, thereby creating several different behavioral situations. A, C, E, and G: cat looks to right of barrier. B, D, F, and H: cat looks to left of barrier. A and B: No food target is present. C and D: Food target on right. E and F: Food target on left. G and H: Food target hidden behind barrier. See text for additional details.

## RESULTS

In this paper we describe the characteristics of a sustained discharge pattern that was recorded from cat TR(S)Ns during periods when an animal's visual axis was *immobile* and located at various positions in relation to a target of interest. The location on the SC's retinotopically coded motor map of the ensemble of TR(S)Ns that was tonically active at any one time depended on the magnitude and direction of the vector between the target of interest and the visual axis. We defined this vector quantity as gaze position error (GPE; Munoz and Guitton 1985). Eighty-seven percent (86/99) of the TR(S)Ns discharged with a sustained rate that could be quantitatively linked to GPE. The optimal GPE vector for each cell was defined as the GPE that yielded the maximum sustained discharge. The 86 cells were divided into two classes. The maximum sustained discharge for fixation TR(S)Ns [fTR(S)Ns,  $n = 12$ ] occurred when the animal attentively fixated a target of interest. These cells were located in the area centralis representation of the rostral SC and had visual receptive fields that included a representation of the area centralis. Orientation TR(S)Ns [oTR(S)Ns,  $n = 74$ ] were activated with a maximum sus-

tained discharge when the animal's visual axis was located at some vector error from a target of interest. These latter neurons had visual receptive fields lacking a central representation and, furthermore, they were at a reduced level of excitability whenever the animal attentively fixated (Guitton and Munoz 1991).

### *oTR(S)N discharges related to eccentric GPEs*

The data illustrated in this section were collected over a 6-day period of recording from an oTR(S)N, cell M8. Chronically implanted microwires were used to record from the same TR(S)N for several days (Guitton and Munoz 1991; Munoz 1988). This neuron was located in the caudolateral right SC and had its visual receptive field situated in the lower left visual field. After a number of exploratory trials, the barrier chosen to generate gaze shifts of optimal amplitude and direction for this cell had a width of  $\sim 45^\circ$  of visual angle and was oriented at  $\sim 45^\circ$  to the vertical meridian (Fig. 2, C-F). Therefore, when the animal looked to the upper right edge of the barrier (right and up, RU), the lower left edge (left and down, LD) fell within the visual receptive field of cell M8.

SUSTAINED DISCHARGES RELATED TO THE PRESENCE OF A VISIBLE TARGET IN THE CELL'S VISUAL RECEPTIVE FIELD. Figure 2 illustrates the activity of cell M8 when the food target was visible on one side or the other of the obliquely inclined barrier. The experiment was performed in both the head-free (Fig. 2A) and head-fixed (Fig. 2B) conditions.

Figure 2A illustrates the typical discharge pattern of this oTR(S)N as the cat performed this simple behavioral task in the head-free condition. Initially, the cat fixated the target located RU. Then, while the target remained RU, the cat looked, spontaneously, first LD and then back to the target at RU. Cell M8 did not fire a single action potential while the target was held RU, even though the cell's visual receptive field was traversed by the barrier's edge (condition C). The target was then moved LD and, after it reappeared from behind the barrier, the cat oriented LD to refixate the food (1st transition in Fig. 2A from conditions E to F).

During the time in Fig. 2A when the target was LD and the cat was still looking RU (see Fig. 2E), the target was within the visual receptive field of cell M8, and it discharged a train of action potentials. When the cat oriented LD to refixate the food target (see Fig. 2F), the cell ceased firing and remained silent for the entire fixation period. After  $\sim 4$  s, the cat looked spontaneously RU, again placing the target back into the cell's visual receptive field. Cell M8 immediately resumed firing in a sustained manner. Firing continued while the animal looked RU and ceased during the gaze shift that reoriented the animal's visual axis LD. This pattern of neural activity continued as the cat looked back and forth from RU to LD. The sustained discharge pattern of cell M8 was observed whenever the gaze axis was directed RU and the target was LD in the neuron's visual receptive field.

When the animal's head was held fixed straight ahead (Fig. 2B), the width of the barrier spanned the approximate limits of the cat's oculomotor range ( $\pm 25^\circ$  from center) so that the visual axis was seldom directed all the way to either

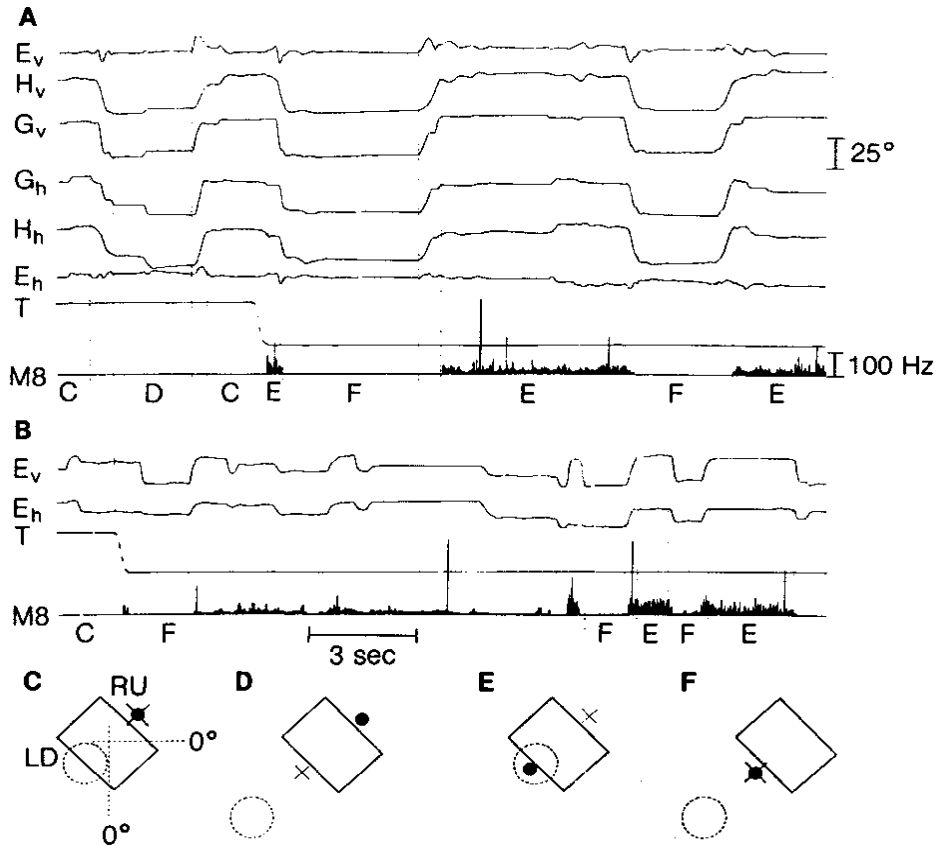


FIG. 2. Activity recorded from *cell M8*, an oTR(S)N located in the caudolateral right SC, when the food target was visible on one side of the barrier in head-free (*A*) and head-fixed (*B*) conditions. Top to bottom: vertical eye ( $E_v$ ), head ( $H_v$ ), and gaze ( $G_v$ ) position traces; horizontal gaze ( $G_h$ ), head ( $H_h$ ), and eye ( $E_h$ ) position traces; target ( $T$ ) position trace; and instantaneous firing frequency of the neuron ( $M8$ ). Upward deflections in vertical and horizontal position traces correspond to upward and rightward movements, respectively. Upward deflections in target trace corresponds to right-up. Vertical dashed lines in *A* and *B* delineate different behavioral situations, identified by letters C-F underneath the firing frequency trace, that are schematically represented in C-F. C: intersection of  $0^\circ$  horizontal and vertical dashed lines marks central gaze position with respect to the animal's body (see METHODS). Right-up (RU) and left-down (LD) edges of the barrier were situated equidistant from this central position. Visual receptive field of *cell M8* (dashed circle) was located to the lower left of the point of fixation (marked by  $\times$ ). Cat fixates the target situated in the middle of the RU edge. Cell's visual receptive field is bisected by the LD edge. D: cat looks spontaneously LD with the target RU. E: cat looks RU, but the target is LD, in the cell's visual receptive field. F: cat fixates the target LD.

side of the barrier. Saccades were still made from RU to LD and back, but the amplitude of these movements never equaled barrier width. Nonetheless, a similar firing pattern was observed. At the extreme left of Fig. 2*B*, the target was located RU and *cell M8* was silent. The target was then moved LD, and whenever the animal looked RU, the target was positioned within the cell's visual receptive field, thereby initiating the sustained discharge from *cell M8*. When the cat looked far enough LD, the target was removed from the neuron's large visual receptive field and the sustained discharge ceased.

The relationship between the intensity of the sustained discharge of *cell M8* and different gaze positions relative to the target is shown in Fig. 3. Figure 3*A* shows the neuron's response, in the head-free condition, when the barrier (having the same orientation as in Fig. 2, C-F) was placed in two different spatial locations relative to the cat's body. In these examples the food target was visible either 1)  $30^\circ$  left and  $10^\circ$  below center position (empty circles on top of dashed vertical lines) or 2) on the vertical meridian and  $10^\circ$  below center (filled circles on top of solid lines). The animal moved its gaze axis to many different positions relative to each target position. The plots were composed of 148 fixations when the target was positioned left of center and 156 fixations when the target was located on the vertical meridian. The data were grouped into bins  $10^\circ$  horizontal by  $10^\circ$  vertical that permitted some smoothing of the data. These bins were not too large in view of the comparatively much larger range of gaze positions associated with the cell's response.

The data in Fig. 3*A* show that the response of this TR(S)N could be described, for each target position, by a bell-shaped curve. Furthermore, when target position was shifted rightward, to the vertical meridian, the location of gaze positions required to evoke the maximum sustained discharge from *cell M8* was also shifted rightward by an equivalent angle. This is more clearly shown in Fig. 3*B*, which represents a vertical cross section through Fig. 3*A* parallel to the horizontal gaze position axis and through the  $15^\circ$  vertical gaze position. A third curve (hollow squares), obtained when the target was located  $15^\circ$  left and  $10^\circ$  below center, is added to Fig. 3*B*. Three discrete peaks of activity were present and centered at different horizontal gaze positions. The curves in Fig. 3*B* are replotted in Fig. 3*C* using horizontal GPE rather than absolute gaze position. The three curves are clearly more superimposed, which would be expected if the sustained discharge was due to the target exciting the neuron's receptive field and if there was no significant modulation of the neural response with absolute spatial location of the target.

A complete, two-dimensional description of the relationship between the intensity of the sustained discharge and the position of the visual axis relative to the target was obtained for *cell M8* by pooling together data obtained during a 6-day period from several different combinations of barrier width and orientation (Fig. 4). GPE is expressed as horizontal and vertical GPE angles. Plots were generated from 698 fixations in the head-free condition (Fig. 4*A*) and 309 fixations in the head-fixed condition (Fig. 4*B*). The point at  $0^\circ$  GPE corresponds to fixation of the target.

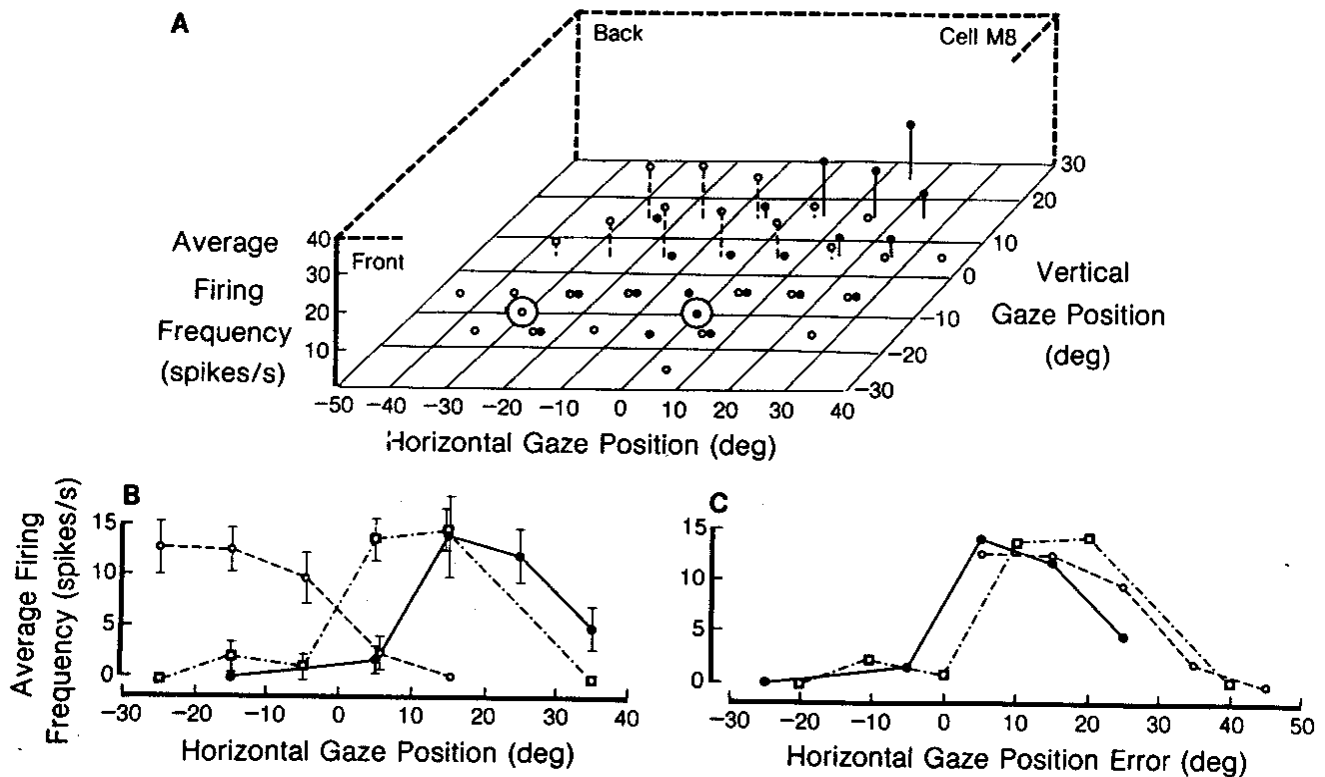


FIG. 3. Lack of influence of spatial location of the target on the sustained discharges of an oTR(S)N, cell M8, recorded in the head-free condition. *A*: plot of absolute gaze position vs. average firing frequency when the target was located in 2 different positions relative to the cat's body. One target was 30° left and 10° below center position, as shown by large circle enclosing small empty circle. Data points corresponding to this target position are empty circles on top of dashed lines. Another target position was on the vertical meridian, 10° below center (filled circles, solid lines). Each data point placed in the middle of a square on the grid of Fig. 3*A* represents the average firing frequency (total number of spikes/duration of fixation) from all fixations within that square area of space (measuring 10° horizontal by 10° vertical). *B*: horizontal section through 15° vertical gaze position in *A*. Solid line through filled circles, and dashed line through empty circles, corresponds to similarly identified data in *A*. Data represented by squares and dot-dash line were obtained using an intermediate barrier position with target held 15° left, 10° below center position. Data are represented by mean  $\pm$  SE. *C*: 3 distinct curves coalesce when data in *B* are replotted using horizontal gaze position error as the abscissae.

By analogy with the concept of receptive field, the plots of Fig. 4, which show the extent of GPEs over which a cell is active, are called gaze position error fields (GPEFs). There was a good correspondence between the head-free (Fig. 4*A*) and head-fixed (Fig. 4*B*) GPEFs for cell M8. This oTR(S)N was activated in both conditions when gaze was directed from  $\sim 5^\circ$  left to  $55^\circ$  right and  $>5^\circ$  above the position of the food target. Note the large range of GPEs over which this TR(S)N was active: over  $60^\circ$  in diameter in the head-free condition. Because of the limits of ocular motility, it was not possible to plot the GPEF over a similar range when the head was fixed.

The relationship between the intensity of sustained discharges and either absolute gaze position or GPE was studied in 40 oTR(S)Ns: 18 cells were tested head free and head fixed, 9 head free only, and 13 head fixed only. GPEFs analogous to that in Fig. 4 were generated for all cells: head-free and head-fixed fields were similar, and no effect of absolute gaze position was found (see below).

**SUSTAINED DISCHARGES RELATED TO THE PRESENCE OF A HIDDEN TARGET.** The GPEF of an oTR(S)N appeared to be coaligned with the cell's visual receptive field, but the sustained discharge was not simply a visual response. Two sim-

ple observations suggest this. First, there was no sustained activity when the cat looked spontaneously about the lit laboratory. Second, the visual responses of most oTR(S)Ns were phasic, not tonic, in nature (Guitton and Munoz 1991). To definitely rule out the hypothesis that the sustained discharge is a pure sensory (i.e., visual) response, we modified the behavioral paradigm used in Fig. 2 so that the food target, initially visible to one side of the barrier, was hidden behind the barrier without reappearing on the other side (see Fig. 1, *G* and *H*). In this situation, the trained cat began looking repeatedly from one side of the barrier to the other, anticipating target reappearance.

Fifty-two oTR(S)Ns were tested in this "hidden target" condition. Forty-nine presented sustained discharges when the food target was hidden behind a barrier having the appropriate width and orientation (Fig. 5, *C-E*). The food target was initially visible RU and the animal fixated it (Fig. 5*C*). The target was then hidden behind the barrier and the cat looked either RU (Fig. 5*D*) or LD (Fig. 5*E*) anticipating its reappearance. When the cat looked RU, the LD edge of the barrier was in the cell's visual receptive field (Fig. 5, *C* and *D*). In the head-free example (Fig. 5*A*), the cat was initially fixating the target RU. It is important here to note that cell M8 was silent, even though the LD edge of the

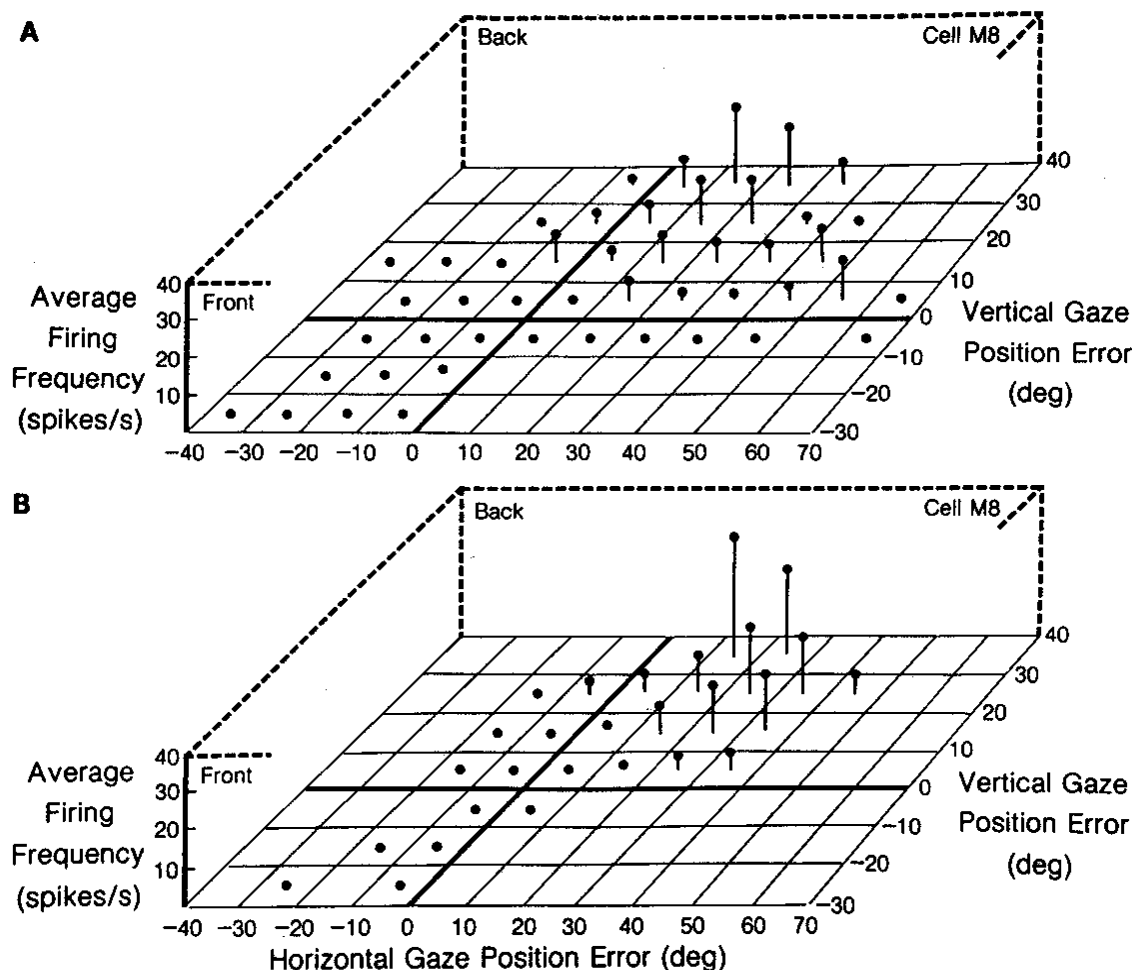


FIG. 4. Gaze position error fields (GPEFs) of oTR(S)N, cell M8, obtained when the target was visible in head-free (A) and head-fixed (B) conditions. Intersection of thick lines marks 0° gaze position error (i.e., fixation of the target). Data were obtained by measuring the cell's average firing frequency at different horizontal and vertical positions of the visual axis relative to the target. For example, a +20° horizontal gaze position error occurs when visual axis is 20° to right of target. Note that cell M8 was maximally activated when visual axis was directed to the right and above the food target.

barrier was in its visual receptive field. The target was then hidden behind the barrier, and shortly thereafter the cat looked LD. The cell was briefly activated, discharging just after the target disappeared but before the gaze shift LD. The cell remained silent while the cat looked LD (condition E). After ~4 s, the cat looked back RU, placing the LD edge in the cell's visual receptive field. Cell M8 now assumed a sustained discharge pattern, which continued until the cat looked back LD. Only in this condition (D) was the cell active. The same pattern of activity continued for the duration of the record. A similar discharge pattern was also recorded in this behavioral situation from cell M8 in the head-fixed condition (Fig. 5B).

GPEFs were also constructed for oTR(S)N responses using this hidden target situation. When the target was behind the barrier, the animal could in principle regard any point around the periphery of the barrier as a potential site for the target to reappear. However, because the cat had been run through many trials with the food disappearing from one particular point on one edge and reappearing at another fixed point on the opposite edge, it knew where the target could be expected to reappear. Therefore, two "imagined" target positions were possible with two zones of sustained

activity present, one in each SC. The sustained discharge pattern recorded from an oTR(S)N was presumed to be related to the vector error between the visual axis and whichever of the two imagined targets lay within the cell's visual receptive field.

The head-free and head-fixed GPEFs of cell M8, in this hidden target condition, were constructed using 237 and 168 fixation values, respectively (Fig. 5, F and G). The similarity between the plots of the head-fixed and head-free conditions implies that it is the position of the visual axis relative to the target, not the position of the head relative to the target nor the position of the eye in the head, that is the critical variable that determines the intensity of cell discharge. Note also that the boundaries and points of maximum discharge, obtained when the target was hidden behind the barrier, are about coextensive with those obtained in the visible target condition (see Fig. 4).

SUSTAINED DISCHARGES RELATED TO BEHAVIORAL CONTEXT. Fixation of the food target (Fig. 5C) drastically reduced oTR(S)N responsiveness and excitability (Guitton and Munoz 1991). Cell M8 never discharged action potentials when the cat fixated the food RU, even though the LD edge

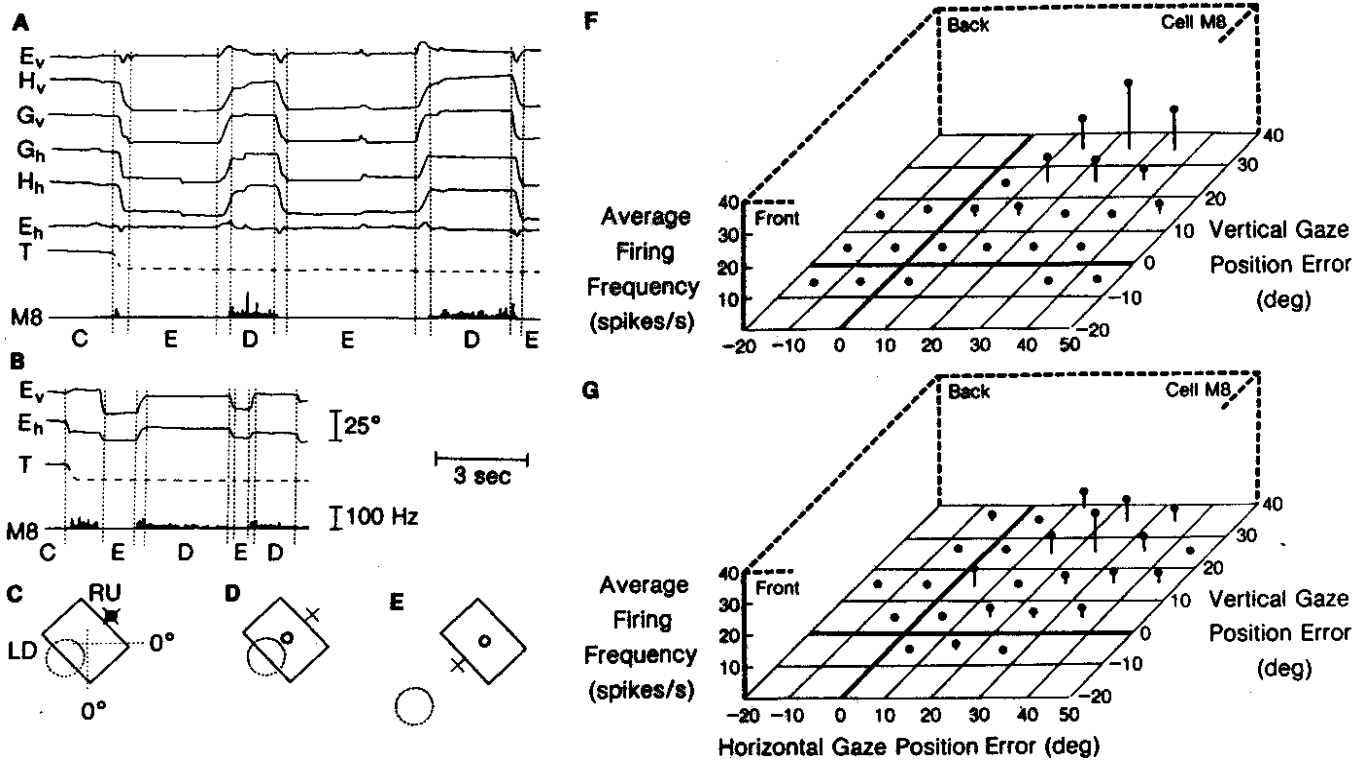


FIG. 5. Activity of oTR(S)N, cell M8, recorded when the food target was hidden behind the barrier in head-free (A) and head-fixed (B) conditions. C-E: schematics illustrating the different behavioral situations. F and G: gaze position error fields of cell M8 obtained when the target was hidden behind the barrier in head-free and head-fixed conditions, respectively. See legends to Figs. 1-4 for additional explanations.

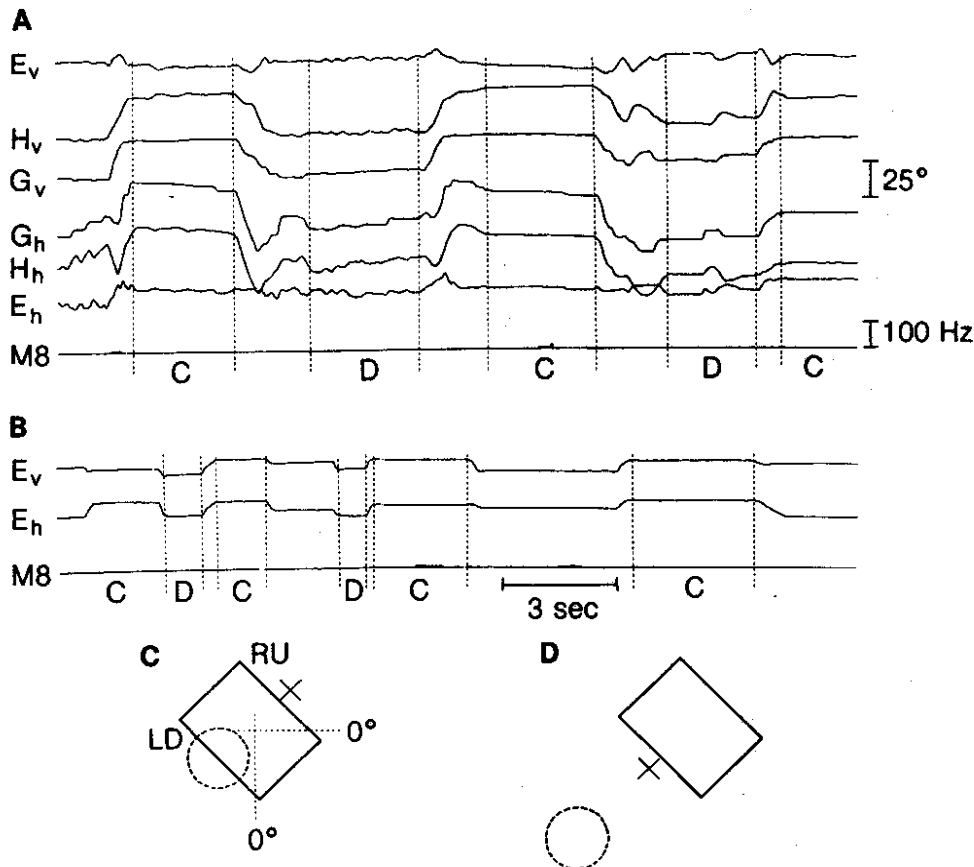


FIG. 6. Lack of activity of oTR(S)N, cell M8, when the food target was absent from the experiment in head-free (A) and head-fixed (B) conditions. C and D: schematics illustrating behavioral situations. See legends to Figs. 1 and 2 for further explanations.

was in its visual receptive field. In Fig. 5D, the food target was hidden behind the barrier and, again, only the LD edge was present in the cell's visual receptive field. However, the cell was tonically active, in contrast with the response relating to Fig. 5C. The differences between the behavioral conditions shown in Fig. 5, C and D, are that in the latter the animal was not fixating the food and furthermore, by virtue of the "cat and mouse" nature of the experimental paradigm, was anticipating reappearance of the target LD when it looked RU. The importance of fixation-elimination versus anticipation for the establishment of the sustained discharge was provided by the following experiments. The same oblique barrier was placed in front of the animal, but the food target was not presented to the cat and the animal was left to look spontaneously about the laboratory for a period of several minutes. Even though the cat frequently looked to and fro from one side of the barrier to the other and the LD edge of the barrier was in the visual receptive field of *cell M8*, the cell did not discharge in this no-target situation in either the head-free (Fig. 6A) or the head-fixed (Fig. 6B) conditions. Thus this cell (like most cells) presented the sustained discharge only when the target either was in its receptive field (Fig. 2E) or was expected to appear in the visual receptive field (Fig. 5D). A minority of TR(S)Ns (13/29) recorded in the no-target condition were sporadically active. This activity was always less than that observed in either the hidden- or visible-target conditions.

To definitely rule out visual inputs as uniquely responsible for generating oTR(S)N sustained discharges, we devised the following behavioral task for one cat. In this experiment, ambient illumination was provided by a stroboscope (see METHODS) that could be turned off unexpectedly during a trial period of 5 s (Fig. 7).

Figure 7A illustrates the responses obtained from an oTR(S)N (*cell Q62*) while the food target was protruded, as shown in Fig. 2, E and F, from the lower left edge of an oblique barrier that was 70° in width and oriented as in that figure. The stroboscope was turned off unexpectedly for ~5 s in the middle of the trial (the time between the 2 vertical dashed lines). *Q62*, like *cell M8*, had a visual receptive field located to the left and below the point of fixation. Note that *cell Q62* was active when the visual axis was directed RU. This pattern of activity did not change when the stroboscope was turned off. *Cell Q62* still discharged when gaze was directed RU. GPEFs were plotted for both the light and dark behavioral conditions. Note that the range of GPEs that produced a sustained discharge did not change between darkness and light. This was true of all 12 oTR(S)Ns obtained from this cat and tested in this paradigm.

COMPARISON OF oTR(S)N SUSTAINED DISCHARGES. We calculated the average firing frequencies of 16 oTR(S)Ns, obtained from seven cats, when cats assumed the optimal GPE for each cell in different behavioral situations (Table 1). The values of optimal GPE of these cells ranged from 10

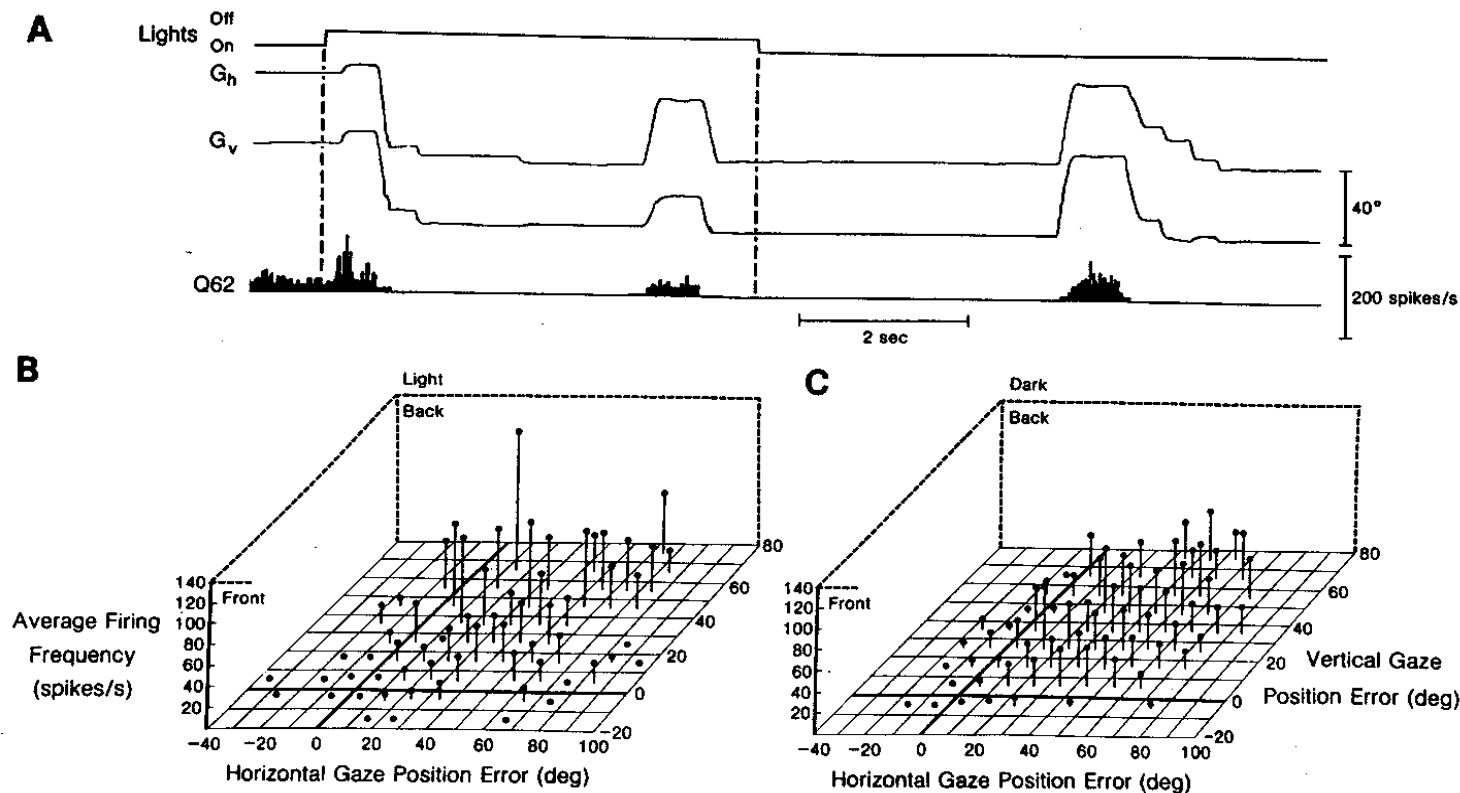


FIG. 7. Sustained discharge can be present even when animal is in total darkness. oTR(S)N, *cell Q62*, represented here had a gaze position error field similar to that of *cell M8*; consequently, barrier was oriented as in Fig. 2, C-F. In these tests, with lights on, the food target was visible left and down. A: *cell Q62* was active, in light and dark, whenever the head-free cat's visual axis was right and up, because then the visible or imagined target was in the cell's GPEF. Top trace and associated vertical dashed lines indicate period when cat was in either the normally lighted laboratory or in total darkness. B and C: gaze position error fields for light and dark conditions. See legends to Figs. 2 and 4 for additional explanations.



TABLE 1. Average peak sustained firing frequency of oTR(S)Ns

Cell	Optimal GPE, deg	Head-Free or Head-Fixed	Target Visible	Target Hidden	Significance
<i>E4.030</i>	30	Free Fixed	49 ± 21 (4) 39 ± 11 (9)		
<i>C9</i>	30	Free	75 ± 10 (4)	44 ± 13 (6)	VIS > HID
<i>T1.NO3</i>	10	Fixed	49 ± 20 (13)		
<i>F3.A28</i>	15	Free Fixed	83 ± 27 (4) 81 ± 24 (4)	67 ± 39 (10) 43 ± 19 (7)	NS VIS > HID
<i>F2.MO1</i>	14	Fixed	34 ± 11 (3)		
<i>F3.MO1</i>	20	Free Fixed	47 ± 15 (9)* 27 ± 9 (20)	27 ± 14 (8) 32 ± 5 (5)	VIS > HID NS
<i>M7</i>	28	Free Fixed	41 ± 18 (6) 33 ± 10 (9)	21 ± 17 (8) 15 ± 7 (9)	VIS > HID VIS > HID
<i>M8</i>	40	Free Fixed	14 ± 6 (7) 23 ± 13 (14)†	11 ± 6 (20) 8 ± 7 (20)	NS VIS > HID
<i>H1</i>	30	Free Fixed	120 ± 13 (4) 92 ± 16 (3)	53 ± 16 (8)* 34 ± 5 (7)	VIS > HID VIS > HID
<i>Q9</i>	50	Free	40 ± 12 (15)	33 ± 18 (24)	NS
<i>Q24</i>	15	Free	140 ± 37 (10)	64 ± 34 (17)	VIS > HID
<i>Q37</i>	55	Free	43 ± 14 (10)	52 ± 14 (11)	NS
<i>Q41</i>	28	Free	24 ± 13 (4)	53 ± 6 (4)	HID > VIS
<i>Q51</i>	50	Free	34 ± 17 (9)	40 ± 14 (17)	NS
<i>Q55</i>	10	Free	76 ± 41 (6)	83 ± 15 (13)	NS
<i>Q62</i>	70	Free	47 ± 20 (6)	50 ± 21 (5)	NS

Values for Target Visible and Target Hidden are mean firing frequencies ± SD; numbers in parentheses are numbers of trials. oTR(S)Ns, orientation tectoreticulospinal neurons; GPE, gaze position error; VIS, target visible; HID, target hidden; NS, not significant. \*Head-free average firing frequency significantly greater than head-fixed (*t* test,  $P < 0.05$ ). †Head-fixed average firing frequency significantly greater than head-free (*t* test,  $P < 0.05$ ).

to 70°. In the visible-target condition the sustained discharge frequencies ranged from 14 to 140 spikes/s and, for all except two cells, were <100 spikes/s. When the target was hidden behind the barrier the frequency ranged from 8 to 83 spikes/s. For a given behavioral condition, similar values were computed for the head-fixed and head-free conditions for all except three cells. These three oTR(S)Ns had significant differences in only one behavioral condition.

When comparing the visible- and hidden-target conditions, we found that seven oTR(S)Ns had significantly higher discharge rates when the target was visible (Vis > Hid, *t* test,  $P < 0.05$ ) and only one cell had a significantly lower discharge rate when the target was visible (Hid > Vis, *t* test,  $P < 0.05$ ). The remaining cells showed no significant (NS) differences between the two behavioral conditions.

#### fTR(S)Ns are active during attentive fixation

We recorded from 12 fTR(S)Ns that were activated in a sustained manner when a cat's visual axis was close to, or aligned on, a visible food target. Four fTR(S)Ns had visual receptive fields centered about the point of fixation. Three of these were studied in some detail. The visual receptive fields of the other eight neurons, although including a representation of the point of fixation, were centered in the contralateral hemifield. None of these latter neurons was held long enough to permit thorough testing.

SUSTAINED DISCHARGES RELATED TO FIXATION OF A VISIBLE TARGET. *Cell J5*, a fTR(S)N located in the rostral left SC, had a rather large (~20° diam), centrally placed visual receptive field. Figure 8 illustrates the activity of *cell J5* when a food target was held stationary to the left or right side of a barrier that was ~20° wide. In the head-fixed condition (Fig. 8, *A* and *B*), the trial began with the target located to the right of the barrier while the cat was looking to the left side of the barrier (Fig. 8*E*). *Cell J5* was sporadically active, firing only a few action potentials. However, when the cat looked at the target (Fig. 8*D*), the neuron began to discharge at a high frequency. This pattern of activity continued throughout the period shown in Fig. 8*A*; *cell J5* was strongly activated only when the cat looked at the target. Figure 8*B* continues directly from Fig. 8*A*, with the target still located on the right side. The target was then moved to the left of the barrier and the cat quickly oriented left and refixated the target. *Cell J5* was now activated with a strong sustained discharge only when the animal fixated the target on the left (Fig. 8*F*). Whenever the cat looked right (Fig. 8*G*), the cell was silent. At the end of Fig. 8*B* the target was moved back to the right and, after a short latency, the cat reoriented to the right side. The sustained discharge pattern was once again observed when the cat fixated the target on the right. A similar discharge pattern was recorded from *cell J5* in the head-free condition (Fig. 8*C*).

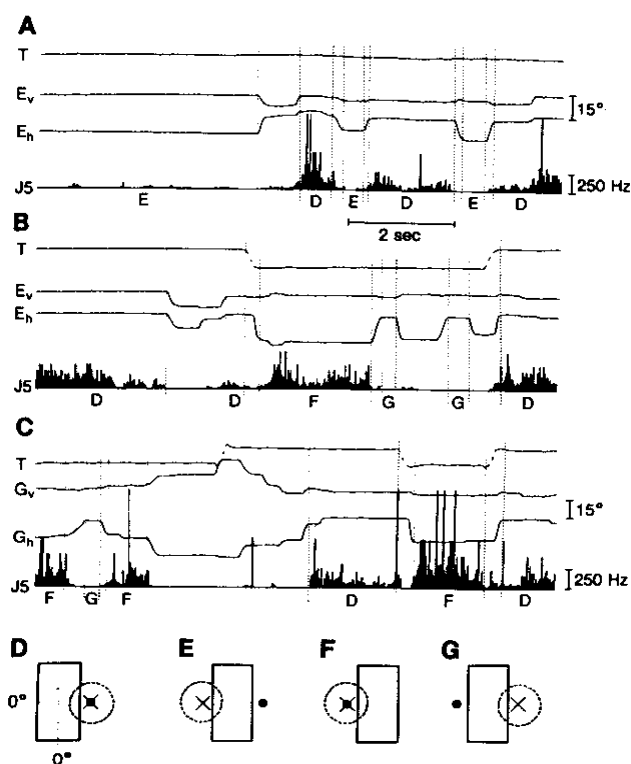
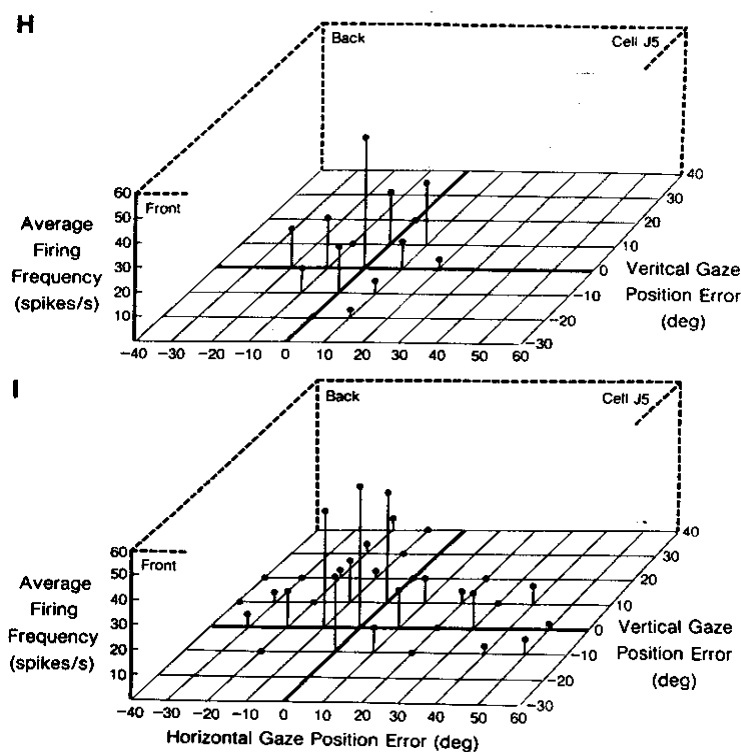


FIG. 8. Activity of *cell J5*, an fTR(S)N located in the rostral left SC, recorded when the food target was visible on one side or the other of the barrier in head-fixed (*A* and *B*) and head-free (*C*) conditions. *D–G*: schematics illustrating different behavioral situations. *H* and *I*: gaze position error fields of *cell J5* obtained when the target was visible in head-fixed and head-free conditions, respectively. Note that *cell J5* was maximally activated when the cat fixated on the food target. See legends to Figs. 2 and 4 for additional explanations.



The GPEF of *cell J5* is plotted for the visible target condition using 234 fixations when the head was fixed (Fig. 8*H*) and 193 fixations when the head was free to move (Fig. 8*I*). The similarity between the plots in the head-fixed and -free conditions implies that the position of the visual axis relative to the target is the critical variable that determines the intensity of cell discharge. All three fTR(S)Ns we studied extensively were maximally active when GPE was at or near zero. The GPEFs were large and appeared to be bell shaped. Thus fTR(S)Ns were not tonically active exclusively during direct fixation of the food target.

In general the concept of GPEF reconciles the sustained activity of fTR(S)Ns with that of the oTR(S)Ns located more caudally in the SC. Indeed, there may be a continuum of optimal GPEs described by the retinotopically coded SC motor map: oTR(S)Ns, located in the posterior SC, are active for large GPEs, whereas fTR(S)Ns, located on the 0° position of the collicular map, are maximally active during direct fixation of the target, when GPE is zero.

**fTR(S)N DISCHARGES RELATED TO THE PRESENCE OF A HIDDEN TARGET.** Figure 8 showed that fTR(S)Ns discharge tonically when the animal fixated a visible food target. Figure 9 illustrates the activity of the same cell, *J5*, when the food target was hidden behind the barrier. The head-fixed trial (Fig. 9*A*) began with the animal's fixating the target, which was visible on the right side (Fig. 9*C*), and the cell's presenting a brisk sustained discharge. The target was then moved behind the barrier, and *cell J5* fired sporadically with a much weaker discharge when the cat looked to either side (Fig. 9, *D* and *E*). When the target again became visible on

the left side of the barrier (Fig. 9*F*), fixation on it produced a vigorous, sustained discharge as before. A similar discharge pattern was recorded from *cell J5* in the head-free, hidden-target condition (Fig. 9*B*). GPEFs were not calculated in this hidden-target condition because, without a target, the GPE vector was ambiguous: for example, when the visual axis was positioned midway between the two edges of the barrier, a fTR(S)N could discharge for both rightward and leftward GPEs (see Fig. 8, *H* and *I*). We conclude from these experiments that to maximally activate *cell J5* the animal had to be fixating the target of interest; fixation of a location where the target's appearance was anticipated produced a much weaker discharge.

**COMPARISON OF fTR(S)N SUSTAINED DISCHARGES.** Enough trials were available for three fTR(S)Ns to permit the calculation of GPEFs in the visible target condition. When the head-fixed animal fixated the target directly, the average sustained frequencies and their associated standard deviations; for *cells F4*, *F3.A30*, and *J5*, were, respectively:  $27 \pm 14$  ( $n = 157$ ),  $102 \pm 22$  ( $n = 5$ ), and  $76 \pm 41$  ( $n = 62$ ). Only *cell J5* was held long enough to be tested when the cat's head was free: during fixation of the visible target, the average frequency was  $63 \pm 30$  ( $n = 32$ ). These values are comparable with the range of oTR(S)N sustained-discharge rates described in Table 1.

#### Size and distribution of TR(S)N GPEFs

The contours of TR(S)N GPEFs were evaluated for 17 cells. The outer boundary of each field was taken as a

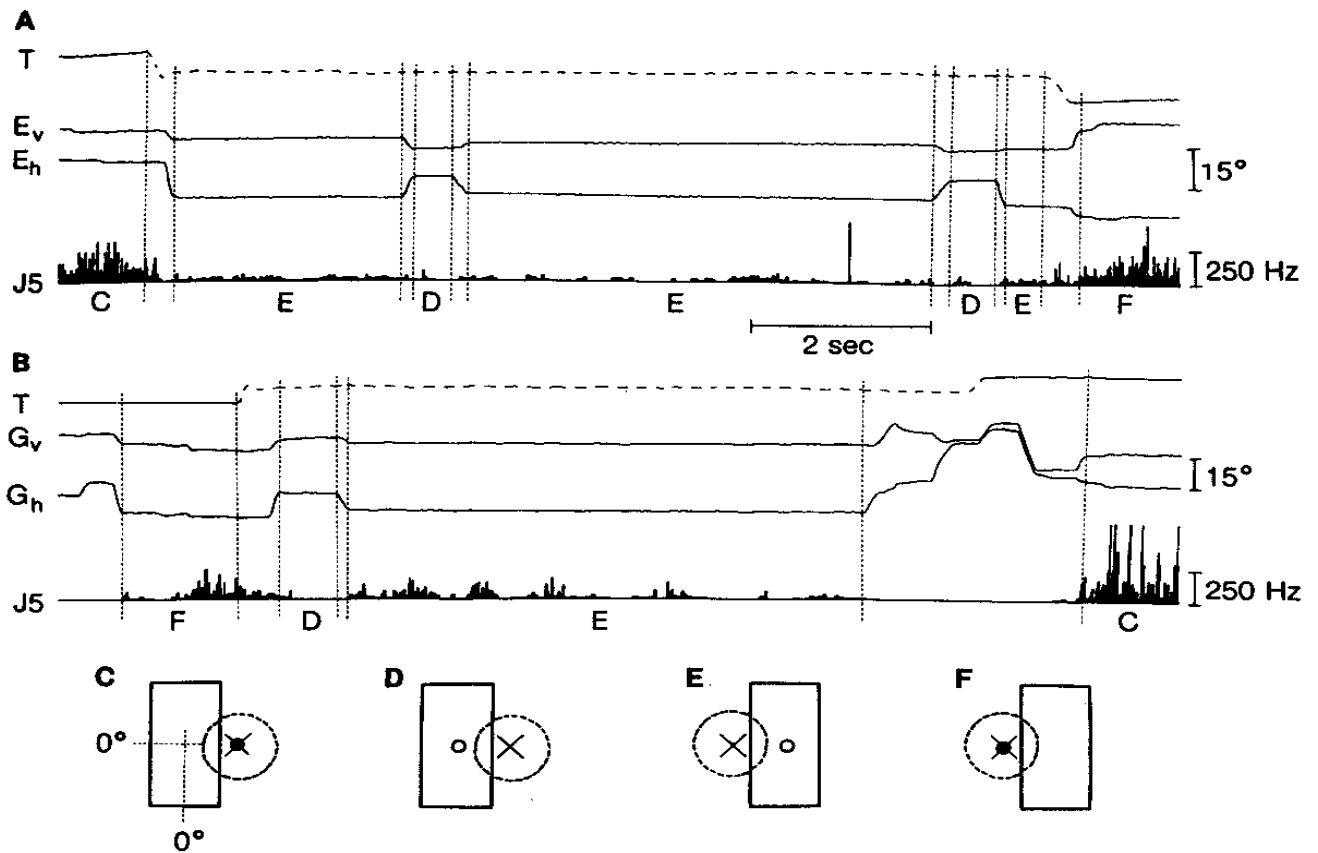


FIG. 9. Activity of cell J5, recorded when the food target was hidden behind the barrier in head-fixed (A) and head-free (B) conditions. C-F: schematics illustrating different behavioral situations. Target was behind barrier in conditions D and E. Cell discharge was much stronger, for an equivalent position of the visual axis, when cat fixated the visible target. (Compare conditions C and D, E and F). See legends to Figs. 2 and 8 for additional explanations.

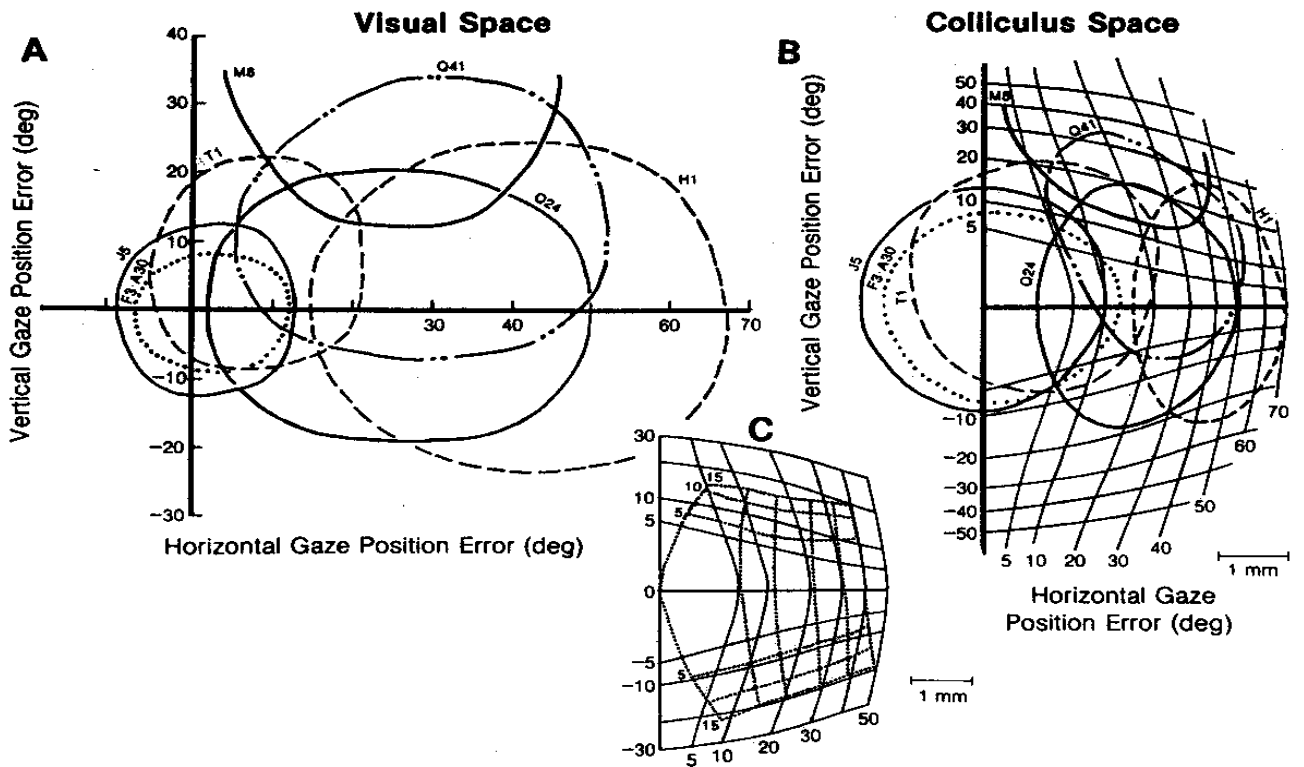


FIG. 10. Gaze position error fields of 7 TR(S)Ns plotted on a 2-dimensional representation of visual space (A) and on an idealized retinotopic coordinate system of the cat SC (B) adapted from McIlwain (1986). Fields are plotted as if each TR(S)N were located in the right SC. Note large size of fields in SC space, thereby suggesting that a large area of the TR(S)N layer is tonically active during either attentive fixation or motor preparation (see text). C: comparison, on a scale smaller than that in B, of the presently used map (solid lines) with McIlwain's map (dotted lines). The former can be considered a flattened version of the latter.

smooth contour encompassing all GPEs that activated the cell to  $\geq 25\%$  of the maximum average firing frequency recorded for the optimal GPE. Figure 10A shows the extent of the GPEFs of seven representative cells, plotted in retinotopic (visual) space. For the sake of comparison, all fields are plotted as if each TR(S)N were located in the right SC. All TR(S)N GPEFs had circular to oval shapes. (To avoid the superior sagittal sinus, we did not explore in detail the medial aspects of the cat SC with vertically oriented electrode penetrations. This sampling bias resulted in a paucity of cells with GPEFs lying below  $0^\circ$  vertical GPE.)

The fields plotted in Fig. 10A are large, with diameters ranging from  $\sim 20$  to  $>50^\circ$ . The size of each cell's GPEF was dependent on the eccentricity of that cell's optimal GPE. The smallest fields belonged to fTR(S)Ns and were centered around  $0^\circ$  GPE. Field size increased approximately with increasing eccentricity from the origin.

## DISCUSSION

We have shown that, during periods when the visual axis was stationary, TR(S)Ns presented sustained discharges, the intensities of which were dependent on the magnitude and direction of the GPE. We devised several behavioral tasks to isolate this component of a cell's discharge from its sensory (Guitton and Munoz 1991) and motor (Munoz et al. 1991a) responses. To discuss this material, we first relate this pattern of discharge to other reports describing the sustained discharge of cells in the cat and monkey colliculus. We then consider the input-output connectivity of the SC and its role in the generation of the sustained discharge. Finally, we postulate that the TR(S)N layer of the SC can function as an attentional map in which mechanisms favoring fixation oppose those driving orientation.

### *TR(S)N discharge patterns*

The average peak rate of sustained discharge of all cells that we studied was  $<150$  spikes/s (see Table 1). Grantyn and co-workers (Grantyn et al. 1983) described three ranges of rhythmic firing that were produced when TR(S)Ns, recorded in the anesthetized cat, were depolarized intracellularly with suprathreshold current steps. For small current steps, TR(S)Ns exhibited low-frequency continuous discharge ( $<200$  spikes/s). As the amount of injected current was increased, TR(S)Ns began to discharge extra spikes that created grouped or burst discharge patterns, with firing rates ranging from 200 to 700 spikes/s. Within this range, small increases in depolarization led to dramatic acceleration of discharge rate, because of the generation of the extra spikes. For the greatest depolarizing steps, continuous, high-frequency discharge (700–1,100 spikes/s) was produced.

The pattern of sustained TR(S)N activity that we recorded in the alert animal falls into the low-frequency range described by Grantyn et al. (1983). Higher frequency, grouped, burst discharges have also been recorded from TR(S)Ns in alert animals, but these patterns of activity, contrary to the sustained discharge, are "motor" and appear to be causally related to the execution of orienting movements (Grantyn and Berthoz 1985; Munoz and Guitton 1986, 1989; Munoz et al. 1991a).

### *Behavioral context and oTR(S)N sustained discharges*

The barrier paradigm that we used was a most convenient technique for enticing the cat to make natural orienting gaze shifts of specific direction and amplitude. Indeed, the animals rapidly learned (2–3 days of 2 h/day practice) this "cat and mouse" game and generated gaze shifts either to spatial locations defined by visible targets or to locations devoid of sensory targets but assigned significance on the basis of both prior experience and the existence of sensory cues at other locations. Through previous training, the animal learned that when the food target was hidden behind the barrier, it would ultimately reappear on one side or the other (Guitton et al. 1990). When the target disappeared from one side, the animal assigned significance to a specific location on the other edge of the barrier, where it anticipated reappearance of the food target. This location on the barrier then became the new target of interest, and a particular zone of the TR(S)N layer in the appropriate SC became depolarized.

The pattern of discharge presented by oTR(S)Ns reflected this process. oTR(S)Ns were silent when the cat attentively fixated the food target. When the target was visible on one side of the barrier, an oTR(S)N maintained a sustained discharge whenever the GPE lay within the GPEF for that cell. Although part of the sustained discharge was determined by the presence of the target in the cell's visual receptive field, there was also a strong anticipatory component of the discharge. For example, in the hidden-target condition, when the target disappeared from one side of the barrier, an oTR(S)N discharged whenever the cat anticipated target reappearance at a specific location. The discharge occurred specifically when the position of the visual axis, relative to the spatial location of the target, lay within the oTR(S)N's GPEF. Furthermore, when ambient light was momentarily extinguished (e.g., see Fig. 7), sustained activity was recorded for the same gaze positions before, during, and after the period of darkness.

It is important to note that there was little or no sustained activation of most oTR(S)Ns during periods when the visual axis was immobile between spontaneously generated gaze shifts when the food target was not present and when the animal did not expect it to appear (e.g., see Fig. 6). Lack of sustained activity existed even though a point on the edge of the barrier lay in the neuron's GPEF and the cat eventually oriented to this point. A few oTR(S)Ns, however, did present weak discharges in this condition. We conclude that the total active population of TR(S)Ns and overall level of sustained activity was greatest in the visible-target condition, reduced somewhat when the target was hidden, and weakest or zero during spontaneously generated gaze shifts in the no-target condition (Table 1).

### *Similarity between cat TR(S)N sustained discharge and primate SC cell activity*

The observation that oTR(S)N sustained discharges are related to GPE recalls the QV cells (Mays and Sparks 1980) and memory-contingent neurons (Waitzman et al. 1987) described for the monkey SC. These two cell types have sustained discharges with similar properties. A QV cell was activated when a visual stimulus was present in its visual

receptive field. Similar to an oTR(S)N, the discharge of the QV cell continued until a saccade removed the stimulus from the neuron's visual receptive field. A QV cell was also activated in the absence of direct retinal stimulation (i.e., in the dark) if the remembered location of the target relative to the fovea was within the cell's visual receptive field. Activation of QV cells was therefore related to the vector of eye position error (i.e., the difference between actual and desired eye position) and not simply retinal error (i.e., location of the stimulus on the retina).

The characteristics of oTR(S)N sustained discharges therefore appear to be the same as those describing QV cell behavior in that 1) both cell types are activated for a specific range of vector errors equal to the direction and magnitude of the distance between desired and actual positions of the visual axis and 2) the discharge does not drive the movement. We have defined this vector as GPE instead of eye position error, as used by Mays and Sparks (1980), because the discharge characteristics of cat TR(S)Ns, in the head-free condition, reveal that the relevant vector is not eye-relative-to-head nor head-relative-to-target, but eye-relative-to-target. This point is considered in greater detail in the next section.

#### *TR(S)N sustained discharge is activated by GPE*

The SC has long been associated with the control of eye movements. Indeed, the literature on the primate SC has focused almost entirely on head-fixed animals (e.g., see Sparks 1986; Sparks and Mays 1990; Wurtz and Albano 1980), the only exception being a study in the head-free monkey (Robinson and Jarvis 1974) that reported unit discharges independent of head displacement. By comparison, studies of the cat SC have supported its role in gaze (i.e., eye + head) control. The retinotopically coded visual map in the superficial layers represents up to  $\sim 80^\circ$  of the contralateral visual field (e.g., see Feldon et al. 1970; Schiller 1984). The motor map in the deeper layers of the cat SC cannot code ocular displacements of up to  $80^\circ$  in amplitude, because the cat's oculomotor range is only about  $\pm 25^\circ$  (Collewyn 1977; Crommelinck and Roucoux 1976; Evinger and Fuchs 1978; Guitton et al. 1980, 1984; Stein et al. 1976; Stryker and Blakemore 1972). This apparent contradiction was resolved in part when electrical stimulation of the SC in the head-free cat elicited gaze shifts with vectors that were compatible with the retinotopic representation (Crommelinck et al. 1990; Guitton et al. 1980; Roucoux et al. 1980).

The discharge characteristics of TR(S)Ns strongly support the role of the cat SC in gaze control. The prime evidence for this comes from our data obtained in the head-free animal (this paper; Munoz et al. 1991a). When the head-free cat looked about the barrier, it fixated different spatial locations with the head aligned along the line of sight and TR(S)Ns discharged. It follows that variations in discharge could not have been dependent on eye position in the orbit because, for each position of gaze, the eye was at or near central position in the orbit.

Similar experiments performed with the animal's head held fixed, however, ruled out the possibility that the sustained TR(S)N discharge was related to head rather than gaze position relative to the target, because the position of the visual axis (i.e., gaze) relative to the target defined a

GPEF similar to the one found for the same cell in the head-free condition. Thus, irrespective of whether target position was varied or the head was fixed or free, the best correlate with the intensity of a TR(S)N's sustained discharge was gaze position relative to the target. Because the sustained discharges of both oTR(S)Ns and fTR(S)Ns were unrelated to any specific head position relative to the body, they were also unrelated to any specific pattern of electromyographic activity expressed by dorsal neck muscles (Munoz et al. 1991b). Hence, some premotor element must have prevented the direct translation of descending sustained collicular output to neck muscle motoneuron activators. Nevertheless, the sustained discharges of oTR(S)Ns could play a role in "warming up" the appropriate circuits that may imminently be called on to activate the neck muscle motoneurons to produce a head movement. Additional data supporting this assertion will be presented in the next paper (Munoz et al. 1991a). In contrast, the sustained discharges of fTR(S)Ns may serve to enhance elements that suppress the generation of eye and head movements.

#### *TR(S)Ns in the rostral SC are active during attentive fixation*

An important feature of collicular organization is that the coding of GPE across the layer of TR(S)Ns extends to the rostral aspect of the SC, where, at the area centralis representation, cells are tonically active during attentive fixation (i.e., when GPE equaled  $0^\circ$ ). To our knowledge, these observations linking rostral TR(S)N discharge to fixation are the first to suggest that this collicular zone may play an active role in the maintenance of this important behavioral act. Fixation-related discharges have previously been recorded from unidentified collicular neurons in the head-fixed monkey (Goldberg and Wurtz 1971; Sparks and Mays 1980) and cat (Peck 1989), but these neurons were not reported to be concentrated in the foveal or area centralis representation. Recently, it has been reported that fixation activity similar to that reported here is indeed concentrated in the rostral pole of the monkey SC (Munoz et al. 1990). However, it still remains to be determined whether output neurons from this region in monkey have their discharges related to the behavioral act of fixation.

#### *Ensemble coding*

A single TR(S)N discharged tonically for a large range of GPEs and therefore cannot by itself code a specific GPE. For example, cell J5 was activated at a similar discharge frequency regardless of whether the animal fixated  $5^\circ$  above or  $5^\circ$  below the food target. The organization of TR(S)Ns into a motor map suggests that a large number of TR(S)Ns are active for a single GPE. It is of interest to determine the spatial characteristics of the resulting zone of sustained activity in the SC's motor layer. Such an analysis is analogous to the "point image" concept in visual neurophysiology, which we now describe.

There is a nonhomogeneous mapping of visual space in the SC, whereby the central, as contrasted with the peripheral, visual field has an expanded representation (e.g., for cat, see Berman and Cynader 1972; Feldon et al. 1970; Lane et al. 1974; McIlwain 1975, 1986a; Schiller 1984).

Furthermore, centrally placed visual receptive fields are smaller than those located in the periphery (McIlwain 1975; McIlwain and Buser 1968; Sprague et al. 1968; Sterling and Wickelgren 1969). The boundary of a collicular cell's visual receptive field, as drawn on the coordinate system of the SC, defines the locus of all collicular cells in that layer of the SC with receptive fields that contain that point of the visual field (defined as a point image; for review see McIlwain 1986a). McIlwain (1975) demonstrated that, when visual receptive fields were imaged onto the coordinate system used in the colliculus, a constant size and shape of point image was produced, independent of receptive-field eccentricity.

The dependence of the size of TR(S)N GPEFs on the eccentricity of the field is also a consequence of collicular spatial coding. In Fig. 10B, the same TR(S)N GPEFs as shown in Fig. 10A are replotted, this time onto the retinotopically coded map of the colliculus. The generation of this map posed a special problem, because there is no agreement as to what it should look like from a dorsal viewpoint and even less when it is unfolded and represented two-dimensionally. [Note the strong disagreement between the maps presented by Feldon et al. (1970) and McIlwain (1986b).] We took the map used by McIlwain (1975, 1986b) because it appears to be compatible with the vectors of his electrically evoked saccades. However, this map is limited in its spatial extent, covering a maximum of 50° in the horizontal direction and ±15° vertically. Our GPEFs covered up to 70° horizontally and 40° vertically. We therefore extrapolated the McIlwain map as follows. The scale on the horizontal meridian could be represented by

$$r = 0.66\theta^{0.46} \quad (1)$$

where  $r$  is in millimeters from the zero representation on the SC map and  $\theta$  is in degrees. We then assumed that the horizontal and vertical meridians were perpendicular to each other and with the same scaling. Figure 10C shows a comparison between our theoretical representation (solid grid) and McIlwain's map (dotted grid). Our map appears to represent approximately an unfolded and flattened SC: the two maps become nearly coextensive if McIlwain's map is imagined to be fixed to the horizontal axis and the anterolateral and anteromedial corners pulled such that the vertical axes on both plots are aligned.

When GPEFs are imaged onto our map (Fig. 10B), the general size of the fields becomes less variable than in retinotopic space. Cells activated by small GPEs had GPEFs that, when imaged onto the SC, were as large as the imaged fields of cells responding to large GPEs. (Note that the skewed appearance of point image Q41 would be more circular in the McIlwain representation.) An important additional conclusion from this exercise is that the size of the imaged fields is large, thereby showing that, during both direct fixation and periods of motor preparation, a large surface area of the TR(S)N layer was depolarized and a very large number of TR(S)Ns were active at any one time. The most active TR(S)Ns in the ensemble were at the center of the image; neuronal activity diminished with distance away from this center.

According to this view there should be cells, say at the 5° location on the SC map, the GPEFs of which, when imaged on the SC motor map, should overlap with the area centra-

lis representation. The message from an active ensemble centered at 5° should contain opposing tendencies: fixation versus preparation for orientation. In such a situation the dominant force defined by "the center of gravity" of the ensemble should presumably determine the relevant behavior.

#### *Connectivity influencing TR(S)N activity*

We have seen that sensory information can interact with cognitive signals to activate an appropriate population of TR(S)Ns. We will now briefly consider extra- and intracollicular connectivity that may influence the locus of TR(S)N activity within the SC.

**SENSORY INPUTS.** In the previous paper (Guitton and Munoz 1991), we showed that visual, auditory, and somatosensory stimuli can activate the same TR(S)N for which motor-related discharge, described in the following paper (Munoz et al. 1991), then drives the gaze-shift that orients the visual axis onto these stimuli. Both direct (i.e., retinotectal and spinotectal) and indirect (i.e., corticotectal) sensory pathways converge on the deeper laminae of the SC (e.g., for review see Huerta and Harting 1984). For example, TR(S)Ns receive at least some monosynaptic input from retinal Y-cells (Berson and McIlwain 1982) and from cells in the extrastriate visual cortex (Berson and McIlwain 1983). The corticotectal projections that convey sensory information to the deeper layers of the cat SC arise from outside the primary sensory cortices (Berson and McIlwain 1983; Clemo and Stein 1984; Ogasawara et al. 1984).

**COGNITIVE INPUTS.** The cognitive process whereby the edge of the barrier assumes significance may have origin from within the cerebral cortex. There is some similarity between our predicted (hidden) target paradigm and the remembered-target paradigm used in several monkey studies, whereby the monkey, in the dark, makes a saccade to the location where a target had previously appeared.

In the monkey, three cortical structures known to contain neurons that are active in the remembered target condition are the frontal eye fields (Bruce and Goldberg 1985; Segraves and Goldberg 1987), the lateral bank of the intraparietal sulcus (Gnadt and Anderson 1988), and the prefrontal cortex within and surrounding the principal sulcus (Boch and Goldberg 1989; Funahashi et al. 1990). Some neurons in each structure present presaccadic sustained anticipatory discharges.

The memory-related information in the frontal eye fields can affect collicular activity via two projections: 1) a direct projection to the deeper layers of the SC (Leichnetz 1981; Segal et al. 1983; Segraves and Goldberg 1987; Stanton et al. 1988) and 2) an indirect route via the caudate nucleus and substantia nigra (reviewed in Guitton 1991; Hikosaka and Wurtz 1983d, 1985a,b; Hikosaka et al. 1989a-c). Cells in the substantia nigra pars reticulata are usually tonically active but respond to certain forms of oculomotor behavior by reducing their rate of discharge (Hikosaka and Wurtz 1983a-c; Joseph and Boussaoud 1985). Several different response types have been described. For example, some cells have memory-contingent visual and saccade-related responses (Hikosaka and Wurtz 1983c), and many of these neurons project to the deeper laminae of the SC (Hikosaka and Wurtz 1983d). Furthermore, it has been demonstrated

in the cat that excitatory corticotectal (of unknown origin) and inhibitory nigrotectal projections converge directly onto TR(S)Ns (Chevalier et al. 1984; Karabelas and Moschovakis 1985). Although it is unknown whether neurons in the posterior parietal cortex, which carry memory-related signals, do indeed project on to TR(S)Ns, anatomic evidence in the monkey (Lynch et al. 1985) and cat (Olson and Lawler 1987) demonstrates a corticotectal route from this region.

**FIXATION INPUTS.** The discharge characteristics of fTR(S)Ns are similar to those described for visual fixation neurons located in monkey: area 7 of the parietal lobe (Lynch et al. 1977; Mountcastle et al. 1975; Sakata et al. 1980), frontal eye fields (Bruce and Goldberg 1985; Segraves and Goldberg 1987), and frontal and prefrontal cortices (Bon and Luchetti 1990; Suzuki and Azuma 1977). In general, cortical visual fixation neurons are inactive during casual fixations as the animal inspects its surroundings but increase their discharge rate considerably when the animal fixates on a visual target having a strong motivational significance (e.g., when the animal is rewarded for maintained fixation). Some of the fixation neurons in the frontal eye fields are known to project to the SC (Segraves and Goldberg 1987). Area 7 of the parietal lobe projects to the SC in both the cat (Olson and Lawler 1987) and monkey (Lynch et al. 1985); but, despite the similarities between fixation cells in area 7 and SC fTR(S)Ns, it remains to be determined whether there is a direct anatomic link between the two cell types.

**INTRACOLLICULAR CONNECTIVITY.** The local connectivity within the SC itself may play an important role in shaping TR(S)N output signals. Both excitatory and inhibitory intracollicular connections have been revealed (Douglas and Vetter 1986; McIlwain 1982). Here we wish to concentrate on the evidence for an inhibitory network within the SC whereby activation of neurons at one collicular locus leads to inhibition of neurons at other loci ipsilateral and contralateral to the activated zone (Behan 1985; Douglas and Vetter 1986; Mascetti and Arriagada 1981). Douglas and Vetter (1986) postulated that an intracollicular inhibitory network may represent a target selection process within the SC that favors the development of only one active locus. However, the role played by TR(S)Ns in such a network is unclear because most of these neurons lack recurrent or commissural collaterals (Grantyn and Grantyn 1982; Moschovakis and Karabelas 1985).

*Relationship between the animal's locus of attention and the collicular locus of TR(S)N activity*

Wurtz and colleagues (Wurtz and Goldberg 1972; Wurtz and Mohler 1976; Wurtz et al. 1980) proposed an attentional hypothesis of collicular function. These authors suggested that the SC was involved in shifting attention to a specific spatial location, which then facilitated the execution of a saccade to that region of the visual field.

The observations presented in this paper, summarized schematically in Fig. 11, do indeed suggest that the locus of TR(S)N sustained activity on the SC motor map, defined

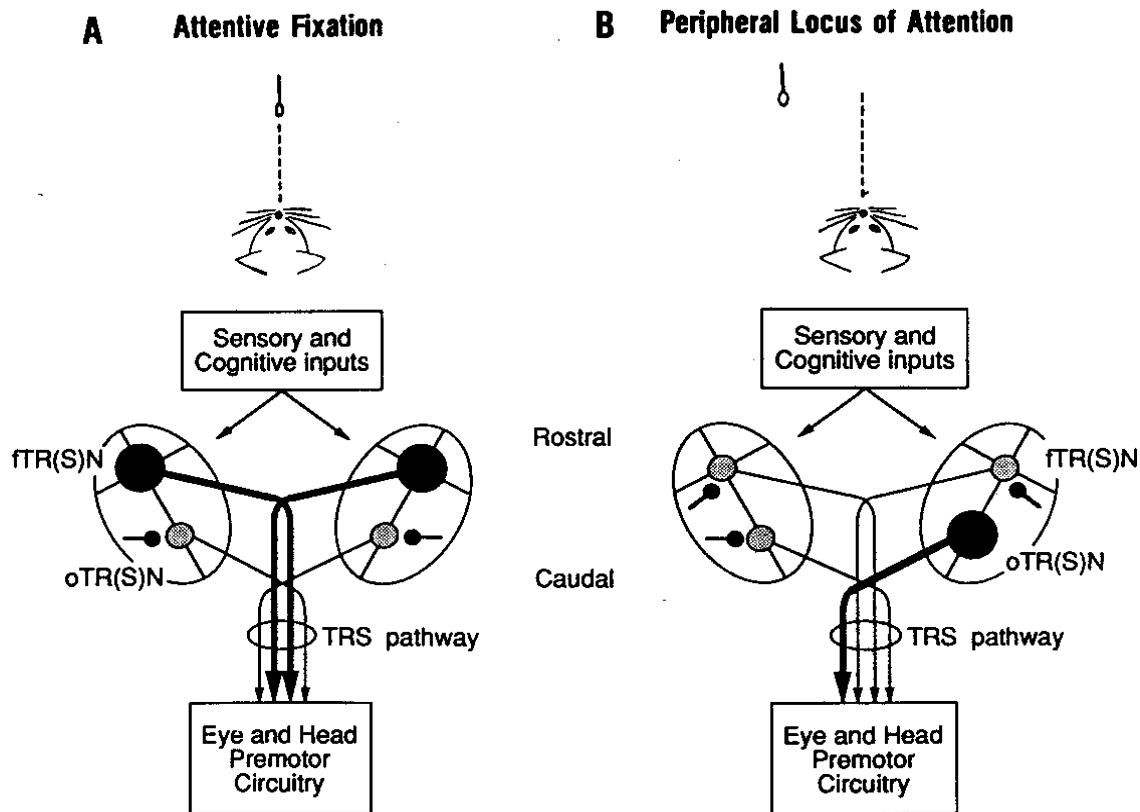


FIG. 11. Summary schematic illustrating how fTR(S)Ns and oTR(S)Ns reciprocally interact to favor fixation (A) or motor preparation (B). Dark circle indicates zone of TR(S)N activity. A: TR(S)N activity is confined to the rostral regions of both colliculi when the animal attentively fixates a target of interest. Remainder of the SC is inhibited. B: zone of activity is located in the caudal right SC when the target of interest is located to the left of the visual axis. Activity of TR(S)Ns located elsewhere is suppressed.

by sensory and cognitive inputs, specifies where, in retinal coordinates, the animal is attending. When the cat was attentively fixating the food target (Fig. 11A), the TR(S)N point image was located in the rostral poles of both colliculi, centered over 0° GPE, and the excitability of other TR(S)Ns [i.e., oTR(S)Ns] was diminished (Guitton and Munoz 1991), at least in part, by postulated inhibition emanating from the rostral SC. This mechanism would make it harder for any sensory input to activate oTR(S)Ns and trigger an orienting movement.

When the cat's visual axis was directed away, say to the right of the food target, the point image shifted to a caudal site in the right SC representing the new GPE (Fig. 11B). This zone of sustained activity could change position on the collicular map as the cat directed its visual axis to different points in space relative to that target. It is postulated that the remainder of the ipsilateral SC and all of the contralateral SC would now be inhibited, thereby reducing the activity of fTR(S)Ns.

In summary we propose that 1) the sustained activity of cells lying outside the area centralis representation [i.e., oTR(S)Ns] reflects the animal's preparation and/or intent to eventually orient, and 2) the activation of cells lying within the area centralis representation [i.e., fTR(S)Ns] reflects the intent to maintain fixation. Thus, when fixating the visible food target, the animal seldom looked away, and fTR(S)Ns appeared to reflect this diligence of fixation by exhibiting strong sustained discharge. When the target was hidden behind the barrier and did not reappear, the animal began looking, to and fro, from one side to the other in search of the target. Fixation cells exhibited weaker discharges in this orientation mode, whereas oTR(S)Ns developed the sustained discharge. Allegorically speaking, the collicular layer containing TR(S)Ns can be imagined as a playing field on which mechanisms favoring fixation are opposed to those driving orientation. Higher centers of the CNS that are involved in directing visual attention could provide the push needed by one side or the other to define, albeit temporarily, the nature of the SC output signal and thus eventual motor behavior. The motor-related discharges of TR(S)Ns are discussed in the next paper (Munoz et al. 1991).

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