FIXATION AND ORIENTATION CONTROL BY THE TECTO-RETICULO-SPINAL SYSTEM IN THE CAT WHOSE HEAD IS UNRESTRAINED

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SUMMARY

The role of the tecto-reticular and tecto-reticulo-spinal neurons (here called TR(S)Ns) in gaze control is described. TR(S)Ns, located in the deeper layers of the cat superior colliculus (SC), project onto the eye and head premotor circuitry. TR(S)Ns located in the caudal SC had sustained and phasic discharges related to the control of gaze movements. The sustained discharge occurred when the visual axis was positioned at some vector quantity away from a target of interest. Each cell has its preferred vector corresponding to the cell's location on the collicular retinotopic map. This tonic discharge acted as a preamble to the phasic discharge and served to pre-excite the relevant oculomotor circuitry. The phasic discharge preceded gaze shifts whose direction and magnitude matched the preferred vector. The intensity of this discharge was correlated to the acceleration and velocity of the movement. TR(S)Ns situated in the rostral SC were maximally active when the cat fixated a target of interest. These neurons decreased their discharge rate during gaze shifts. Thus, TR(S)Ns provide both fixation and orientation signals to the eye and head premotor circuitry. A scheme is proposed where TR(S)Ns lie within a gaze feedback loop that controls eye and head movements via inputs to long lead burst neurons and omnipause neurons.

Contrôle de la fixation et de l'orientation par le système tecto-réticulo-spinal chez le chat dont la tête est libre.


RéSUMÉ

Le rôle des neurones tecto-réticulaires et tecto-réticulo-spinaux (TR(S)Ns) dans le contrôle du regard est décrit. Les TR(S)Ns, situés dans les couches profondes du colliculus supérieur (CS) du chat, projettent sur les circuits prémoteurs oculaires et céphaliques. Les TR(S)Ns situés dans le CS caudal avaient des décharges soutenues et phasiques en rapport avec le contrôle des mouvements du regard. La décharge soutenue survenait quand l'axe visuel était positionné au-delà de la cible. Chaque cellule avait un vecteur préférentiel correspondant à sa localisation sur la carte colliculaire retinotopique. Cette décharge tonique agissait comme un préambule à la décharge phasique et servait à pré-activer les circuits oculomoteurs correspondants. La décharge phasique précédait les déplacements du regard dont la direction et l'amplitude correspondaient au vecteur préférentiel. L'intensité de cette décharge était corrélée avec l'accélération et la vitesse du mouvement. Les TR(S)Ns situés dans le CS rostral étaient pleinement activés quand le chat fixait une cible. La décharge de ces neurones diminuait pendant les déplacements du regard. Ainsi, les TR(S)Ns transmettaient des signaux de fixation et d'orientation aux circuits prémoteurs oculaires et céphaliques. Un schéma est proposé dans lequel les TR(S)Ns forment partie d'une boucle à « feedback » qui contrôle les mouvements de l'œil et de la tête par des différences sur les neurones « burst » et sur les neurones « omnipause ».

INTRODUCTION

Within the complex neural processes that lie between a pure sensory response and a motoneuron discharge there are two structures which appear necessary for the initiation of saccadic eye movements: the frontal eye fields (FEF) and superior colliculus (SC). Ablation of both the SC and FEF in the primate leads to an inability to generate saccades (Schiller et al., 1980), although monkeys can still make saccades when only one of these structures is removed. Many single unit recording studies in alert monkeys have shown that neurons in both the SC (Schiller and Koerner, 1971; Wurtz and Goldberg, 1971, 1972; Goldberg and Wurtz, 1972; Mohler and Wurtz, 1976; Wurtz and Mohler, 1976a; Mays and Sparks, 1980) and FEF (Wurtz and Mohler, 1976b; Goldberg and Bushnell, 1981; Bruce and Goldberg, 1985; Segraves and Goldberg, 1987) have sensory and motor-related components in their discharge patterns. For example, the visual responses of many neu-

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rons located in the superficial layers of the monkey SC can be enhanced if the stimulus triggers an orienting response (Goldberg and Wurtz, 1972; Wurtz and Mohler, 1976a). «Saccade-related burst neurons», located in the deeper layers of the monkey SC, discharge high frequency bursts of spikes prior to saccadic eye movements (Schiller and Koenner, 1971; Wurtz and Goldberg, 1971, 1972; Sparks et al., 1976). If a visual stimulus fails to evoke a saccade then these neurons may still be activated but they lack the high frequency saccade-related burst component of their discharge (Sparks, 1978).

To establish how the SC communicates with brainstem premotor circuits it is essential to determine the discharge characteristics of collicular output cells. This has been done in a limited number of studies describing the discharge of identified tecto-reticular neurons (TRNs) in alert animals (Keller, 1979; Grantyn and Berthoz, 1985; Berthoz et al., 1986; Munoz and Guitton, 1985a, 1986a; Moschovakis et al., 1988a,b). These neurons form the descending collicular efferent projection to the contralateral brainstem saccadic premotor circuitry (Keller, 1979). Although, as we shall see, the discharge of these cells is considerably more complex than hitherto suspected, the results do confirm that TRNs can indeed carry the presaccadic burst discharge.

An intriguing and important aspect of collicular organization is its relation to the control of eye-head orienting movements. The superficial layers of the SC are organized into a retinotopically coded map subtending up to about 80° of the contralateral visual field (Feldon et al., 1970). The central visual field is represented in the rostral SC, the peripheral visual field in the caudal SC. The organization of the motor map in the deeper layers presents a special problem. The oculomotor range is less than ±80°, such that an eye movement alone cannot attain a target, say at 80°. This problem is extremely well illustrated in the cat whose visuo-oculomotor system has been well studied and whose gaze (head-free) control system appears similar to that of man (Guitton, 1988). The cat has a restricted ocular motility yielding an oculomotor range of only ±25°. Consequently combined coordinated eye-head movements must be used to attain targets outside the oculomotor range.

The cat's tecto-reticulo-spinal (TRS) pathway forms a potentially powerful neural substrate for carrying gaze-related motor signals since it projects to both eye and head premotor centers within the brainstem and spinal cord (Grantyn and Grantyn, 1982; Grantyn and Berthoz, 1985). Furthermore, microstimulation of the deeper laminae of the cat SC, where tecto-reticulo-spinal neurons (TRSNs) are located, elicits coordinated eye and head movements (Hess et al., 1946; Syka and Radil-Weiss, 1971; Guitton et al., 1980; Roucoux et al., 1980) whose organization appears to be based on principles similar to those of naturally occurring eye-head orienting movements (Guitton et al., 1984). The evoked gaze movements are retinotopically coded as determined by the underlying visual projection.

To date, only a few studies in either cat (Straschill and Schick, 1977; Harris, 1980) or primate (Robinson and Jarvis, 1974) have reported single unit recordings in the SC of head-free animals. However, due to the very limited amount of data, none of these observations have yielded significant insight into how neural elements within the colliculus may be involved in gaze control in the animal whose head is unrestrained. This was the object of a number of studies of which this paper is a part (Munoz, 1988). It will be shown that TRNs and TRSNs (together called TR(S)Ns) provide the brainstem with both vector error and eye and head movement velocity and acceleration signals.

METHODS

Twelve cats were trained to perform several visuomotor tasks when their heads were either held immobile (head-fixed) or unrestrained (head-free) (Munoz and Guitton, 1985a, 1986a). Eye, head, and food target movements were measured by the search-coil-in-magnetic-field technique (Guitton et al., 1984). Animals were prepared for chronic recording in one surgical session, performed under Nembutal anaesthesia. An eye coil was sutured to the sclera of one eye. Extracellular single unit recordings were obtained from tectal efferent neurons using either glass micro-pipettes (Munoz and Guitton, 1985a) or stainless steel microwires (Palmer, 1978). Glass micro-pipettes were driven into the brain using a hydraulic microdrive attached to a stainless steel recording chamber. Bundles of ten 25 micron diameter stainless steel microwires were implanted into the SC. A bipolar concentric stainless steel electrode was inserted into the predorsal bundle, immediately rostral to the abducens nucleus, to antidromically activate the TRNs. The recording chamber or microwire connector pins, 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 expant that was anchored to the skull with stainless steel screws.

TRNs, located in the intermediate and deep layers of the cat SC, were identified antidromically by their responses following stimulation of the predorsal bundle. The antidromic nature of the response was verified using a number of criteria that included collision testing (Munoz and Guitton, 1985a). At least 2/3 of TRNs appear to project to the spinal cord (Grantyn and Grantyn, 1982). To underline this feature we have called our identified cells TR(S)Ns, since an unknown fraction of the population projected to the spinal cord.

In our experimental paradigm, the animal could be rapidly trained to make gaze shifts to both visual and predicted targets. Initially, the cat fixated a food target that was visible to one side of a barrier. The target then disappeared behind the barrier and reappeared to the other side. Following the reappearance of the target, the cat oriented to the visible target and was rewarded. The animal
quickly learned the above task and began predicting that the disappearance of the food target from one side of the barrier meant future reappearance of the target on the other side. On some trials the cat oriented from one side of the barrier to the other before the target reappeared, thereby orienting to a predicted target. The barrier width and orientation were adjusted to have the cat generate gaze shifts of various amplitudes and directions. The movement vector that was associated with the best response from the cell could then be determined.

RESULTS

A total of 259 TR(S)Ns were antidromically identified in 12 alert cats. While recording from a neuron, a battery of tests were undertaken that ranged from studies of the cell's visual responses to studies of its discharge during visuomotor orienting. Forty-seven percent (122/259) of these neurons were recorded from long enough to yield significant data.

In the subsequent paragraphs we present examples illustrating 3 important features of TR(S)N organization. (1) TR(S)Ns situated in the area centralis representation of the retinotopic map (to be called «rostral TR(S)Ns») present sustained discharges during fixation. (2) TR(S)Ns situated off the area centralis representation (to be called «caudal TR(S)Ns») present discharges that control eye-head orienting movements. These cells are driven by signals of both sensory and cognitive origin. Their discharge pattern can be subdivided into sustained and motor related components. (3) The profile of the frequency of discharge of caudal TR(S)Ns influences the velocity and acceleration profiles of eye and head trajectories. The data is presented for the head-free cat but recordings made in the head-fixed condition show similar results with identical interpretations.

CAUDAL TR(S)Ns: SUSTAINED AND PHASIC MOTOR RELATED DISCHARGES PRECEDING AN ORIENTING MOVEMENT.

Figure 1A shows the typical response of a TR(S)N located in the caudal SC, when a cat oriented to the predicted target in the head-free condition. The paradigm is schematically represented in fig. 1B-D. This cell, located in the caudal right SC (fig. 1F), had its visual receptive field (dashed circles in parts B-D) situated to the left of the fixation point (marked by an «X»). The food target (represented by the small filled circle) was initially visible to the right side of the barrier so that when the cat looked at the target, the left edge of the barrier was within the cell's visual receptive field (fig. 1B). The target was then hidden behind the barrier (fig. 1C) and the trained animal oriented to the left side (fig. 1D), since prior training had taught it to anticipate the reappearance of the target on that side.

To clearly demonstrate the presence of an increase in TR(S)N discharge that had both sustained and motor related components it was necessary to increase the duration between target disappearance and onset of the gaze shift. Repeating the target trajectory illustrated in fig. 1B-D several times without rewarding the animal generated some trials in which the animal's behavioral response, the leftward gaze shift, lagged the disappearance of the target by several hundred milliseconds.

Figure 1A illustrates one such trial in which the head-free cat oriented to the predicted target almost one second after the food disappeared from the right side of the barrier. The cell began to discharge in a sustained manner shortly after the target was hidden (dashed line denotes target disappearance). This sustained discharge continued until the gaze shift was made (onset marked by solid vertical line). Note also a small increase in the firing rate of the neuron which occurred immediately prior to movement onset and was associated with the orienting response itself; it was clearly dissociated from the initial onset of sustained activity that followed target disappearance.

We will consider the nature of this movement-related phasic discharge in greater detail below. First, let us concentrate on the sustained firing pattern. Note that the TR(S)N was silent in condition B, whereas it was active in C. The visual input to the cell was the same in both conditions; namely, the left edge of the barrier passed through the cell's receptive field. However, the two behavioural conditions are different. First, in B the cat attentively fixated the target whilst in C no specific target was being fixated; the animal's visual axis was essentially «parked» to one side of the blank barrier. In other experiments, which we cannot elaborate on here, we have shown that the behavioural act of attentive fixation inhibits TR(S)Ns located off the area centralis representation: i.e., the elimination of attentive fixation increases caudal TR(S)N excitability (Munoz and Guittion, 1986b, 1987a). Second, in C the animal's behavioural set was such that it anticipated the reappearance of the target on the left side (Munoz and Guittion, 1985a). The combination of these two mechanisms created the sustained discharge pattern of TR(S)N activity whose functional role appeared to be to maintain, at a light level of discharge, a specific zone of the SC which in turn depolarized its associated «downstream» neural machinery in anticipation that this SC-reticular formation ensemble might eventually be used to trigger a movement. Thus, the sustained activity for a given neuron was specific to a limited family of vectors (gaze position error vectors) drawn between the current gaze position and the target: visible or imaginary as in the predicted target condition. This is illustrated in fig. 1E for this neuron. The intersection of the horizontal and vertical axes represents the target. Each tick mark on the axes marks 10° eccentricity. The outermost circle encloses a surface within which any position of the visual axis will be associated with a sustained discharge of this TR(S)N and is defined as the neuron's gaze position error field (GPEF). The vector from the circle's center to the origin is the optimal gaze position error vector for this cell and is associated with the highest level of sustained discharge. Vectors that begin off center are associated with a lower discharge frequency. The GPEF
Fig. 1. — Motor related discharges of a caudal TR(S)N. A. Single trial showing cell discharge when cat oriented to the predicted target. Shown from top to bottom are the horizontal target (Th), head (Hh), eye (Eh), and gaze (Gh) position traces followed by the instantaneous frequency histogram of cell H1 discharge. B-D. Schematics illustrating the different behavioral situations. Cell has its visual receptive field (dashed circle) located to the left of the fixation point (marked by X). B. The cat fixes the food target (filled circle) located to the right of the barrier. The left edge is in the cell's receptive field. C. Food-target (empty circle) is moved behind the barrier. D. Trained cat orient to the left side of the barrier, anticipating target reappearance. E. Plot of this cell's gaze position error field. Target is located at the intersection of the horizontal and vertical lines. Tick marks are placed 10° apart. Outermost contour encloses all gaze position errors for which cell H1 was active. We call this a gaze position error field. Innermost contour encloses gaze position errors yielding maximum discharge. The arrow represents the optimal movement vector for this neuron. F. Schematic view of the right SC. This TR(S)N was located in the caudal SC along the representation of the horizontal meridian.

Décharges en rapport avec l'activité motrice d'un TR(S)N caudal. A. Expérience unique montrant une décharge cellulaire lorsque le chat était orienté en direction de la position prévue de la cible. De haut en bas : cible horizontale (Th), tête (Hh), œil (Eh), regard (Gh). Les traces sont suivies de l'histogramme de fréquence instantanée de la décharge cellulaire H1. B-D. Schémas illustrant les différentes situations comportementales. La cellule a un champ visuel réceptif (cercle hachuré) à la gauche du point de fixation (marqué par un X). B. Le chat fixe la cible « aliment » (cercle plein) située à droite de la barrière. Le bord gauche est dans le champ réceptif de la cellule. C. La cible « aliment » (cercle vide) est déplacée derrière la barrière. D. Un chat entraîné s'oriente du côté gauche de la barrière, anticipant la réapparition de la cible. E. Coordonnées de l'erreur de position du regard de cette cellule. La cible est située à l'intersection des lignes horizontales et verticales. Les marques sont placées à 10°. Le contour situé le plus à l'extérieur englobe toutes les erreurs de position du regard pour lesquelles la cellule H1 était active. Nous avons nommé cet ensemble champ d'erreur de position du regard. Les contours les plus internes englobent les erreurs de position du regard produisant les décharges maximales. La flèche représente le vecteur du mouvement optimal pour ce neurone. F. Aspect schématique du SC droit. Ce TR(S)N était situé dans le SC caudal le long de la représentation du méridien horizontal.

for the neuron illustrated in fig. 1 is large, subtending some 45°, and centered at about 30° on the horizontal meridian (fig. 1E). The broad tuning of TR(S)N GPEFs implies (McIwain, 1986) that a large number of TR(S)Ns are active for a given gaze position error.

Note that the sustained discharge ultimately yields to a phasic discharge which precedes the movement. In cases where there is no movement the sustained discharge gradually disappears (Munoz and Guitton, 1985a).

The movement related discharge pattern that was illustrated in fig. 1 was characteristic of most of the TR(S)Ns located in the caudal SC. Eighty-six percent (50/58) of the caudal TR(S)Ns were activated with a sustained discharge, coding the gaze position error to a predicted target. Sixty-four percent (32/50) of the TR(S)Ns that presented a sustained discharge, subsequently increased their firing rate prior to the onset of a particular vector of orienting movement to a predicted target. The remaining cells (18/50) continued to discharge at an approximately constant sustained rate until the end of the gaze shift to the predicted target. Almost all caudal TR(S)Ns studied (66/70) increased their rate of discharge prior to visually-triggered orienting movements (Munoz and Guitton, 1986a). TR(S)N discharges related to spontaneous movements were not studied in detail since cats rarely generated large amplitude spontaneous gaze shifts. Nonetheless, some TR(S)Ns were active, albeit weakly, for some spontaneous movements made in the dark. Caudal TR(S)Ns were most active during movement to the visible target and least active, or silent, for spontaneous movements.
ROSTRAL TR(S)Ns: SUSTAINED DISCHARGES RELATED TO ATTENTIVE FIXATION

TR(S)Ns located in the rostral SC were maximally active when a cat attentively fixated a target of interest (i.e., 0° gaze position error). Their excitability was reduced when the animal's locus of attention was disengaged from fixation and directed peripherally (Munoz and Guitton, 1988). When the cat oriented and subsequently fixated upon a peripheral stimulus, the pattern of discharge recorded from rostral TR(S)Ns manifested itself as the inverse of the pattern described above for caudal TR(S)Ns.

Figure 2A illustrates the activity of a TR(S)N located in the area centralis representation of the rostral left SC, when the head-free cat generated a leftward orienting movement towards a predicted target. The TR(S)N was active at the start of a trial, while the cat fixated the target on the right side of the barrier (fig. 2B). Shortly after the target disappeared behind the barrier (fig. 2C), the rate of discharge began to decrease. Firing resumed at the termination of the gaze shift (fig. 2D), when the eye and head were still in motion. Note however that the rate of discharge usually (unlike in this example) did not reach pre-movement values since in fig. 2D the visual axis was now not fixated upon the visible food target. If rather than moving the target from the right side to behind the barrier, the target was moved from the right to the left side, the pattern of activity was similar to that shown in A. The cell was tonically active during fixations and silent both when fixation was broken and during the gaze shift.

As in fig. 1 and by analogy with caudal TR(S)Ns, the gaze position error field of this neuron is plotted in fig. 2E. For this neuron, the optimal gaze position error vector was zero. When the visual axis was within the outermost circle, the cell presented a sustained discharge. Maximum firing frequency occurred when gaze was on target. Note that the food target need not be visible: it was only necessary that the cat be attentive to a specific point in its visual surround (as in the condition of fig. 2D).

These results also imply that a large number of TR(S)Ns,
centered on the « zero » representation of the retinotopic map, are active (fig. 2F). When the cat fixes an object of interest, TR(S)Ns located at 0° are most active and the active zone extends to a radius of about 10° on the map.

**RELATIONSHIP BETWEEN TR(S)N FIRING FREQUENCY PROFILE AND GAZE VELOCITY PROFILE**

We will now present evidence linking the discharge patterns of caudal TR(S)Ns to the metrics and velocity characteristics of eye, head, and gaze orienting movements. To facilitate a description of this relationship, we will consider a family of orienting responses, triggered in a paradigm in which the food target was not halted behind the barrier but was instead moved in a continuous motion from one side of the barrier to reappear on the other side. In an experienced cat, gaze shifts to reorient the visual axis onto the food were triggered either before or after target reappearance. Examples of such orienting movements are shown in fig. 3 along with the associated neuronal activity of the same TR(S)N as shown in fig. 1. The left and right vertical dashed lines correspond to target disappearance and reappearance respectively. The solid vertical line denotes onset of the leftward orienting movement. Each trial began with the cat fixing the food target located on the right side of the barrier, thereby placing the left edge in the visual receptive field of this neuron (see fig. 1B). The target was then moved behind the barrier and reappeared on the left. The orienting movement was triggered either before or after target reappearance. There was a continuum of response latencies between these two conditions. Each trial terminated with the cat fixing the target on the left.

In each of the trials illustrated in fig. 3, the TR(S)N began its sustained discharge shortly after the target disappeared from the right side and continued to fire until the end of the leftward gaze shift. In fig. 3A the movement began when the target was still in motion and before it had reappeared from behind the barrier. In association with these predictive movements, the neuron discharged a low frequency train of action potentials. Furthermore, the gaze velocity profile appeared somewhat flattopped or blunt.

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**Fig. 3.** Effects of prediction and vision on characteristics of cat’s orienting movement and caudal TR(S)N’s discharge pattern. Food target was moved from the right side of the barrier (left dashed line) to reappear on the left (right dashed line). The cat generated the leftward gaze shift (solid line) at different times relative to target reappearance. Shown from top to bottom are the horizontal target (Th), head (Hh), eye (Eh), and gaze (Gh) position traces; the horizontal gaze (Gh), eye (Eh) and head (Hh) velocity traces; followed by the instantaneous firing frequency histogram. A. Leftward gaze shift initiated before target reappears on left. B. C. Leftward orienting movement initiated after target reappears on left. See text for further details.

_Effets de la prédiction et de la vision sur les caractéristiques du mouvement d’orientation du chat et de la décharge du TR(S)N caudal. La cible « aliment » s’est déplacée sur le côté droit de la barrière (ligne hachurée gauche) pour reapparaître sur le côté gauche (ligne hachurée droite). Le chat a généré un changement de regard vers la gauche (ligne pleine) à différents intervalles de temps en rapport avec la réapparition de la cible. De haut en bas : tracés de position de la cible horizontale (Th), de la tête (Hh), de l’œil (Eh), et du regard (Gh) ; tracés des vitesses du regard horizontal (Gh), de l’œil (Eh), de la tête (Hh) ; suivis de l’histogramme de fréquence instantanée de mise en jeu. A. Mouvement du regard vers la gauche initié avant la réapparition de la cible sur la gauche. B. C. Mouvement d’orientation vers la gauche initié après la réapparition de la cible sur la gauche. Voir le texte pour d’autres détails._
When the orienting movement began at least 50 ms after the target reappeared (fig. 3C), the cell, in addition to carrying the low frequency sustained discharge, also presented a high frequency burst of spikes shortly after the target reappeared (about 40 ms) and immediately before (about 25 ms) the onset of the gaze shift. In association with this high frequency burst from the TR(S)N, the eye, head, and gaze velocity profiles had greater accelerations and reached higher velocities than the profiles of movements triggered in the absence of the burst.

A transition zone existed between movements that were either predictive or visually guided: gaze shifts in this category were initiated 0-50 ms after the target reappeared. An example of a head-free gaze shift triggered within this transition zone, is illustrated in fig. 3B. This gaze shift was initiated about 15 ms after target reappearance and the initial slowly rising gaze, eye, and head velocity profiles suggested a movement to a predicted target. Following the initial increase in velocity there exists, in each of the eye, head, and gaze traces, a deceleration phase which suggests that peak velocity would soon be attained. The velocity at each arrow is comparable with the peak velocity in the adjacent traces of fig. 3A thereby suggesting that the eye, head, and therefore gaze in fig. 3B are driven, at least initially by discharges characteristic of movements to predicted targets. However, as evidenced by the inflection point on each trace (marked by arrows) the trajectory of the orienting response was modified in mid-flight: all profiles showed a reacceleration, thereby assuming a new shape that was more characteristic of a gaze shift to a visible target (see fig. 3C). Most interestingly, the discharge pattern of the TR(S)N showed comparable changes. At the onset of the gaze shift, the neuron was only firing at a low frequency rate, a pattern of activity characteristic of movements to the predicted target. Shortly after target reappearance, but within the gaze shift, the cell discharged a high frequency burst of spikes whose onset preceded the modification of the gaze and eye trajectories by 9 ms and the head trajectory by 29 ms. It was possible to mimic these modified trajectories with different patterns of electrical stimulation applied to the deeper laminae of the cat SC (Munoz and Guitton, 1987b).

QUANTITATIVE RELATIONS BETWEEN TR(S)N. DISCHARGES AND MOVEMENT METRICS

The examples shown in fig. 3 suggest that eye, head, and consequently gaze maximum velocities are greater when the orienting movement is made to a visible target compared to a predicted target. This is shown more explicitly in fig. 4A for the maximum gaze velocity of the cat whose TR(S)Ns are being described. The data are grouped into 5° bins of movement amplitude and expressed at the mean ± standard error. For a given amplitude gaze shift, the peak velocity attained in the visible target condition (filled circles) was always greater than when the target was predicted (empty circles). These differences were statistically significant (p < 0.01). It follows that gaze duration should show the opposite effect (fig. 4B). The asterisk marks the only nonsignificant difference between the target conditions.

In discussing fig. 3, we suggested that the intensity of TR(S)N movement related discharges covaried with gaze velocity. In order to quantify this relationship, we measured the average firing frequency of the neuron and plotted it against the average gaze velocity of the movement. The average firing frequency was measured across an interval from 50 ms before movement onset through to its termination. This time period was chosen because high frequency TR(S)N bursts could precede: (1) movement onset by up to 50 ms; and (2) mid-flight modifications of gaze trajectory by as little as 7 ms. The data plotted in fig. 4C and D compare movements to predicted (empty circles) and visible (filled circles) targets. Gaze shifts that could not be classified as either predictive or visually triggered (e.g., fig. 3B), were omitted from this analysis. The data set are matched for equal direction and amplitude of movement. Gaze shifts were leftward and 24° to 32° in amplitude. The average firing frequency of our representative caudal TR(S)N increased with the average gaze velocity of an orienting movement (fig. 4C). A linear regression analysis of these data produced the solid line with a correlation coefficient of 0.66.

Recall from fig. 4A, B, that, not only was a movement to the visible target faster, it was also shorter in duration than a movement of comparable amplitude directed toward the predicted target. In fig. 4D we have plotted the number of spikes, counted from 50 ms before movement onset through to its termination, against the average gaze velocity for the same trials described above. The correlation between the number of spikes and the average gaze velocity was poor (r = 0.10). Hence, for a given amplitude and direction of movement the number of action potentials discharged remained independent of whether the gaze shift was made to a visible or predicted target, and therefore of movement velocity.

DISCUSSION

FIXATION VERSUS ORIENTATION: CHANGES IN THE SITE OF SC ACTIVITY

Figure 5 summarizes, in a cartoon-like fashion, the results presented above and illustrates how the site and intensity of collicular efferent activity varies in an orienting task. Each part of the figure depicts schematically the retinotopic map obtained by slicing through the deeper collicular layers at the level where TRNs and TRSNs are located. In fig. 5A the animal is attentively fixating an object of interest: hence there is a zone of activity centered on the area centralis representation which is the «zero» of the map. The most
active TR(S)Ns are at the center of this zone and the level of activity of these neurons decreases with their distance from zero.

At some time later, the object being fixated is still of prime importance to the animal, but we indicate in fig. 5B that new targets of secondary interest are now being retained in spatial register. This is done by maintaining small zones of depolarized activity at each target's appropriate location on the coordinates of the SC motor map which is in register with the overlapping retinotopic map. These secondary discharges are what we have called the sustained discharge (fig. I): an activity which is similar to that described for collicular "quasi-visual" cells by Mays and Sparks (1980). We suggest that this discharge essentially acts as a preparatory signal which depolarizes collicular and associated brainstem neural circuits in the eventualty that they will be called upon to initiate a gaze shift.

The level of the sustained discharge is very dependent on the level of activity at 0. Indeed, we have shown that attentive fixation (= activity at the 0) actively inhibits inputs onto TR(S)Ns in the caudal SC (Munoz and Guittot, 1986b, 1987a). Experiments by others have shown inter-and intra-collicular inhibitory mechanisms (Mascetti and Arriaga, 1981; Douglas and Vetter, 1986). We propose that activity at 0 inhibits the rest of the SC.

If the animal's attention is now shifted to one of the peripheral targets, say the one on the horizontal meridian, then the intensity of discharge at that new site will increase.
Fig. 5. — A. Spatial variations in collicular efferent discharges during an orienting movement. Each oval-like drawing represents an idealized oblique view of a tangential plane through the collicular layers where TR(S)Ns are located. Cat is fixating a target of interest and there is a raised profile indicating an increase in activity at the area centralis representation of the retinotopic map. The height of any point on this "hill" is a measure of the firing frequency of a TR(S)N below it. D. The "hill" is now centered on a point in the more caudal aspects of the SC and the discharge controls a gaze shift to a new target. B and C. Intermediate stages in the target selection process. See text for details.

Variations spatiales dans les décharges éfferentes colliculaires au cours d'un mouvement d'orientation. Chaque ovale représente une vue oblique idéale d'un plan tangenti à travers des couches colliculaires où se trouvent les TR(S)Ns. Le chat fixe une cible et est indiqué par une élévation de l'activité au niveau de la représentation de l'aire centrale de la carte rétinoto-lique. La hauteur de chaque point sur ce "monticule" est une mesure de la fréquence de mise en jeu d'un TR(S)N au-dessous. D. Le "monticule" est cette fois centré sur un point de niveau plus caudal du SC et la décharge contrôle un déplacement du regard vers une nouvelle cible. B et C. Étapes intermédiaires dans le processus de sélection de la cible. Voir le texte pour les détails.

(the most caudal site in fig. 5B-D) while activity at 0 decreases. The intensity of the activity at the new locus is determined by two causes: (1) For a cognitively defined target (i.e., one that is not defined by direct sensory cues) the collicular motor-related phasic discharge will be generated presumably by direct and indirect frontal lobe inputs (Guitton et al., 1985; Hikosaka and Wurtz, 1985a, b; Segraves and Goldberg, 1987). (2) If, on the other hand, the new target is defined by a direct sensory cue (e.g., a mouse that moves), then the rise of activity will be due to the TR(S)N's sensory inputs. If either or both of the sensory and cognitive drives are strong then the caudal zone of the SC will grow at the expense of all others including the activity at 0.

Our data indicate that the zone of sustained activity, corresponding to a single target of interest, moves about the collicular map as the cat fixates different points in space relative to that target. Thus, sustained activity appears to be dependent on whether or not the target is worth orienting to. We have observed this activity to last more than 10s (Munoz and Guitton, 1985a). By comparison, the increase of activity leading to the burst discharge that drives eye and head movements, occurs very rapidly. This rapid increase could be due, at least in part, to the positive feedback effects of the mutually inhibitory relations between the new active site and fixation activity at 0.

In summary, we have proposed that the collicular layer containing TR(S)Ns can be imagined as a playing field upon which mechanisms favouring fixation are opposed to those driving orientation. Higher centers of the CNS such as the frontal eye fields could be responsible for providing the "push" needed by one side or the other to define, albeit temporarily, the nature of the SC output signal.

Movement related phasic discharges modulate gaze velocity

We have seen that a collicular zone of phasically active
Fig. 6. — A. Proposed links between SC and brainstem oculomotor circuitry. Schematized dorsal view of the left and right SC is shown at top. Two TRS axons leave each colliculus. The cell body of one is situated on the area centralis representation (where the two axes meet) and projects to omni-pause neurons (OPNs). The other originates from a more caudal site and projects to long lead burst neurons (LLBNs). The contents of the box labelled oculomotor system are described in the text. The TRS system also projects to the head motor system whose contents are left blank. The outputs of the eye and head motor systems are eye-position-relative-to-head (E/H) and head-position-relative-to-space (H/S). These are used in the feedback loop shown at the top to calculate gaze position error (E/T) which is the input to the SC. See text for details. B. Schematized discharge patterns of various neurons in the adjacent circuit when a cat, with its gaze (G) first on a fixation point (FP), orients to a target (T). Dashed line on left indicates offset of FP and onset of T. Middle and right dashed lines indicate start and end of gaze shift. rTRSN: rostral, cTRSN: caudal, fixation type, TRSN. Other abbreviations and explanations in text.

A. Relations hypothétiques entre le SC et les circuits oculomoteurs du tronc cérébral. En haut, vue dorsale schématique des SC gauche et droit. Deux axones TRS partent de chaque colliculus. Le corps cellulaire de l'un se trouve sur la représentation de l'aire centrale (où les deux axes se rejoignent) et projette sur les neurones omni-pause (OPNs). L'autre naît d'un site plus caudal et projette vers les neurones « à déclenchement long » (LLBNs). Le contenu du cadre nommé système oculomoteur est décrit dans le texte. Le système TRS projecte aussi vers le système moteur de la tête dont le contenu est laissé en blanc. Les sorties des systèmes moteurs de l'œil et de la tête sont de types « position de l'œil par rapport à la tête » (E/H) et « position de la tête par rapport à l'espace » (H/S). Elles sont utilisées dans la boucle de rétro-contrôle montrée en haut afin de calculer l'erreur de position du regard (E/T) qui est l'entrée vers le SC. Voir texte pour les détails. B. Niveaux de décharge schématiques de différents neurones du circuit ci-contre lorsqu'un chat, dont le regard (G) se fixe d'abord sur un point (FP), s'oriente ensuite vers une cible (T). La ligne hachurée sur la gauche indique la terminaison de FP et le début de T. Les lignes hachurées au milieu et à droite indiquent le début et la fin du déplacement du regard. rTRSN: TR(S)N rostral, de type fixation ; cTRSN: TR(S)N caudal, de type orientation. Pour les autres abréviations et explications, voir le texte.
neurons drives a coordinated eye-head movement thereby yielding a gaze shift whose vector is determined by approximately the "center of gravity" of the active zone. In a prior communication we suggested that TR(S)N discharges influence gaze velocity in the head-fixed and free cat (Munoz and Guitteny, 1985b, 1986a). The similarity between the TRSN temporal activity profile and the eye velocity profile, in the head-fixed cat, was shown by Berthoz et al. (1986). Rohrer et al. (1987) also showed that there is a link between saccadic velocity and the discharge intensity of saccadic related burst neurons in the head-fixed monkey SC. It is of considerable additional interest that a sudden increase in the intensity of TR(S)N discharge is related to an abrupt acceleration of the eyes and head at latencies of about 10 and 30 ms, respectively. In the oculomotor system this suggests strongly that the TRS system is part of the saccade burst generator and we will consider this in the next section. Such results also complement well the observed decrease/increase in saccadic velocity following pharmacologically induced deactivation/activation of the monkey SC (Hikosaka and Wurtz, 1985a, 1986; Lee et al., 1988).

FUNCTIONAL INTERACTIONS BETWEEN TR(S)N ACTIVITY AND BRAINSTEM PREMOTOR CIRCUITRY

Saccadic eye movements are generated by a burst of neural activity in the agonist motoneurons and inhibition of the antagonist motoneurons. These signals are provided to motoneurons by excitatory (EBN) and inhibitory (IBN) burst neurons (see Fuchs et al., 1985 for review). Figure 6 illustrates some of the neural elements linking the SC to EBNs. Long-lead burst neurons (LLBNs) begin to discharge a low frequency preambles up to 100 ms before a saccade, followed by a high frequency burst immediately prior to initiation of the eye movement (Luschei and Fuchs, 1972; Keller, 1974; Curthoys et al., 1981). These neurons presumably mediate collicular activation of the EBN; they receive monosynaptic collicular input and begin their high frequency bursts after collicular saccade related burst neurons but before the EBNs (Raybourn and Keller, 1977; Keller, 1981). Another population of premotor cells, tonically active omnipause neurons (OPNs), pause for saccades in all directions (Luschei and Fuchs, 1972; Keller, 1974), providing a potent inhibition of EBNs (Curthoys et al., 1984) and IBNs (Nakao et al., 1980) during the inter-saccade interval, thereby gating out any LLBN activity not related to saccade initiation. Collicular stimulation produces monosynaptic activation of OPNs followed by a potent polysynaptic suppression (Raybourn and Keller, 1977). From the time course of LLBN activation and OPN suppression that follows collicular stimulation, Raybourn and Keller (1977) postulated that some LLBNs may inhibit the OPNs. In addition, recent morphological studies of OPNs (Ogaki et al., 1987; Strassmann et al., 1987) have revealed axonal projections, not only to regions of the reticular formation containing EBNs and IBNs, but also to those areas known to contain LLBNs. Therefore, OPNs may also exert inhibition onto LLBNs. Further evidence in favour of this hypothesis is provided by measurements of OPN excitability changes in relation to the initiation of the quick phases of nystagmus (Kamogawa et al., 1983). There is a moderate decrease in OPN excitability 40-50ms prior to the initiation of the fast phase. This time corresponds to the mean onset of the LLBN "preamble" discharge in this preparation (Curthoys et al., 1981). There is a more intense reduction in OPN excitability that occurs at fast phase onset and continues until the end of this rapid eye movement (Kamogawa et al., 1983). This stage corresponds to the time of cessation in OPN discharge. If LLBN and OPN populations maintain reciprocal inhibitory interconnections, then once OPN discharge is halted, LLBN excitability increases, leading to the generation of a burst which then further inhibits the OPNs. An alternative mechanism has been hypothesized whereby IBNs and OPNs mutually inhibit one another (Scedder, 1988). However, Ito et al. (1986) have argued that such a connection from the IBN onto the OPN may not exist. The requirement for mutual inhibition between burst and pause cell pools has been postulated in order to maintain accurate control of the burst duration (Robinson, 1975; Keller, 1977). The reciprocal inhibition between LLBNs and OPNs could satisfy this requirement.

We speculate here that caudal TR(S)Ns, active for non-zero gaze position errors, exert excitation onto LLBNs to facilitate the initiation of a movement. On the other hand, TR(S)Ns in the rostral SC, active for 0° gaze position error (i.e., visual axis fixed upon a target of interest), may convey excitation to OPNs, thereby suppressing the initiation of movement. These connections are shown in fig. 6A. The movement-related discharge patterns of TR(S)Ns described in this paper and in more detail elsewhere (Munoz and Guitteny, 1985a, 1986a, 1987b, 1988; Munoz, 1988) support this hypothesis. Caudal TR(S)Ns whose optimal gaze position error vectors correspond to the direction and amplitude of the gaze shift increase their rate of discharge immediately prior to movement onset, as shown schematically in fig. 6B. Meanwhile, as we have discussed in relation to fig. 5, there is a concomitant reduction in the activity emanating from the rostral fixation zones. We propose that the enhanced discharge of caudal TR(S)Ns and reduced firing by rostral TR(S)Ns could produce excitation of LLBNs and simultaneous disinhibition of OPNs, thereby making the latter cells vulnerable to LLBN inhibition. When LLBN inhibition of OPNs supersedes the diminished excitation emanating from the rostral SC, OPN discharge should cease and LLBNs begin to burst, thereby providing direct activation of EBNs. The different motoneuron pools would then receive the appropriate excitatory or inhibitory burst to drive the saccade. At the termination of the gaze shift, activity in the caudal SC subsides while TR(S)Ns in the rostral SC are reactivated. Concurrently, LLBN discharge
ceases and OPNs resume their tonic rate of firing, thereby inhibiting the EBNs and IBNs.

What about the head movement control? We have shown that TR(s)N discharges influence head acceleration and velocity profiles. This is indicated in fig. 6a by the schematic input of the TRS system onto the head motor system. This box is left blank both because of our scant knowledge of its contents but also because it is beyond the scope of this paper to consider them.

THE GAZE CONTROL FEEDBACK SYSTEM

Considerable evidence now shows that the position of the visual axis in space is controlled by a feedback loop which compares current gaze (G = eye position relative to the head (E/H) + head position relative to space (H/S)) to desired gaze (GD) to yield a gaze position error signal (E/T) which drives the eye and head motor systems towards the target (see Guitton and Volle, 1987; Guitton, 1988 for reviews). Experiments also indicate that E/H is a corollary discharge while H/S is obtained from integration of the semicircular canal output.

Robinson (1975) first proposed a local feedback model to control the saccade burst generator. Keller (1981) incorporated the SC and known brainstem circuitry into this scheme, whereby feedback of E/H passed through the SC. We have modified this version in fig. 6a to include gaze feedback through the SC. Our recordings from TR(s)N indicate these neurons code E/T: a discharge, say at 60° on the cat SC retinotopic map, drives a 60° gaze shift. This implies that the E/T signal is an input to the SC, as shown at the top of fig. 6a, and acts not only to select the appropriate collicular locus of discharge, but also to decrease the causal TR(s)N discharge and initiate rostral TR(s)N activity once gaze is on target. Such a feedback circuit would also naturally incorporate the link between TR(s)N discharge frequency and gaze acceleration and velocity profiles as discussed in previous sections.

REFERENCES

GAZE FIXATION AND ORIENTATION CONTROL AND TECTO-RETICULO-SPINAL SYSTEM


