Stimulation of the Superior Colliculus in the Alert Cat

I. Eye Movements and Neck EMG Activity Evoked when the Head is Restrained

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Summary. Electrical stimulation of the cat superior colliculus (SC), in conjunction with the accurate measurement of elicited eye movements and histologically verified electrode positions, has revealed a striking antero-posterior variation in collicular organization. Three zones could be defined in the SC on the basis of eye movement patterns and associated neck muscle EMG activity evoked from the deeper layers. The *Anterior* zone was coextensive with the central 25° of the visual retinotopically coded map contained in the superficial layers. Saccades evoked from this zone were also retinotopically coded, and the latency of EMG activity depended on the position of the eye in the orbit. A similar observation applies to the entire monkey SC. The *Intermediate* zone was coextensive with the 25°–70° of visual projections. Saccades evoked from this region were "goal-directed" and were associated with invariant, short latency EMG responses. The *Posterior* zone was found in the extreme caudo-lateral portion of the SC. Eye movements evoked from this zone were centering saccades associated with constant latency EMG activity. The present results in conjunction with previously demonstrated antero-posterior variations in projections to the SC, suggest that the motor strategies controlling gaze shifts toward visual targets vary depending on the location of the target in the visual field.

Key words: Cat – Stimulation – Superior colliculus – Eye movements – Eye-head coordination

It is well known that electrical stimulation applied to the deeper layers of the monkey superior colliculus

(SC) evokes saccadic eye movements that are retinotopically coded (Robinson 1972; Schiller and Stryker 1972). When a specific collicular point is stimulated, the amplitude and duration of the evoked movements are constant and independent of the initial eye position. A characteristic feature of these saccades is that they displace the visual axis to the part of the visual field which is projected onto that part of the colliculus (Schiller and Koerner 1971; Schiller and Stryker 1972). It has also been shown that units in the deep layers of the monkey SC discharge before saccades that are similar in direction and amplitude to those evoked by electrical stimulation (Schiller and Stryker 1972). Taken together, this evidence suggests that, in monkey, the electrical stimulus mimics a motor command that in the normal animal plays a role in controlling the orientation response to new visual stimuli appearing in the peripheral field.

The situation in the cat appears more complex. In this species, the range of eye movements is relatively small and does not exceed about 25° from the central gaze position (Stryker and Blakemore 1972; Crommelinck and Roucoux 1976; Stein et al. 1976; Collewijn 1977; Crommelinck et al. 1977a; Evinger and Fuchs 1978). However, the retinal projection to the superficial layers covers up to 80° of the visual field (Feldon et al. 1970). Of particular interest, therefore, is the nature of the motor signal controlling orientations toward visual targets appearing more than 25° from the cat's primary eye position. Important clues to the understanding of this motor organization may be obtained by studying the eye and head movements evoked by stimulating the deep layers of the cat colliculus.

In spite of numerous experimental studies, there is still considerable debate as to the nature of the evoked eye movements. Hyde and Eason (1959) reported that stimulation of the cat SC evoked eye

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movements that bring the eye to the same final position, independent of the initial one. They called this pattern of responses "goal-directed". Other authors have reported that, depending on the collicular site being stimulated, either retinotopic or goal-directed saccades can be evoked (Straschill and Rieger 1973; Roucoux and Crommelinck 1976; Crommelinck et al. 1977b). Some experimenters, however, have not been able to elicit goal-directed saccades in cat and have put forward the hypothesis that such movements result from mechanical constraints which disturb the trajectory of evoked saccades as they approach the limits of the oculomotor range (Schiller 1972; Stein et al. 1976). A further controversy exists regarding the sites from which goal-directed saccades can be evoked. Straschill and Rieger (1973) have suggested that goal-directed movements are evoked from deep layers, whereas retinotopically coded movements are evoked from the superficial layers. On the other hand, Roucoux and Crommelinck (1976) and Crommelinck et al. (1977b) have suggested that goal-directed movements are only evoked from the caudal region of the S.C.

In this study, we describe the eye movements and neck muscle EMG activity evoked when the cat's head is held fixed. In a second paper, we describe the coordinated eye and head movements evoked when the animal's head is released, free of any mechanical constraints. Portions of these studies have been described elsewhere (Crommelinck et al. 1977b; Guitton et al. 1977).

Methods

Experiments were performed on 6 adult cats.

Eye Movement Recording

Eye movements were recorded with the electromagnetic technique (Robinson 1963), using frequency coding. The sensitivity of the system (10 mV/degree for a 3 turn coil around the eye) together with its frequency response (1 kHz) permitted the detection of eye movements smaller than 15 min arc. The DC drift in the system was very low and could be continuously monitored.

Animal Preparation

Surgery was performed in two separate sessions. In the initial session, each cat was anesthetized and a coil, made of 3 turns of teflon-coated stainless steel wire, was sutured to the sclera in a plane approximately perpendicular to the optical axis of the eye. The tightly twisted wire was lead out near the outer canthus following the method of Fuchs and Robinson (1966). Two neck EMG electrodes were thrust into the left biventer cervicis muscle.

Final surgery was performed some 14 days after the first session. A stainless steel well was secured by dental acrylic over an opening that had been stereotaxically located in the skull to permit a vertically driven microelectrode to reach the colliculus. Threaded sleeves designed to attach the cat's head were also anchored to the acrylic implant.

Calibration of the Eye Coil

While the animal was still anesthetized, an accurate calibration of eye position was done. Calibration of the eye's primary position was first undertaken using previous results (Crommelinck et al. 1977a). The output voltage from the demodulating electronic circuitry was adjusted to zero when the eye was in its primary position. The sensitivity of the eye coil was then calibrated by two methods. First, by means of threads anchored to the conjunctiva, the eye was rotated through known angles. Second, the field coils themselves were rotated. The mean of the two calibration values was used.

Experimental Procedure

Experimental sessions began after a recovery period of one week after the second intervention. The right SC was stimulated by delivering trains of 0.5 ms cathodal pulses at a frequency of 400 Hz through a steel microelectrode (impedance 3–5 MΩ at 1 kHz). In each cat, selected sites were tested to determine a stimulus threshold, defined as the current required to evoke saccades in 50% of the trials. To obtain the experimental data, the stimulus was set equal to twice the threshold. The resulting current ranged from a few µA to 100 µA depending on the collicular layer being stimulated. The electrical stimulus was applied while the animal looked spontaneously about the room in response to various novel stimuli, such as morsels of a favorite food, movements of the experimenters, noises, etc. Care was taken to assure that the animal was utilizing its full oculomotor capabilities.

Eye movements were visualized and recorded on the face of a storage oscilloscope operating in the X-Y mode. The Z-axis was modulated with a train of 1 ms pulses at a frequency of 400 Hz for the duration of each evoked saccade.

Selected sites were marked by passing a DC current through the steel stimulating electrode. At the end of the last experimental session, the animal was anesthetized and perfused with a ferri-ferrocyanide, 10% formalin solution, and the blue spots thus produced were used to reconstruct the electrode tracks.

Results

The Cat's Oculomotor Range

The oculomotor range (OMR), defined as the locus of maximum ocular deviations, was measured in every cat. The OMR, as viewed in the X-Y mode, was roughly circular with a mean diameter of 46° for 6 cats. The OMR is represented as a dotted contour in subsequent figures. The center of this contour corresponds approximately to the cat's primary visual position (Crommelinck et al. 1977b) and, in all figures, this point is marked by the intersection of the horizontal and vertical axes.
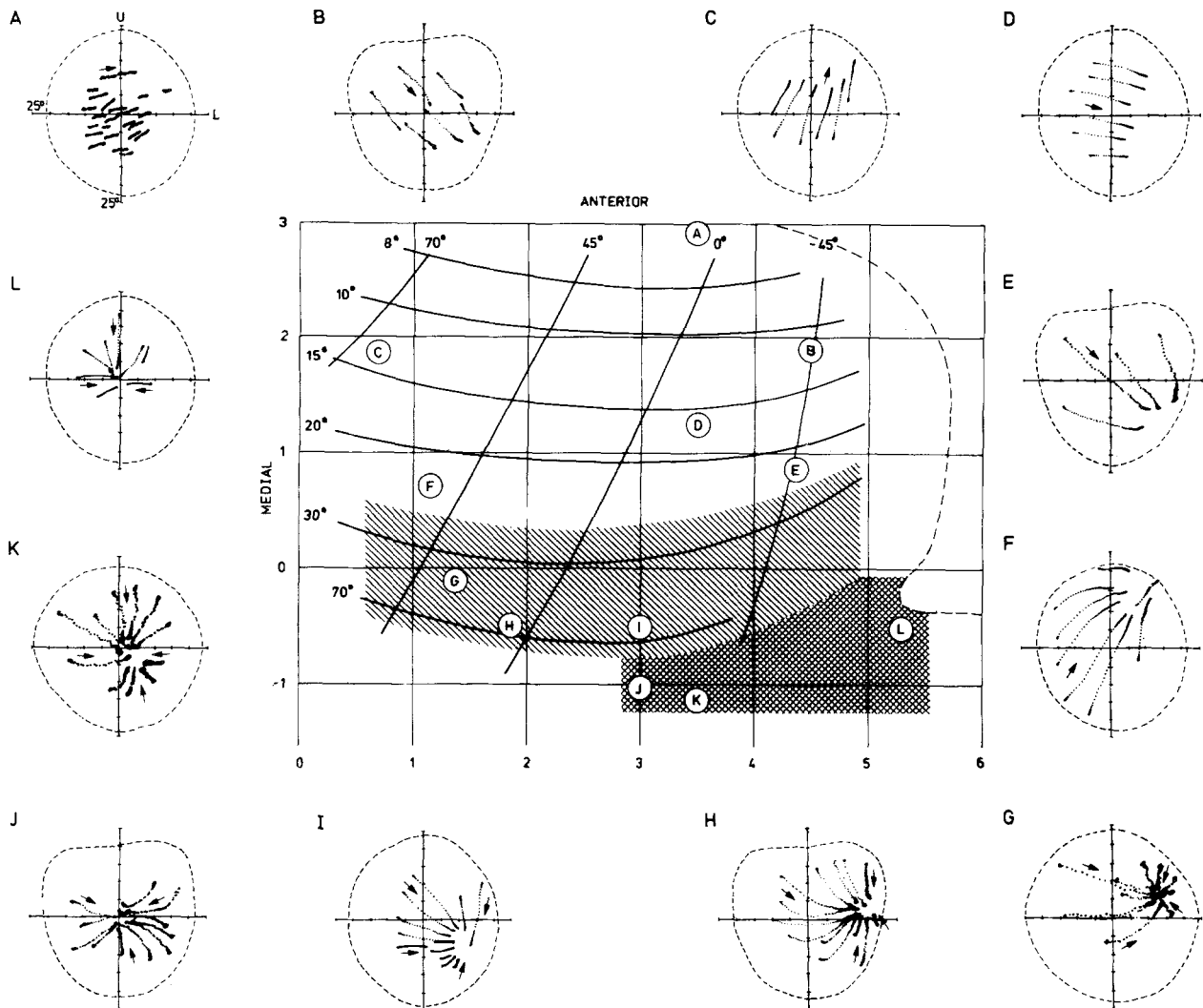
Fig. 1A–L. Examples of eye movements evoked at different sites of cat S.C. The central portion of the figure shows the dorsal view of the cat right superior colliculus (SC). The superimposed orthogonal grid lines represent the antero-posterior and medio-lateral stereotaxic coordinates. The retinotopically coded visual projection to the SC is represented by the heavier, oblique, and curved grid pattern (after Feldon et al. 1970). Isopleths of constant amplitude run approximately in the medio-lateral direction (8°–70°), while those of constant direction are indicated by the values 70°, 45°, 0°, and –45°. Circled letters indicate penetrations of the stimulating electrode, and the pattern of saccadic eye movements evoked by stimulating the deep collicular layers below these points are shown in the correspondingly identified satellite figures surrounding the central portion. To obtain these figures, saccades were directly photographed from the screen of an X-Y memory oscilloscope. The Z input was modulated with 1 ms pulses at 400 Hz for the duration of the saccade. The approximately circular dotted contours represent, in each case, the limits of the cat's oculomotor range. Arrows indicate the direction of saccades. U is up; L is the cat's left. Saccades elicited from the unhatched area (*Anterior* zone) were retinotopic (examples A–D). Saccades evoked from the hatched area (*Intermediate* zone) were craniotopic (examples G, H and I). A transition zone yielded the intermediate pattern of saccades shown in E and F. Stimulation within the double-hatched region (*Posterior* zone) evoked centering saccades (examples J, K, L)

Eye Movement Vectors Related to Stimulus Parameters and Collicular Sites

Before considering the pattern of eye movements evoked from the SC, a brief description will be given of the effects of varying the stimulus parameters.

The threshold varied with the depth of the stimulating electrode, from 70 to 100 µA and more in the upper layers, to values as low as 5 µA in the deeper layers. The threshold was slightly higher for the most caudal sites. Apart from a drop in threshold, a variation in depth of the electrode had a minimal effect on the characteristics of the evoked saccades.

For a given current and train duration, doubling or halving the pulse width or the pulse frequency had little or no effect on the amplitude, direction or latency of an evoked eye movement. However,
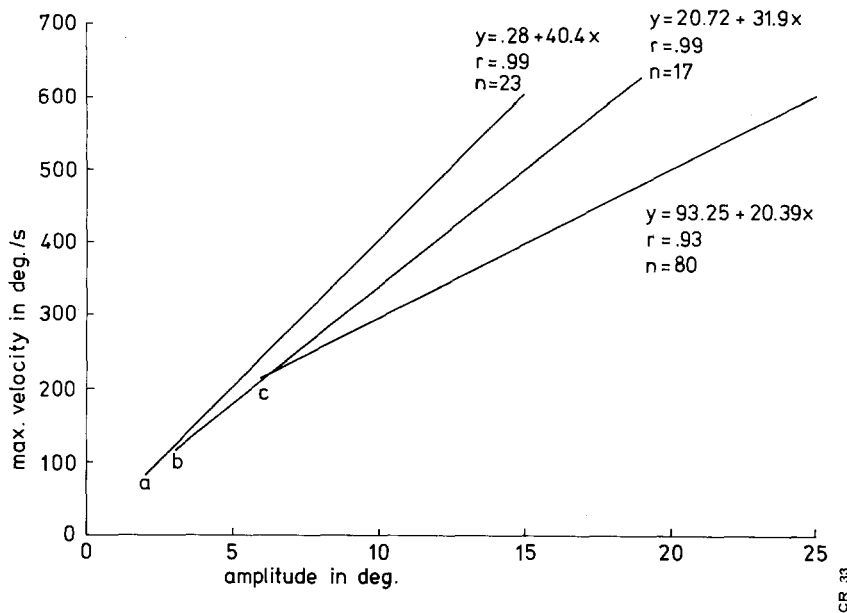
Fig. 2. The relationship between maximum velocity (V) and amplitude (A) of evoked saccades depends on stimulus train duration. c: V vs A linear regression line for "unit" saccades; r: correlation coefficient; N: number of saccades used to obtain regression. b and a: V vs A linear regression lines for saccades evoked with train durations equal to the mean latency of a saccade plus 10% (line a) or 50% (line b) of unit saccade duration

increasing the current beyond threshold both increased its amplitude (in the anterior collicular region only; see below) and reduced its latency. For a current equal to twice threshold, the mean latency was 25 ms. The most influential factor affecting the saccade characteristics was the train duration.

Stimulating the SC of alert cats evoked three types of rapid conjugate ocular displacements corresponding to three distinct zones. All three evoked eye movement patterns are illustrated in Fig. 1 and are considered in detail below.

Anterior Zone

The anterior zone, or approximately the anterior ⅔ of the SC, comprises the portion of the map roughly corresponding to the 25 central degrees of the retina. Saccades evoked from this zone were contraversive, retinotopically coded and defined a motor map which was coextensive with the overlying retinotopic one. For example, stimulation of point A in the SC evoked small saccades of about 5° amplitude, directed almost horizontally (Fig. 1A). Similarly, stimulation of point C evoked saccades of about 15° amplitude directed about 70° above the horizontal line (Fig. 1C). The same correspondence between sensory and motor maps clearly existed for points B and D. This organization is similar to the relation between sensory and motor maps found in the monkey SC (Robinson 1972).

The largest evoked saccades in the anterior zone were roughly 25°–30° in amplitude and are shown in Fig. 1, E and F. It is clear from the trajectories shown in these figures that the large saccades had different

directions, depending on the eye's initial starting point in the orbit, in fact, the ocular movements tended to converge. An obvious explanation for this convergence is that one or either of the horizontal or vertical components of a movement was restricted, the eye having attained its mechanical limits. This is obviously the case for the topmost saccade in Fig. 1F, where the vertical component was blocked. Similarly, the most lateral saccade in Fig. 1E had its horizontal component limited. However, mechanical limitations do not seem to fully explain the convergence since, convergence of evoked saccades was frequently seen even when the eye did not appear to be near those limits (e.g. compare the two lowest saccades in Fig. 1E). Points E and F lie in a transition region between the anterior and the more caudal intermediate zone, to be considered in the next section.

The amplitude of an evoked movement was partly determined by the duration of the stimulus train. The amplitude of the evoked saccade linearly increased as the duration of the stimulus train was increased, until a plateau was reached. This saccade amplitude was defined as the *unit* saccade and was characteristic of a given collicular site. If the train duration was sufficiently increased, a second evoked eye movement occurred, provided that the eye was not near its mechanical limits. For unit saccades of small amplitude and with very long stimuli, a "staircase" of saccades was evoked (see Fig. 3A).

The observation of a linear relationship between amplitude and stimulus duration suggests that an evoked eye movement smaller than the plateau value is in fact a unit saccade whose trajectory was inter-
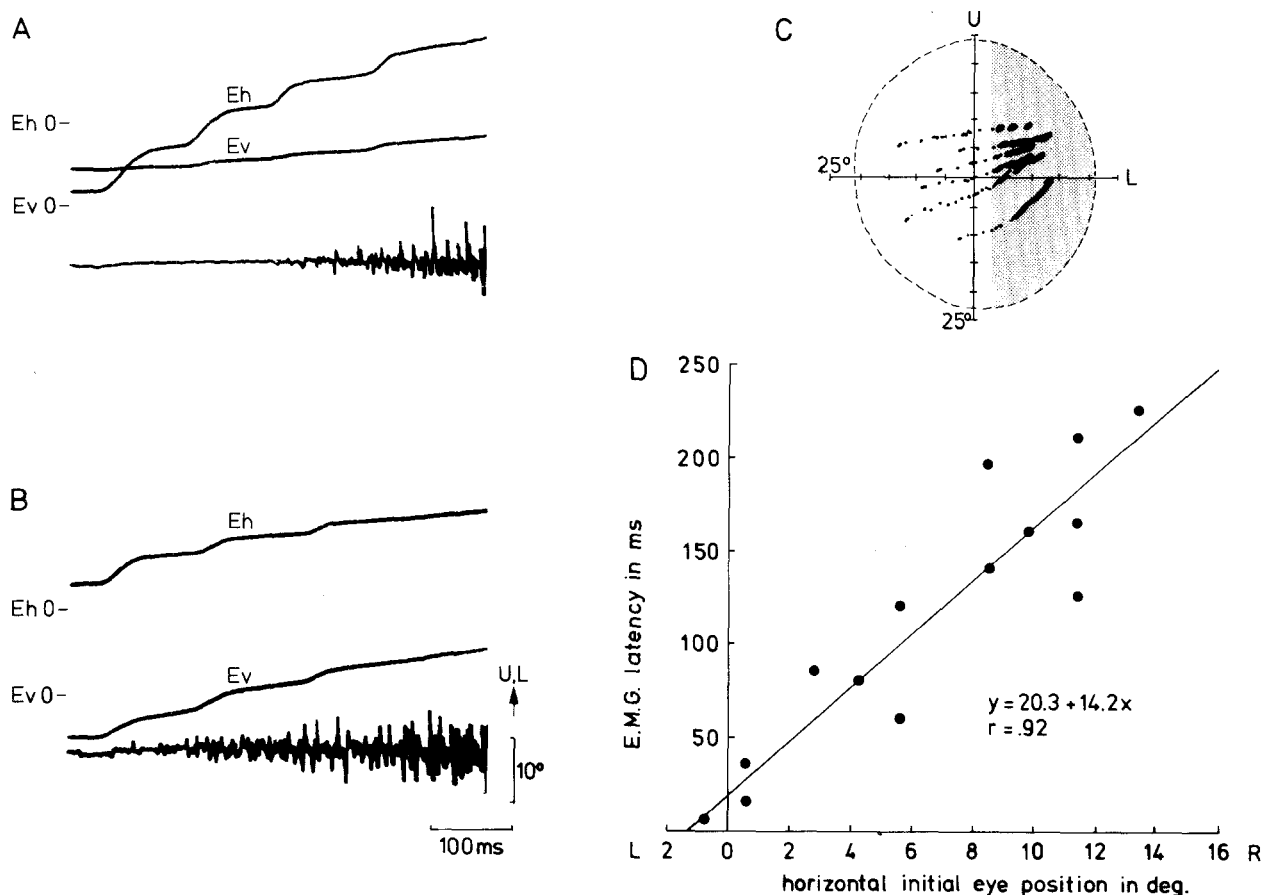
Fig. 3A–D. Anterior zone: dependence of evoked neck muscle EMG activity on initial eye position. **A** and **B** Staircase of saccades evoked with a stimulus train lasting 400 ms. Bottom trace in each part shows that latency of EMG activity is longer if eye begins its trajectory on side ipsilateral (right) to stimulated colliculus. E_h0 and E_v0: horizontal and vertical central gaze positions. Eye movement traces directed upward indicate movement to cat's left (E_h trace) or upward (E_v trace). (See small arrow to lower right). **C** The saccades shown in **A** and **B**, plus others, are visualized on an X-Y memory scope. Saccade trajectory is emphasized (darkened in figure) during EMG activity by modulating Z axis intensity with the EMG signal. The stippled area is that part of the OMR in which EMG bursted. **D** Linear relationship between latency of EMG activity and horizontal initial eye position for the saccades shown in **A**, **B**, and **C**. L and R: left and right sides for the cat

rupted in mid-course. This can be shown by comparing the relationship between maximum velocity (V) and amplitude (A) for unit and "interrupted" saccades. Line c of Fig. 2 illustrates the normal V versus A relationship for unit saccades. It has been computed from a sample of eye movements evoked by a stimulus train whose duration was chosen to be longer than the sum of the mean latency value (25 ms), plus duration of the unit saccade. This train duration was found adequate to assure that evoked saccades were not cut off in mid-flight. Note that the slope of this line is approximately two times steeper than the spontaneous saccades made by the same cats in the experimental environment. Line a of Fig. 2 represents the V vs A relation calculated from eye movements evoked using a stimulus train whose duration was set equal to the sum of the latency value

plus 10% of the unit's saccade duration. The train used to obtain line b had its duration adjusted to equal latency plus 50% of the unit saccade's duration. Comparing the three lines shows that for a given amplitude, the lowest maximum velocity was associated with a saccade evoked by a long train (line c). The maximum velocity associated with the same amplitude the shorter the train (lines a or b) was higher and this suggests that evoked eye movement associated with short trains was the initial portion of saccadea of greater amplitude.

The EMG activity in the biventer cervicis neck muscle contralateral to the stimulation site was continuously monitored throughout each experimental session. Two examples of the relationship between evoked saccades and EMG activity are illustrated in Fig. 3, A and B.
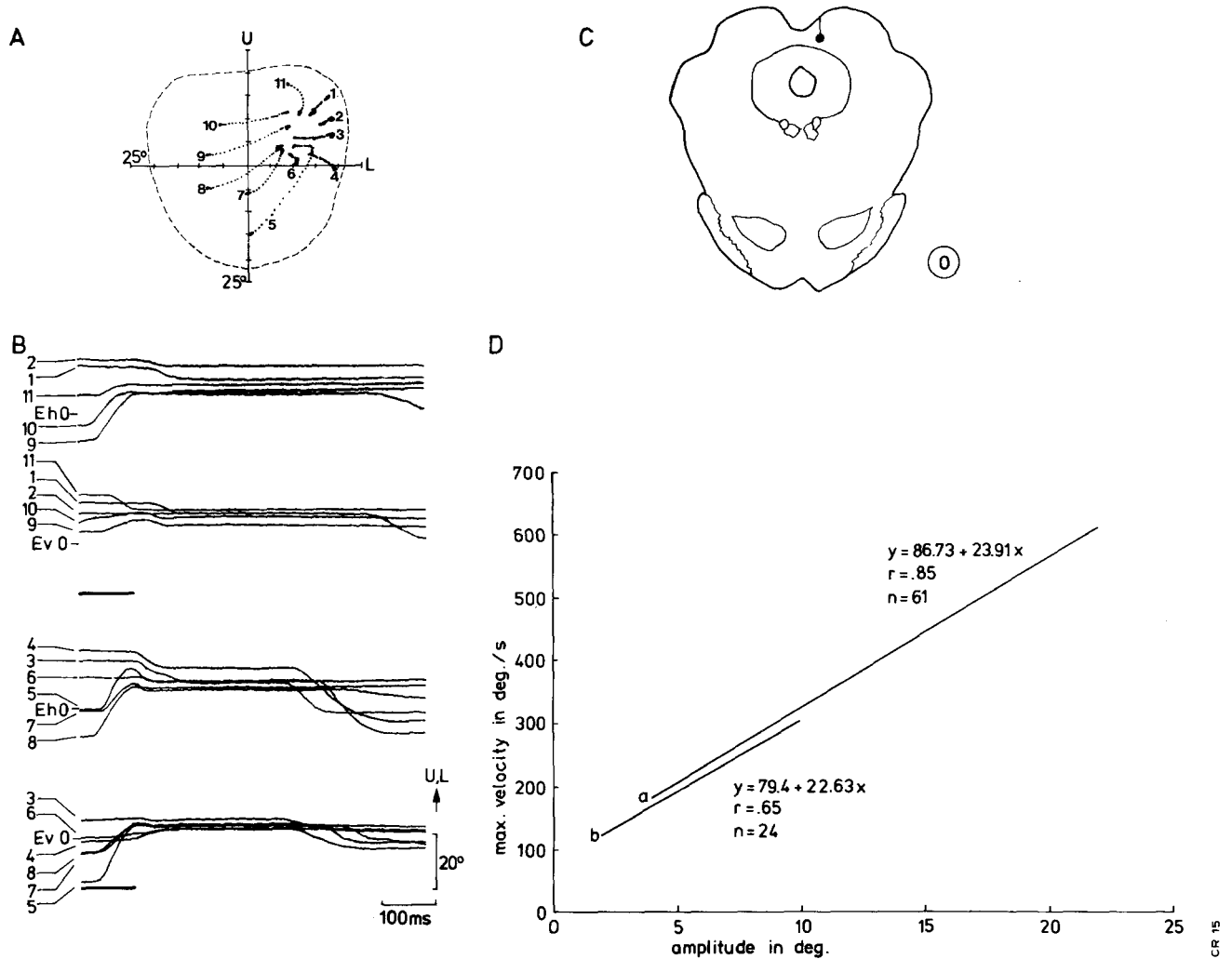
Fig. 4A–D. Intermediate zone: characteristics of "goal-directed" saccades. A example of craniotopic movements evoked by stimulating the SC at point shown in the coronal section in C (frontal plane O). B time dependence of horizontal and vertical components of saccades shown in A. Numbers correspond. Note both longer latency for ipsiversive saccades (nos. 1, 2, 3, 4), and curved trajectories. D V vs A relation for evoked ipsiversive (line b) and contraversive (line a) saccades. These linear regression lines are similar to each other and to the one for unit saccades evoked from the anterior zone (Fig. 2, line c). For symbols and traces, see previous figures

In this figure, the onset of the 400 ms stimulus train coincided with the beginning of the traces. The horizontal and vertical components of an eye movement are shown relative to the center of the OMR (EhO and EvO). In Fig. 3A, the evoked staircase movement began well to one side of the primary position and the eye was driven towards the side ipsilateral to the muscle. In Fig. 3B, the saccades began closer to the eye's mechanical limit on the ipsilateral side and, therefore, there were fewer saccades in the staircase. Comparing Figs. 3A and B, it can be seen that the latency of EMG activity depended on the initial position of the eye in the orbit. When the evoked eye movement began its trajectory past the midline, the latency was much shorter. In Fig. 3C, the evoked EMG activity was

used to modulate the Z-axis intensity of an oscilloscope. The EMG activity appeared when the eye was just beyond the midline. Fig. 3D shows a linear relationship between EMG latency and the horizontal initial eye position. When the eye movement began just a few degrees past the midline on the side ipsilateral to the muscle whose activity was recorded, the latency was actually very short. Extrapolation of the linear relationship shows that the ideal zero latency point occurred when the eye started its movement about 1°–2° past the midline.

Intermediate Zone

The approximate extent of the intermediate zone is shown by the lightly shaded area in Fig. 1. The
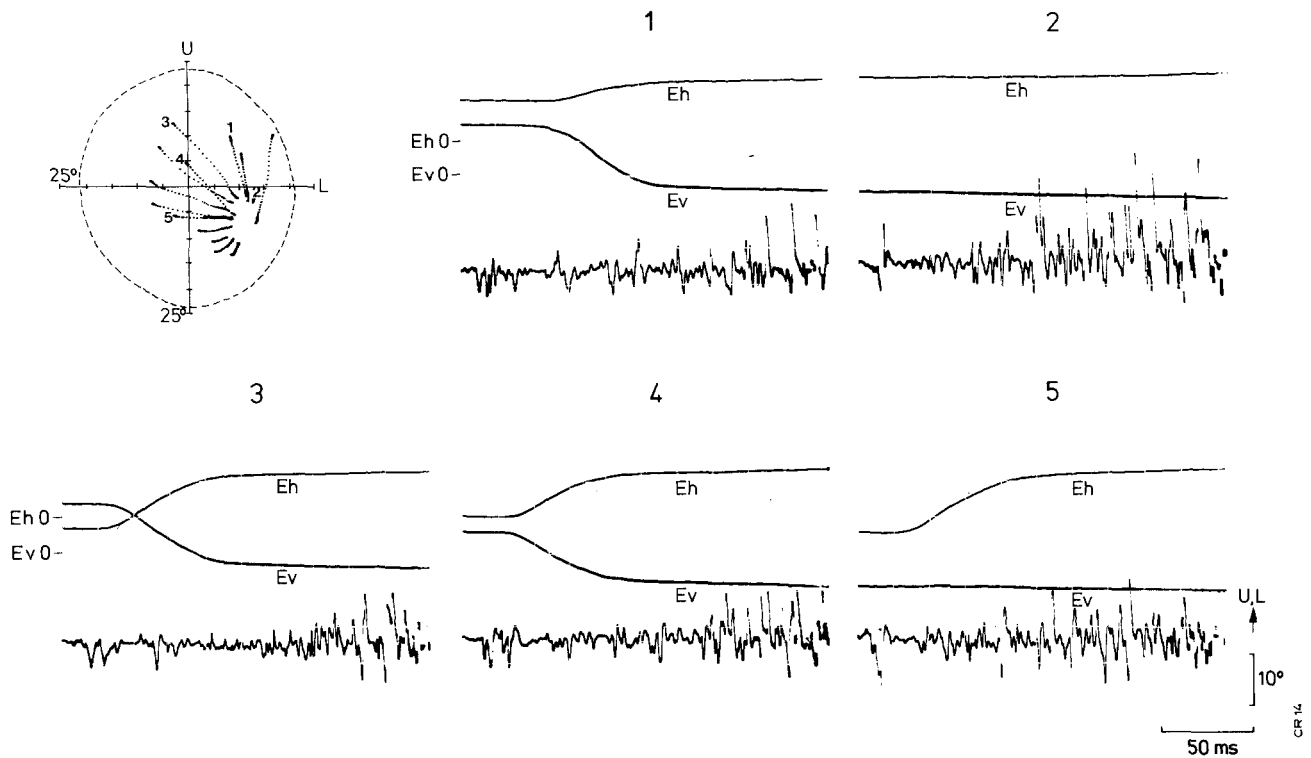
Fig. 5. Intermediate zone: goal directed saccades evoked from right SC and their associated neck muscle EMG activity recorded in left biventer cervicis. Stimulus train duration 400 ms. Note initial burst at short latency (7–10 ms) followed by short silent period, and then long lasting intense activity. This pattern of EMG activity is independent of initial eye position and is even observed when the eye is already on the goal (example 2) and no eye movement is evoked. Note also that with this long train no further saccades are evoked once the eye is on target

characteristic feature of this collicular region is that evoked saccadic eye movements were "goal-directed": i.e. the eye was brought towards, and stopped within, a rather restricted region of the OMR. "Goal-directed" saccades are illustrated in Fig. 1, G, H and I and in Fig. 4A. An important feature of these movements was the presence of *both* contraversive and ipsiversive movements. The latter were difficult to obtain and were only seen when the initial eye position was sufficiently close to the extreme limits of the OMR.

All eye movements evoked in this zone were saccades. This is illustrated in Fig. 4D by the similarity between the V vs A relation for both contraversive and ipsiversive evoked displacements. However, ipsiversive saccades had much larger latencies (80–100 ms) than the contraversive ones (20–25 ms) (Fig. 4B).

Saccades evoked from the intermediate zone resembled those evoked from the anterior zone in that their duration and amplitude depended on the stimulus train. This means that evoked saccades only reached the goal if the train duration was sufficiently long. For very long train durations, say 400 ms (see Fig. 5), the eye reached the goal and stayed "glued"

there while stimulation continued. Unlike for the anterior zone, staircase saccades were never observed. If perchance the eye was already on the goal when stimulation was applied, no evoked eye movement could be observed (Fig. 5, example 2).

A further property of "goal-directed" saccades was that their trajectory was frequently curved. Two striking examples of curved trajectories are shown in Fig. 4A (saccade numbers 5 and 11). Unlike the curved saccades sometimes seen when stimulating the anterior zone, the trajectory of those evoked from the intermediate one was not influenced by the mechanical limits of the eye.

It can be seen from Fig. 1, G, H and I and Fig. 4A that the goal was always situated in the OMR half contralateral to the stimulated SC. Positions of the goal within the semi-OMR varied in a special way according to the collicular site being stimulated. The direction of the goals with respect to the center of the OMR corresponded to the retinotopic map. The eccentricity – the distance of the goals from the center of the OMR – was fairly constant and did not correspond to this map (Fig. 1). In Fig. 1, G, H and I the directions of the goals varied from about 30° up to 25° down, but the eccentricities were similar
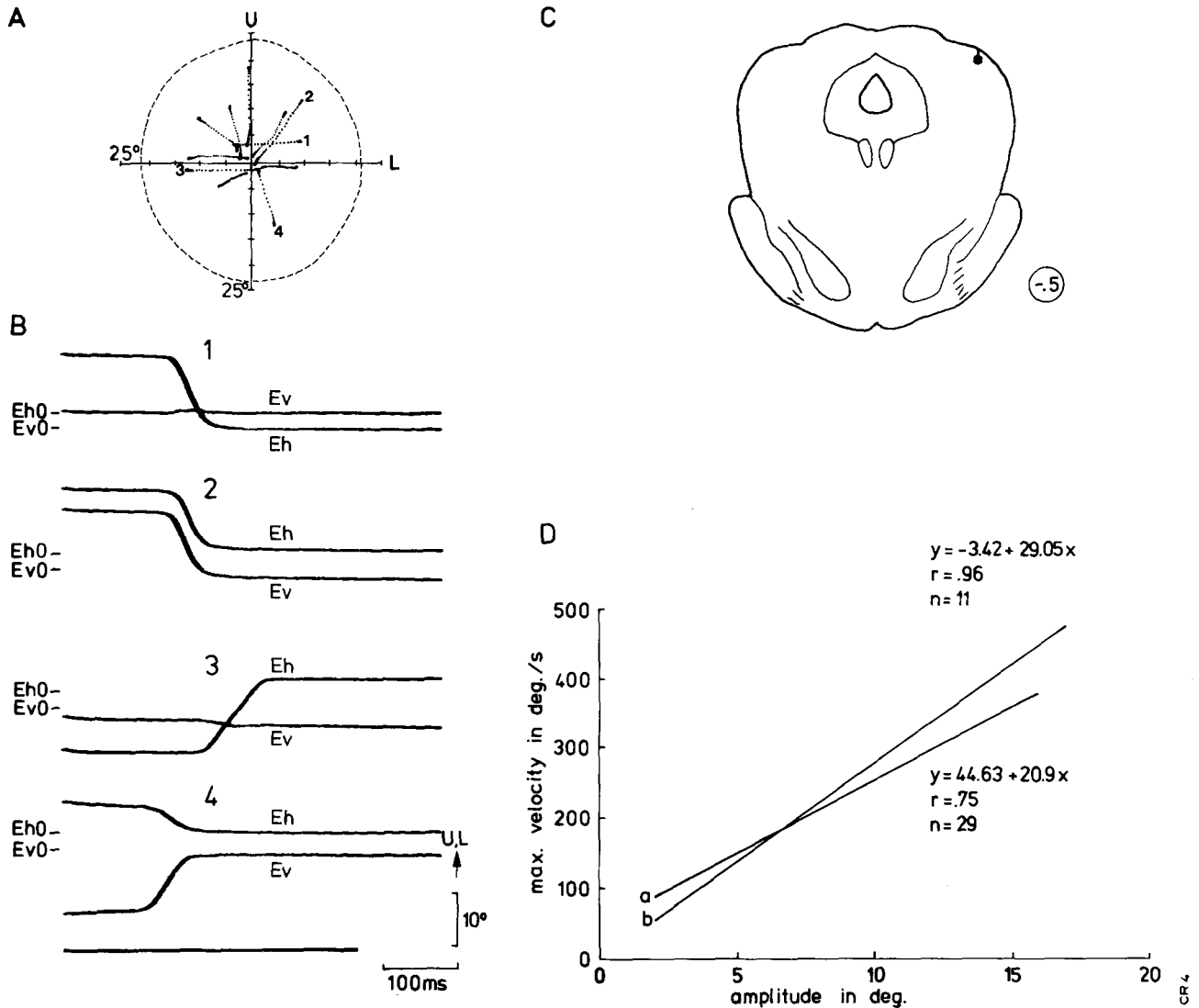
Fig. 6A–D. Saccades evoked in Posterior zone: A centering saccades evoked by stimulating the point indicated in the coronal section of part C taken at stereotaxic coordinate –0.5. B Time variation of horizontal and vertical components of some of the saccades shown in A. Train duration was 400 ms. Note equal and long latency for ipsilateral and contralateral saccades. Symbols as in other figures. D V vs A relation for ipsiversive (line b) and contraversive (line a) saccades

(12°–15°), even though the overlying retinotopic projection corresponded to eccentricities varying between 40° and 70° from the area centralis. In Fig. 5 the evoked eye movements and their associated EMG activity is shown. When the train was sufficiently long (400 ms in Fig. 5), the evoked EMG activity appeared in two distinct bursts, neither of which depended on the initial position of the eye in the orbit. The initial burst had a latency of about 7 ms (range 5 to 10). This burst was followed by a period of relative silence and then by a second intense discharge whose duration lasted as long as the stimulation. The latency of the second burst was about 40–50 ms. This overall pattern of evoked EMG activity was also observed when the initial eye

position coincided with the goal and no eye movement could be evoked (Fig. 5, example 2).

Posterior Zone

This zone is situated in the extreme caudo-lateral portion of the SC. Some stimulation sites, as verified histologically, were clearly within the intermediate and deep collicular layers. Other, more lateral sites were probably outside the SC in the region of the inferior colliculus brachium.

Stimulation of this zone evoked centering saccades (Figs. 1J–L and 6A). These movements brought the eye towards the center of the OMR,

irrespective of the eye's initial position in the orbit. Ipsiversive saccades were as numerous and as large as contraversive ones, and their V vs A characteristics were similar to those observed for saccades evoked from the anterior and intermediate zones (Fig. 6D). For some stimulated points (Fig. 1, J and L, and 6A), the eye was driven rather precisely onto the OMR center. For other points (e.g. Fig. 1K), there was some discrepancy between this center and the eye's final position. It might be supposed that these off-center goals belong to the same family of "goal-directed" movements as those evoked from the intermediate zone. This was not thought to be the case because there was a clear discontinuity between the intermediate and posterior zones, as reflected in three observations. First, unlike the intermediate zone, the mean latencies of ipsiversive and contraversive saccades evoked from the posterior zone were similar (Fig. 6B). These latencies were variable and occasionally quite large, the mean being 81 ms (S.D. = 31 ms). Second, unlike the intermediate zone again, the direction of the near-center goals observed in the posterior zone did not correspond to the overlying retinotopic map. Third, and most important, the pattern of head movements evoked from the posterior zone was quite characteristic and will be described in a subsequent paper (see Roucoux et al. next article).

Discussion

The results of this investigation confirm and extend our previous findings (Crommelinck et al. 1977b) which suggested that the cat's SC may control ocular orienting responses by using distinct strategies that depend on the position of the target in the animal's visual field. Retinotopic saccades evoked from the anterior zone may disclose a strategy for reaching a visual target that lies within the cat's oculomotor capabilities. "Goal-directed" eye movements evoked from the intermediate zone could more appropriately be called craniotopic saccades. In combination with the appropriate head movements (Roucoux et al. 1980), they may reveal a mechanism for the control of an orienting response to a visual target lying outside the cat's oculomotor range. At the very posterior SC border, a third region existed where centering saccades could be evoked. This zone may be implicated in a third strategy for the control of an orienting response.

The difference between the cat and monkey SC may be intimately linked to the cat's oculomotor range which is quite small as compared to that of the monkey.

Effect of Stimulus Parameters

For both cat (Straschill and Rieger 1973; Roucoux and Crommelinck 1976; Stein et al. 1976) and monkey (Robinson 1972; Stryker and Schiller 1975) and for stimuli above threshold, it is generally agreed that changing pulse width or frequency does not affect either duration or amplitude of the evoked saccades. Increasing the stimulus current beyond threshold shortens the latency. In cat, however, unlike monkey, higher intensity stimulation tends to evoke larger saccades. Saccades evoked from the normal alert cat SC are considerably faster than normal spontaneous ones. This is not the case in monkey (Robinson 1972). Evoked saccades that are faster than spontaneous ones have also been reported following stimulation of the frontal eye field in the alert cat (Guitton and Mandl 1978). These findings could suggest that these rapid eye movements evoked in the cat are not normal saccades. However, the characteristics of cat saccades are highly variable (Crommelinck and Roucoux 1976; Evinger and Fuchs 1978), the fastest ones occurring when the head is free (Collewijn 1977; personal observation). Saccades performed in this latter condition have almost the same speed as the ones evoked in the present study, suggesting that evoked saccades, though very fast, are still within a "normal" range.

The most striking difference between cat and monkey is that a cat's saccade could be halted in mid-course if the train duration was not sufficiently long. In a previous study, Roucoux and Crommelinck (1976) reported that two small evoked saccades can be fused together to produce a larger one when the time interval between two short stimulus trains is reduced to zero. In light of the present results, this observation can now be explained as resulting from the dependence of saccade duration on that of the train.

The effect of further increasing the train duration beyond that required to produce a unit saccade depended on the collicular zone being stimulated. For the anterior zone, further increases in stimulus duration produced no eye movement until a value was reached, at which time a second saccade began and the whole process was repeated. For the intermediate and posterior zones no further eye movements could be evoked once the eye was on the "goal".

In monkey, the dependence of saccade duration on train duration has not been reported. The evoked rapid eye movements in this species have always been described as "all or none" phenomena and increases in train duration have generated a staircase series of saccades having near constant amplitudes (Robinson

1972; Stryker and Schiller 1975). Our observations suggest that, in cat, stimulation does not trigger a ballistic movement whose amplitude and direction are determined before the saccade even starts but rather generates an error which is nulled when stimulation is turned off.

Anterior Zone

The finding of a restricted region from which retinotopically coded eye movements can be evoked is in general agreement with a previous study by two of the present authors (Roucoux and Crommelinck 1976). That study, however, limited the anterior zone to the 12–15 deg of retinal projection. The discrepancy between the old and new results is due to the short stimulus train duration (50 ms) that restricted saccade amplitude in the early experiments. A retinotopic distribution of evoked saccades has also been described by other authors, but none have confined this type of motor map to the anterior portion of the colliculus. Straschill and Rieger (1973) suggested that retinotopically organized saccades could be evoked by stimuli restricted to the superficial layers but applied to the entire horizontal extent of the SC. In that study, goal-directed movements were elicited from the deeper layers. Stein et al. (1976), in a more recent investigation, reported that only retinotopically coded saccades could be evoked by stimulating the cat SC.

The relationship between evoked eye movements and neck muscle EMG activity suggested that the electrical stimulus would drive a head movement directed, like the eye, to the contralateral side. The onset of EMG activity was critically dependent on the horizontal position of the eye in the orbit and appeared when the eye was just beyond the central position. A similar result has been found by Stryker and Schiller (1975) in the monkey, save that in this species, EMG activity began when the eye was turned considerably more towards the periphery (20°-30° in monkey vs 1–2° in cat). The nature of the eye-head coordinated evoked response suggests that head motion is triggered by the position of the eye in the orbit. This will be further discussed in a subsequent paper (Roucoux et al. 1980).

Intermediate Zone

Low level electrical stimulation applied to either the intermediate or deep layers of the SC, but restricted horizontally to a region lying below the 25°–70° of visual retinotopic projection, evoked saccades

directed to a fixed point relative to the orbit. Hyde and Eason (1959) were the first to report that such "goal-directed" or craniotopic ocular displacements could be evoked from the SC. Subsequently, Straschill and Rieger (1973) reported that craniotopic saccades could be evoked from the entire horizontal extent of the SC by a stimulus restricted to the intermediate and deep collicular layers. Roucoux and Crommelinck (1976) first suggested the existence of the intermediate zone, the boundaries of which have been more accurately determined in the present study.

Craniotopic movements were evoked from a collicular zone underlying a visual projection whose neurons would discharge in relation to targets appearing outside the cat's OMR. The results showed an important discrepancy between the eccentricity of a goal (e.g. 15° for point H in Fig. 1) and the retinotopic eccentricity (70° for the same point). Although there was no correspondence between eccentricities, there was good agreement between the direction of a goal and the corresponding retinotopic direction. Thus, stimulating below a visual projection corresponding approximately to the horizontal meridian (point H in Fig. 1) yielded a goal located on this axis.

The EMG activity accompanying goal-directed saccades is compatible with the existence of synchronized coordinated eye-head movement. The contralateral biventer cervicis muscle is activated with a latency that is constant and independent of the initial eye position. This pattern is quite different from that observed following stimulation of the anterior zone. The EMG activity evoked from the intermediate zone presents two components (Fig. 7). The first, at short latency (5–10 ms), is compatible with either the mono- or di-synaptic activation of cervical motoneurons via the tecto-spinal or reticulospinal projections (Anderson et al. 1971). It is noteworthy that a number of findings now concur that the tecto-spinal tract originates in the caudal portion of the SC (Coulter et al. 1979; Kawamura and Hashikawa 1978; Rose and Abrahams 1978), a site approximately coextensive with our intermediate region. The short latency EMG response is brief and ceases after some 50 ms, even though stimulation persists. In contrast, the second response continues with increasing amplitude as long as stimulation is applied. The longer latency of this component suggests the involvement of more complex pathways.

Posterior Zone

The pattern of saccadic eye movements evoked from the posterior zone differed from those evoked from

the intermediate one with respect to their longer latency and the relationship between their goal and the retinotopic map. The posterior zone is situated, in part, under a retinotopic projection whose visual receptive fields are located in the extreme retinal periphery. However, the role of the eye centering saccades in a mechanism controlling gaze shifts towards such peripheral targets is obscure and may become apparent only in experiments in which the cat is free to move its head (Roucoux et al. 1980).

Conclusion

The results of this study support earlier findings showing that stimulation of the cat SC can evoke different patterns of eye movement depending on the collicular region being excited. Stimulation of a caudal portion of the SC (the intermediate zone) yields craniotopic saccades coupled with synchronous short latency neck muscle EMG activity. The link between caudal colliculus and head movements is also emphasized by the tecto-spinal tract which originates principally from this region of the SC.

A question that arises from the present results is whether the three patterns of evoked eye movements described herein reveal different real-life strategies employed by the cat's nervous system for reaching visual targets that appear in different parts of its visual field. Some clues to answering this question will be considered in the following paper where the eye and head movements evoked from the presently described three collicular zones are to be discussed.

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