

## TECTAL AND TEGMENTAL EXCITATION IN DORSAL NECK MOTONEURONES OF THE CAT

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*(Received 10 January 1992)*

### SUMMARY

1. Intracellular recordings were made from 116 splenius (SPL) and 103 biventer cervicis and complexus (BCC)  $\alpha$ -motoneurones in nineteen cats anaesthetized with  $\alpha$ -chloralose.

2. Electrical stimulation in the contralateral tectum evoked disynaptic excitatory postsynaptic potentials (EPSPs) in the motoneurones when a train of stimuli was applied in the ventral layers throughout the superior colliculus. In the rostral half of the superior colliculus, these EPSPs were due to stimulation of ascending collaterals of tectofugal neurones. EPSPs of a presumed trisynaptic linkage could only be evoked from the dorsal and intermediate tectal layers in the caudal half of the superior colliculus. It is concluded that the tectofugal neurones which evoked the disynaptic EPSPs are mainly located in the caudal half of the superior colliculus.

3. Disynaptic EPSPs were evoked in the motoneurones by a train of stimuli in the contralateral fields of Forel and Zona incerta, which were due to stimulation of ascending collaterals from the tectofugal neurones.

4. Spatial facilitation experiments revealed that tectal disynaptic EPSPs in the neck motoneurones were mediated via reticulospinal neurones with convergent input from cortico-reticular neurones.

5. A train of stimuli in the ipsilateral tectum evoked EPSPs with latencies compatible with a trisynaptic linkage, while disynaptic EPSPs at low threshold could be elicited from the underlying tegmentum. Similar disynaptic EPSPs could be evoked from the ipsilateral fields of Forel. It is suggested that some of the disynaptic tectal EPSPs in SPL and BCC motoneurones can be mediated via a tectento-reticulospinal pathway which originates in the cuneiform nucleus.

### INTRODUCTION

The first investigation of effects from the superior colliculus in dorsal neck motoneurones was made by Anderson, Yoshida & Wilson (1971) who found that

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disynaptic excitation from the contralateral tectum could be mediated via reticulospinal neurones. They also reported that disynaptic excitation could be evoked from the ipsilateral tectum, but provided no conclusive evidence concerning the origin of the effect. These authors made rostrocaudal tracks in the superior colliculus through its caudal three-quarters and found no systematic differences in the effects.

We have now reinvestigated the effects in dorsal neck motoneurones by systematic stimulation throughout the tectum and the underlying tegmentum and also rostrally in the diencephalon ipsi- and contralaterally. The results suggest a longitudinal organization of the tecto-reticulospinal pathway mainly restricted to the caudal half of the superior colliculus. In addition, it was found that the same tecto-reticular neurones have ascending collaterals which terminate in the fields of Forel and Zona incerta (Berman, 1968) in the diencephalon. A new disynaptic excitatory pathway from the ipsilateral tegmentum to the dorsal neck motoneurones is also described. The functional significance of these pathways is discussed.

#### METHODS

The results have been obtained from 116 splenius (SPL) and 103 biventer cervicis and complexus (BCC) motoneurones recorded in nineteen cats. Only motoneurones with initial spike amplitudes larger than 60 mV have been included.

*Preparation.* The animals were anaesthetized with ether during surgery and subsequently with  $\alpha$ -chloralose (50 mg/kg). Additional doses of  $\alpha$ -chloralose (25–75 mg/kg) were added during the course of the experiments. The criteria for adequate depth of anaesthesia were the persistence of miotic pupils, stable blood pressure and respiratory rate and absence of the withdrawal reflex to noxious stimulation. Pneumothorax and artificial respiration were always performed, the animal being immobilized with gallamine triethiodide (Flaxedil). After paralysis, the criteria for adequate anaesthesia were: miotic pupils and stable blood pressure, even with painful stimuli. Rectal temperature was maintained at 36–38 °C, and the arterial blood pressure and expiratory CO<sub>2</sub> were monitored continuously. Noradrenaline (0.04 mg/ml) was infused if the blood pressure fell below 80 mmHg.

A laminectomy was performed that exposed the spinal segments C1–C4. Nerve branches from the C2 and C3 segments innervating the lateral head flexor SPL and head elevators BCC were dissected and mounted on bipolar stimulating electrodes.

*Stimulation and recording.* Stereotaxically placed monopolar tungsten electrodes were used for stimulation of cortico- and tectofugal fibres. The former fibres were stimulated in the contralateral pyramid at about 5 mm rostral to the obex level with an electrode which was calibrated at the obex. The latter fibres were stimulated with an electrode which was placed in the tectum according to the Horsley–Clarke co-ordinates given in Berman's atlas (1968; see Results). Stimulating strengths ranged usually from 20 to 200  $\mu$ A. Only in the collision experiments was a higher stimulus strength of 500  $\mu$ A used in order to ensure activation of all tectofugal fibres (cf. Fig. 6). In all cases, 100  $\mu$ s pulse duration was used. Trains of impulses were given at 300 Hz. Intra- and extracellular records were obtained by using glass microelectrodes filled with 2 M-potassium citrate. Silver electrodes were used for cord dorsum recordings.

Histological reconstruction of electrode tracks was made by using stereotaxically placed electrolytical lesions in the brain stem and from traces of electrode penetration. In the spinal cord, tracks were reconstructed by leaving the glass microelectrode in each patch.

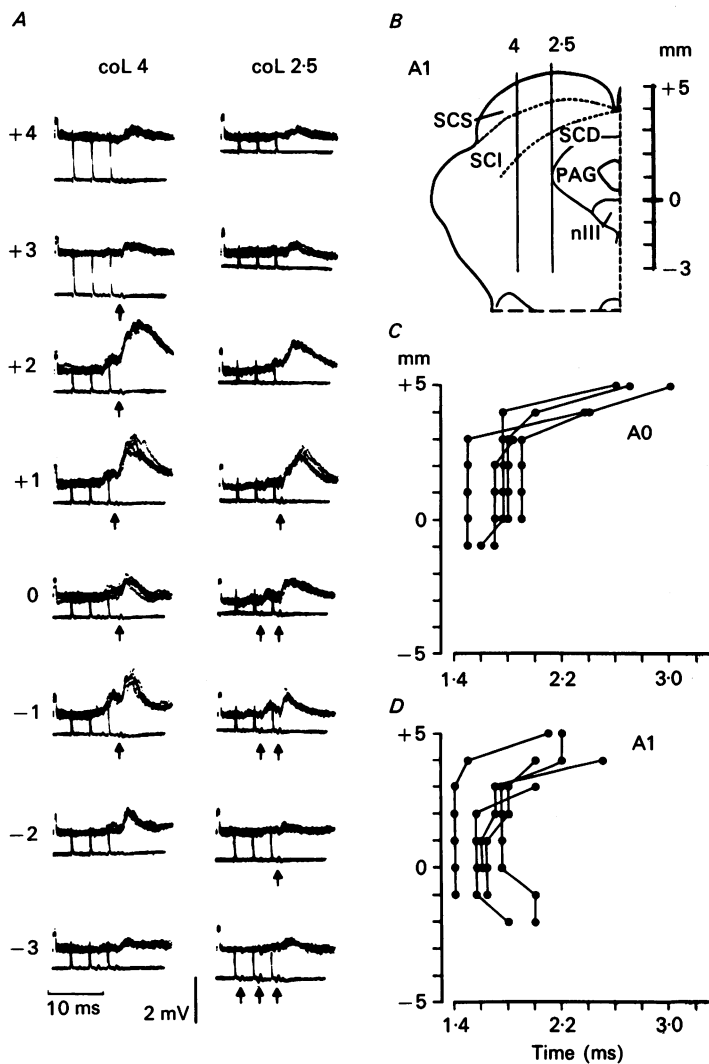


Fig. 1. Transverse tracking in the contralateral tectum and tegmentum at the level defined by Horsley-Clarke co-ordinates as anterior 1 mm (A1). *A*, tracking at laterality 4 respectively 2.5 mm from the midline. Intracellular recording (upper traces) are from a SPL motoneurone. Three stimuli were given at 100  $\mu$ A. Lower traces were recorded from the cord dorsum in C3. *B*, histological reconstruction of the electrode penetrations. *C*, latencies measured from the third stimulus at 100  $\mu$ A to the onset of the EPSPs plotted *versus* the depth of stimulation at contralateral (*coL*) 2.5 mm for A0. *D*, as in *C* but for A1. Arrows indicate synaptically evoked volleys at depths +3 to -2 and the direct rubrospinal volley at depth -3. Abbreviations: oculomotor nucleus (nIII); periaqueductal grey (PAG); superior colliculus, superficial layer (SCS); intermediate layer (SCI); deep layer (SCD).

## RESULTS

*Contralateral excitation**Transverse tracking*

Excitatory postsynaptic potentials (EPSPs) could be evoked in SPL and BCC motoneurons when a train of electrical stimuli was applied in the contralateral tectum. Figure 1*A* and *B* illustrates the results from a SPL motoneuron at different stimulus positions at the level of anterior 1 mm (A1; Horsley-Clarke co-ordinates). The effect of using trains of three volleys at 20, 50, 100 and 200  $\mu\text{A}$  were usually tested. The EPSPs shown in Fig. 1*A* were evoked at a stimulation strength of 100  $\mu\text{A}$ . Temporal facilitation was required to elicit the EPSPs, which were stimulus linked either to the second or third volley. Dorsally in the tectum, small EPSPs were evoked at 2.5 ms (contralateral (coL) 4 mm, depth +4 mm) and 2.2 ms (coL 2.5 mm, depth +4 mm) from the third tectal stimulation. Ventrally in the tectum (+2, +1, 0) the amplitude of the EPSPs increased markedly in parallel with a shortening of the latencies to 1.5–1.6 ms. Note that a small EPSP could be evoked from the second volley. Deeper (-1, -2, -3), in the tegmental region, stimulation resulted in gradually smaller EPSPs and longer latencies (1.7–2.0 ms). Although the threshold for evoking the tectal EPSPs varied slightly from one experiment to another, the lowest thresholds were between 20 and 50  $\mu\text{A}$  all the way from depth +5 to -2 mm. More ventrally the threshold was usually 100–200  $\mu\text{A}$  or above 200  $\mu\text{A}$ .

Figure 1*C* and *D* illustrates the relationship between the EPSP latency from the third stimulus of the train at 100  $\mu\text{A}$  and stimulation depth for different SPL motoneurons from tracking at 2.5 mm contralaterally at A0 (*C*) and A1 (*D*). Marked shortening of the latency was observed of 0.6–0.9 ms from depth +5 to +3. In contrast, from depth +3 and ventrally to depths +2 and -1, the latencies remained either constant or decreased slightly by between 0.1 and 0.4 ms. Grading the strength of stimulation from 50 to 200  $\mu\text{A}$  revealed shortening of the latencies of 0.1–0.3 ms, which presumably reflects earlier firing on faster rising EPSPs in the intercalated neurones. Thus, the observed shortening of the latencies described in Fig. 1 (using 100  $\mu\text{A}$ ) of < 0.4 ms could be explained by differences in the number of activated tectofugal neurones, but those of 0.6–0.9 ms could not. The latter shortenings of the EPSP latencies most likely reflect the activation of one intercalated neurone with monosynaptic connections to the tectofugal neurones.

Stimulation in the contralateral tectum and tegmentum evoked IPSPs at almost the same latency as the EPSPs in BCC motoneurons (B. Alstermark, M. Pinter & S. Sasaki, in preparation). The thresholds of the IPSPs were often lower than of the EPSPs, which made the analysis more difficult for BCC motoneurons. However, similar results to those shown in Fig. 1 for SPL motoneurons were also observed among BCC motoneurons.

*Synaptic linkage*

It can be seen in the lower paired records of Fig. 1*A* (arrows), which were obtained from the cord dorsum in C3, that a synaptic volley appeared after the second and third stimuli. A causal relationship between this synaptic volley and the evoked

EPSPs is suggested, because of the fixed linkage in time (cf. depth -1 mm at coL 4 vs. coL 2.5). Measurements from the synaptic volley to the onset of the EPSPs gave latencies from 0.4 to 0.6 ms, which are compatible with a monosynaptic linkage. Subtraction of these values from the minimal latencies of 1.5–1.6 ms measured from

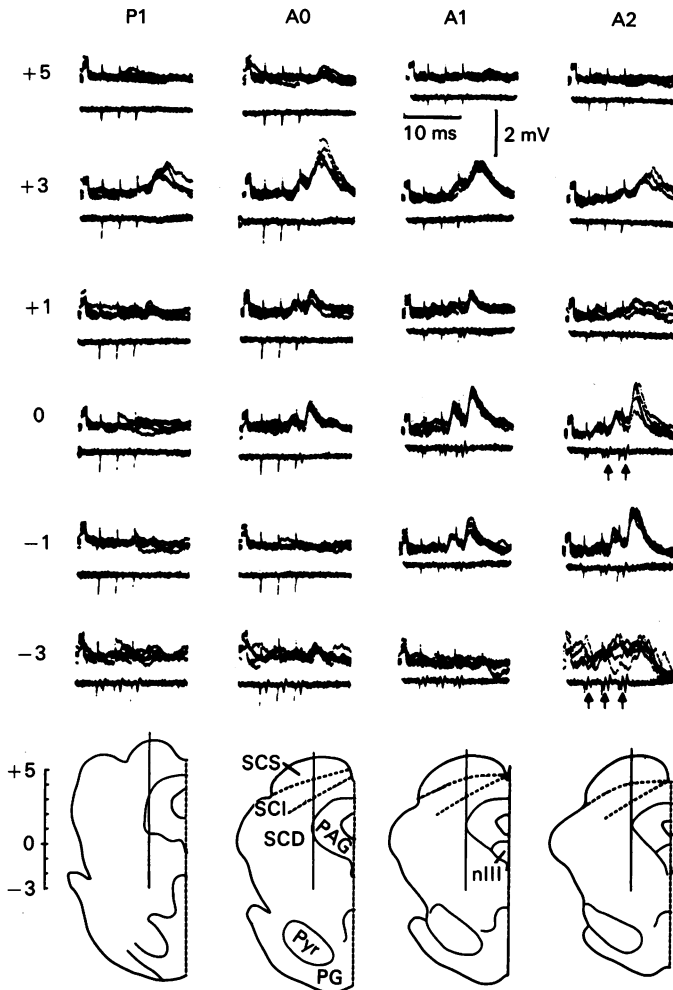


Fig. 2. Longitudinal tracking in the contralateral tectum and tegmentum from P1 to A2 in a SPL motoneuron which was recorded in C2. Stimulation strength was 100  $\mu$ A. The laterality was coL 2.5 mm for all levels. Arrows indicate synaptically evoked volleys at depth 0 and the direct rubrospinal volleys at depth -3. Abbreviations: see Fig. 1; pontine grey (PG); pyramid (Pyr).

the effective second or third tectal stimuli gives values of 0.9–1.2 ms, which include the conduction time to the spinal cord, one synaptic delay and time to firing in the intercalated neurones. If a conservative assumption of a maximal velocity of 70 m/s for tectofugal fibres is made (Grantyn & Grantyn, 1982), then 0.7 ms is the required

conduction time from tectum to the C2–C3 segments. Since the remaining 0.2–0.5 ms can only allow for one synaptic relay it is concluded that the shortest latencies of 1.5–1.6 ms from tectum to SPL and BCC motoneurons show a disynaptic linkage.

The observation that the short latency EPSPs were evoked from depths +1 to -1 at coL 2.5 fits well with the known projection of the tectofugal fibres as they traverse ventrally around the periaqueductal grey on their way to the decussation (Kawamura, Brodal & Hoddevik, 1974). No monosynaptic EPSPs were recorded in the SPL and BCC motoneurons when stimulation was applied in the ventral part of the tectum, which suggests a lack of direct tectospinal connections with dorsal neck motoneurons.

These results are in agreement with the results of the study by Anderson *et al.* (1971). In addition, our findings showing a stepwise shortening of 0.6–0.9 ms from the most dorsal layers and lateral part of the tectum to the intermediate and medial parts, strongly suggest that one intercalated neurone prior to the tectofugal neurone has been activated and thus that the EPSPs from the former regions were trisynaptically mediated.

#### *Longitudinal tracking*

Serial tracks at different antero-posterior levels ('longitudinal tracking') were made at coL 2.5 (stimulation strengths of 20–200  $\mu$ A were regularly used but only 100  $\mu$ A is illustrated from P1 to A8), as illustrated for a SPL motoneuron in Figs 2, 3 and 4. Similar results were found in ten SPL and in seven BCC motoneurons. Figure 2 shows that EPSPs could be evoked from the intermediate layers (+3) at different levels in the caudal half of the tectum at A1–A2, while no or only small (A0) EPSPs were elicited from the dorsal tectal layers (+5). It is interesting to observe the disappearance of the EPSPs at depth -1 for P1 and A0 and also that the EPSP from A1 but not from A2 was decreased in amplitude as compared to depth 0. This finding suggests that the fibres of the most caudal tectofugal neurones (P1–A1) turn slightly rostrally before they reach the decussation. Further ventrally at depth -3 there was only a small EPSP evoked from A2 but no effects from P1 to A1.

Small synaptic volleys which appeared after the second and third tectal stimuli can be seen in the lower cord dorsum records of Figs 1, 2, 3 and 8 (arrows). Since these volleys decreased in amplitude more ventrally, it is likely that they were evoked by activation of tectofugal fibres. The large synaptic volley (-2) and direct volley (-3) in Figs 1, 2, 3, and 8 which were evoked already after the first stimulus are caused by activation of rubrospinal neurones (Baldissera, Lundberg & Udo, 1972).

Figure 3 shows that in the rostral half of the tectum at A3–A5 no EPSPs were evoked in the intermediate layer (+2). No effects were evoked by stimulation in the dorsal layer (+5; not illustrated). At depth +1 there was only a small EPSP evoked at A3 and at A4 the EPSP had a longer latency. Distinct short latency EPSPs could be evoked from the depths 0 and -1 but not ventrally in the red nucleus at -2 or -3. In summary, the results from the tracking experiments show that the disynaptic excitation in dorsal neck motoneurons is mainly evoked from the dorsal and intermediate tectal layers in the caudal half of the contralateral superior colliculus (cf. Discussion).

*Ascending collaterals*

Surprisingly, rostral to tectum at A7 and A8 (Figs 3 and 4) distinct EPSPs with a disynaptic latency could still be evoked but were only evoked at low threshold ( $50 \mu\text{A}$ ) from depth  $-1$ . More rostral tracking was not performed in this cell, but

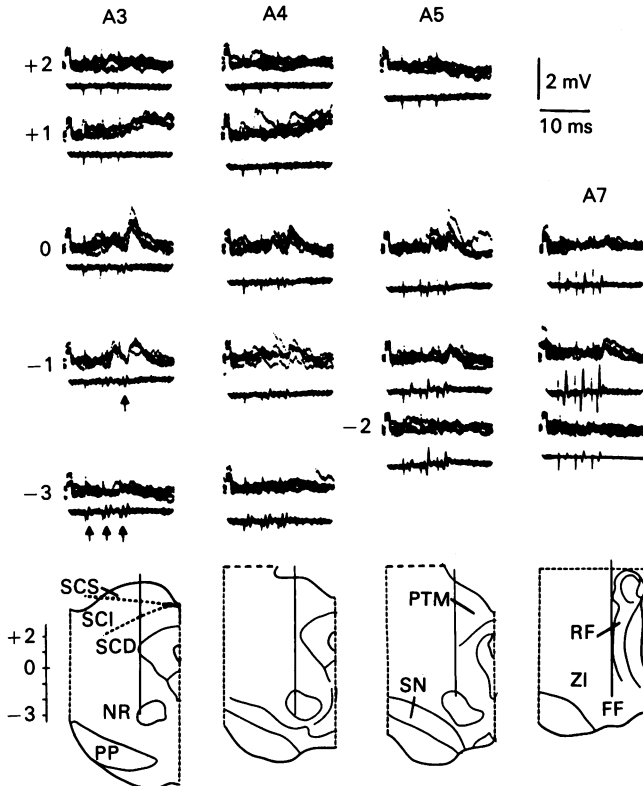


Fig. 3. Continuation of the longitudinal tracking for the cell shown in Fig. 2 at A3–A7. Arrow at depth  $-1$  is the synaptically evoked volley, while arrows at depth  $-3$  indicate the direct rubrospinal volleys. Abbreviations: see Figs 1 and 2. Fields of Forel (FF); medial pretectal area (PTM); retroflex bundle (RF); substantia nigra (SN); zona incerta (ZI).

EPSPs could not be evoked from A9 and A10 in other SPL ( $n = 2$ ) and BCC ( $n = 2$ ) motoneurons. At A8, EPSPs could be elicited at  $-1$  from coL 1.5–4.5 with a threshold below  $100 \mu\text{A}$ , as shown in Fig. 4. More laterally the threshold increased, but EPSPs were still evoked from depth  $-1$  at coL 7 and 8 when the stimulus strength was raised to  $200 \mu\text{A}$  (Fig. 5D). This region corresponds to the fields of Forel and Zona incerta.

The similarities of the shapes and latencies of these rostral EPSPs with those evoked from the tectum suggest the possibility of a common origin. A characteristic feature of the tectal disynaptic excitatory pathway to dorsal neck motoneurons is that it is mediated via reticulospinal neurones (Anderson *et al.* 1971; Alstermark, Pinter & Sasaki, 1983, and unpublished observations), which receive convergent

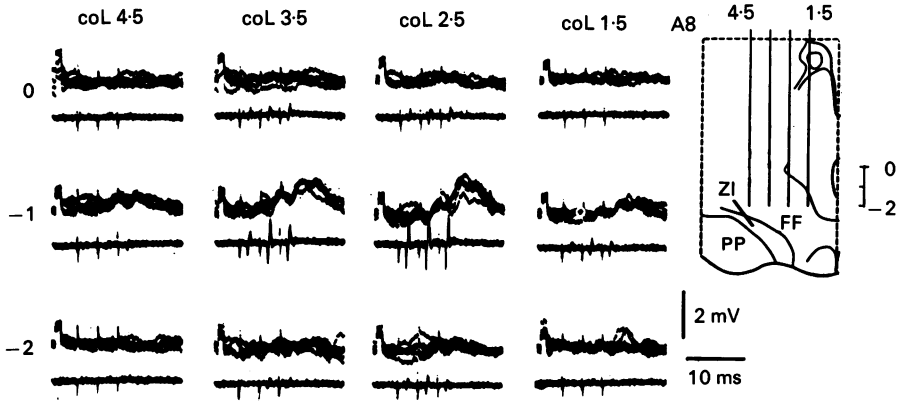


Fig. 4. Continuation of the longitudinal tracking for the cell shown in Fig. 2 at different lateralities at A8.

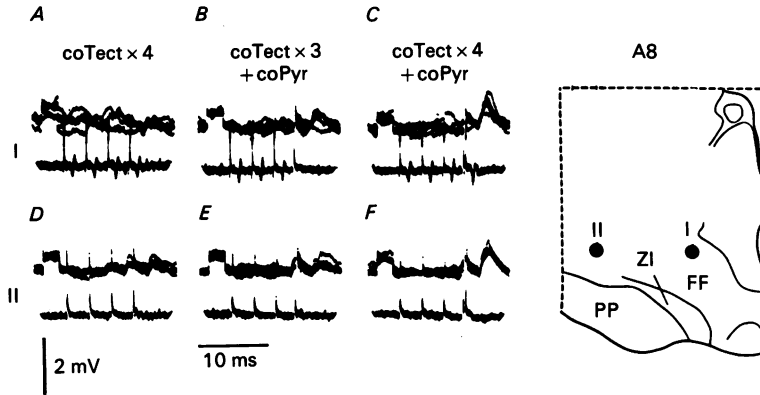


Fig. 5. Convergence on reticulospinal neurones which mediate disynaptic excitation to a SPL motoneurone from cortico-reticular fibres and presumed ascending collaterals of tecto-reticular neurones (coTect) that project to the fields of Forel (FF). The cortico-reticular fibres were stimulated in the contralateral pyramid (coPyr) rostral to a pyramidal transection which was made at 3 mm rostral to the obex. Stimulation at two different lateralities (I, II) in the FF evoked a small disynaptic test EPSP (A and D) which was facilitated by a single conditioning pyramidal volley (C and F). The facilitation was linked to the fourth tectal volley as shown in B and E.

input from corticofugal fibres (Alstermark *et al.* 1983, and unpublished observations). In order to investigate if the rostral EPSPs could be of tectal origin, spatial facilitation experiments were performed with a conditioning stimulation of fibres in the contralateral pyramid as shown in Fig. 5 for two different stimulus positions at A8. The pyramid had been transected a few millimetres rostral to the decussation and the corticofugal fibres were stimulated rostral to the lesion in order to assure that a possible interaction occurred on reticulospinal neurones. Small test EPSPs were evoked in A and D which were facilitated by a single pyramidal volley as shown in C and F. This interaction was linked to the fourth tectal volley as proven by the



disappearance of the facilitation when the fourth volley was withdrawn (*B* and *E*). Thus, these experiments support the possibility that the disynaptic excitation evoked from the region of the contralateral fields of Forel and Zona incerta could be due to direct activation of ascending collaterals of the tectofugal neurones.

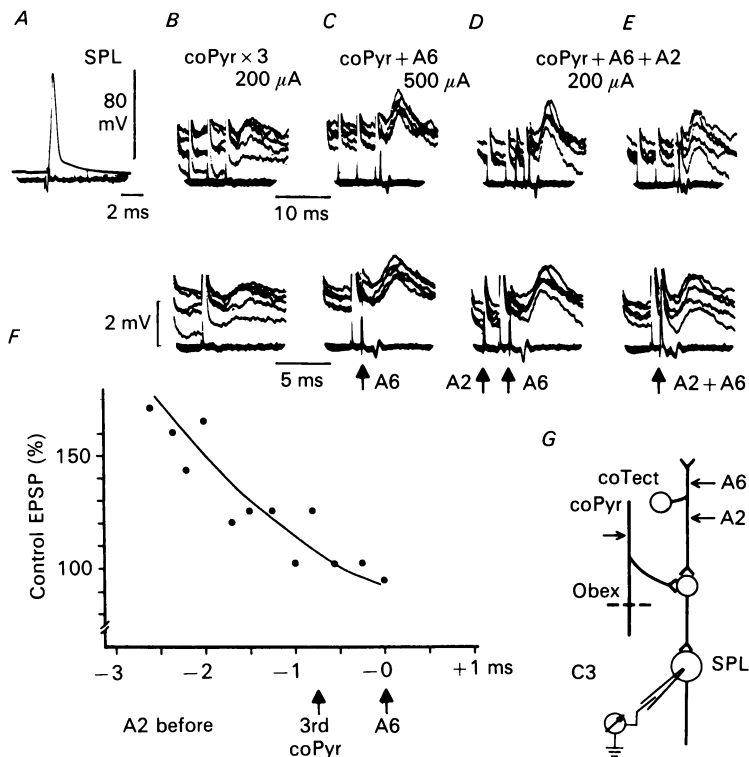


Fig. 6. Convergence on reticulospinal neurones which mediate disynaptic excitation to a SPL motoneurone (*A*) from cortico-reticular fibres and fibres of tectofugal neurones which have a bifurcating projection to the fields of Forel (FF) and to the reticular formation. *B*, a disynaptic test EPSP was evoked by stimulation of cortico-reticular fibres at 200  $\mu$ A in the contralateral pyramid (coPyr) rostral to the pyramidal transection which was made at 3 mm rostral to the obex. The lower pairs of records were taken at a faster sweep speed and show only the later part of the upper records. *C*, facilitation of the pyramidal disynaptic EPSP by a maximal conditioning stimulation of the ascending branches of the tecto-reticular neurones in A6 (marked with arrow). The facilitation was linked to the third pyramidal volley. This facilitated EPSP is denoted the control EPSP in *F*. *D*, interaction of the control EPSP with maximal stimulation of the tecto-reticular fibres in A2. Note the temporal facilitation when the A2 stimulation preceded the A6 stimulation by 2.5 ms. *E*, lack of spatial facilitation when the A2 and A6 stimuli were given simultaneously. *F*, time course of facilitation of the control EPSP. *G*, experimental arrangement.

Additional evidence for this possibility was provided by the results of the experiment illustrated in Fig. 6. A pyramidal disynaptic EPSP was used as a test of transmission via reticulospinal neurones (*B* and *G*). The pyramidal EPSP was facilitated by a maximal conditioning of the presumed ascending

tectofugal collaterals in A6 where they are located close together (*C* and *G*). The peak amplitude of the facilitated EPSP is denoted the control EPSP (*F*). The tectofugal fibres were also stimulated maximally by a separate electrode in A2 at an optimal position for activating the fibres just as they funnel together and leave the tectal

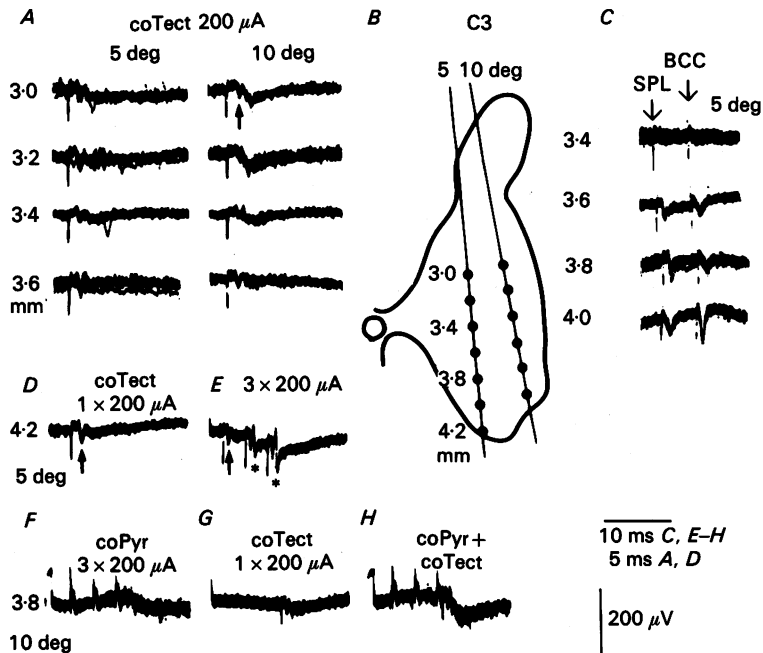


Fig. 7. Termination of tectospinal neurones and of the reticulospinal neurones which could be activated from the contralateral pyramid and tectum in the grey matter of the C3 segment. *A*, extracellular recording of focal synaptic potentials (FSPs) which were evoked by a single stimulus in the contralateral tectum, (A1, coL 2.5, -1). The arrow indicates the direct tectospinal volley which preceded the FSP. *B*, histological reconstruction of the electrode penetrations. *C*, extracellular recording of the motoneuronal field potentials from the SPL and BCC motor nuclei, which were evoked by antidromic nerve stimulation. *D*, a single stimulus applied in the contralateral tectum evoked only a very small FSP. The arrow indicates the arrival of the direct tectospinal volley. Note that the record was taken with the fast sweep speed. *E*, recording from the same position as in *D* but a train of three tectal stimuli was given which caused a marked potentiation of the FSP after each stimulus. Note the appearance of the synaptic volley (marked with asterisk) after the second and third stimuli and that this record was taken with the slow sweep speed. *F*, a train of three pyramidal shocks evoked a small FSP. *G*, a single tectal stimulus evoked only a very small FSP. *H*, facilitation of the pyramidal FSP by the conditioning tectal stimulation in *G*.

layers (*G*). In contrast to spatial facilitation between two different systems where the optimal time interval is near zero (synchronous arrival of the volleys at the relay neurones), it would be expected that if the same system is stimulated twice, the resulting temporal facilitation should be minimal (because of refractoriness) when the time interval approaches zero. This was found to be true as shown for different time intervals in *D*, *E* and *F*. Note the almost complete collision between stimulation

of A2 and A6 when given synchronously in *E* and the temporal facilitation in *D* when the time interval was 2.5 ms. It is concluded that the same tectofugal fibres, which mediate disynaptic excitation via reticulospinal neurones to dorsal neck motoneurones, have ascending collaterals which terminate in the region of the fields of Forel and/or in Zona incerta (cf. Discussion).

#### *Field potential analysis in the spinal cord*

Termination in the neck segments of tectospinal and reticulospinal neurones which were monosynaptically activated by tecto-reticulospinal neurones was investigated by extracellular recording of the focal synaptic potential (FSP) in various parts of the grey matter as illustrated in Fig. 7. A single stimulus in the tectum evoked a monosynaptic FSP from depth 3.0 to 3.4 which was larger in the lateral track at 10 deg than medially at 5 deg (*A* and *B*). Note that the tectospinal volley is largest at depth 3.6 in the medial track. These findings are consistent with the anatomical studies which have demonstrated that the tectospinal fibres are located in the ventral funicle and that they terminate laterally in the intermediate zone of the grey matter (Nyberg-Hansen, 1964). Also electrophysiological experiments have demonstrated that tectospinal neurones terminate on propriospinal neurones (Illert, Lundberg, Padel & Tanaka, 1978) and on segmental interneurones (Alstermark, Lundberg & Sasaki, 1984) which are located laterally in the intermediate zone of the C3–C4 segments.

Figure 7*C* shows that the antidromically evoked motoneuronal field potentials for the SPL and BCC motoneurones were largest at depths 3.8–4.0 in the medial track. Recording from the motor nuclei when a single tectal stimulus was given (*D*) showed a small FSP after the tectospinal volley (arrow). When a train of three tectal stimuli was applied (*E*), it resulted in a synaptic volley after the second and third stimuli (asterisk) which was followed by an FSP. This FSP was potentiated by the second and third tectal stimuli and was presumably mediated by reticulospinal neurones. Figure 7*F–H* illustrates that a small FSP, which was evoked by the third pyramidal stimulus (*F*), could be facilitated (*H*) by a single conditioning tectal stimulus (*G*). These results suggest that reticulospinal neurones, which mediate disynaptic pyramidal and tectal excitation, terminate in the motor nuclei of SPL and BCC motoneurones.

#### *Ipsilateral excitation*

The results of transverse tracking (100  $\mu$ A) at four lateralities through the ipsilateral tectum and tegmentum at the level of A1 are illustrated in Fig. 8*A*. No EPSPs were evoked from the dorsal tectal layers (+4) and only small EPSPs with long latencies were elicited at depth +3. More ventrally (+2 to –2), the amplitude of the EPSPs increased and the latency became shorter. The EPSPs with the largest amplitude and shortest latency (1.7 ms) from the third stimulus were evoked from depth –2 at ipsilateral (iL) 2.5. More ventrally at depth –3 the EPSPs became smaller and the latency increased (2.0 ms). Figure 8*B* and *C* summarizes the depth–latency profiles for different SPL and BCC motoneurones respectively. In Fig. 8*C* it is shown that at lateralities 2 and 2.5 the latencies decreased gradually from 2.0 to 3.0 ms between depths +3 and 0, and to about 1.6 ms at depth –2. With a position of lateral 3–4 mm (in *B*) the same pattern was observed except that the minimal

latencies were longer (1.75–2.0 ms) and were observed more dorsally at depth 0. These depth–latency profiles differ considerably from those obtained from the contralateral side (cf. Fig. 1) in two respects: (i) the shortest latencies of around 1.6 ms were only found ventrally at depth –2, (ii) dorsal to depth 0, the latencies were

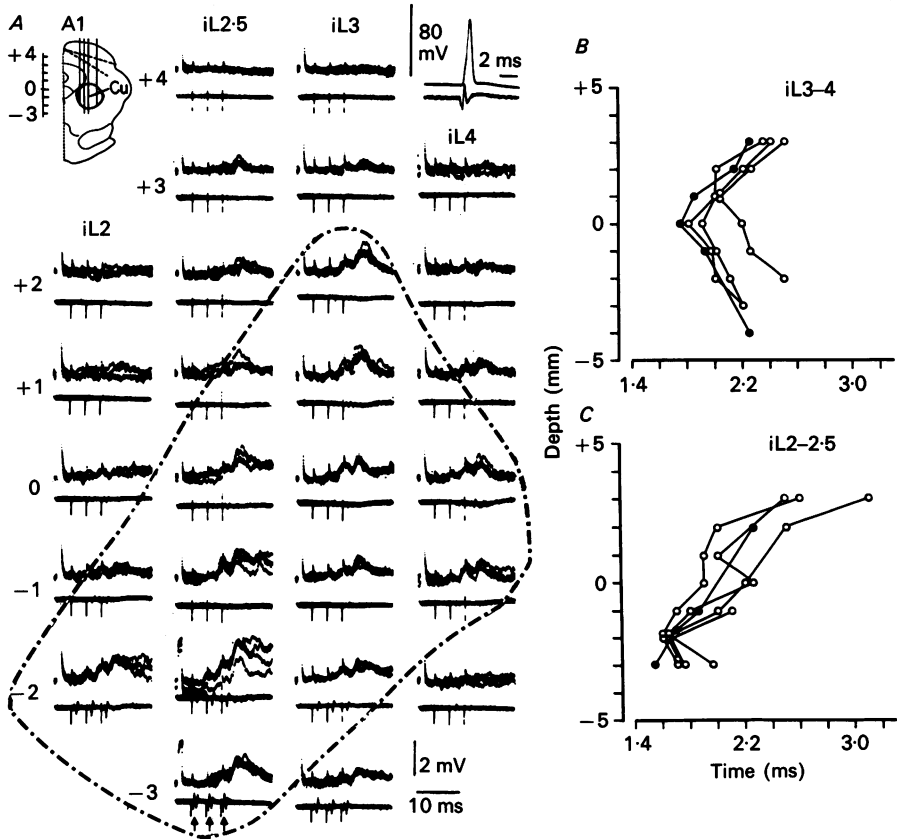


Fig. 8. Transverse tracking in the ipsilateral tectum and tegmentum at the level of A1 for a SPL motoneurone. *A*, the electrode tracks from the different lateralities are shown in the histological reconstruction. The stimulation strength was 100  $\mu$ A. Upper traces are from intracellular recordings and the lower traces are from cord dorsum recordings in C3. The interrupted line indicates the border for thresholds below 50  $\mu$ A. *B*, latencies measured from the third stimulus at 200  $\mu$ A to the onset of the EPSPs plotted *versus* the depth of stimulation at iL 3–4 mm for A1.  $\circ$  indicate BCC motoneurones and  $\bullet$  SPL motoneurones. *C*, as in *B* but for iL 2–2.5 mm. Abbreviations: cuneiform nucleus (Cu).

longer than 1.8 ms. By analogy with the analysis of contralateral tectal EPSP latencies (see above), it is concluded that the minimal latencies for the ipsilateral tegmental EPSPs are disynaptic.

In Fig. 8*A* (interrupted line) is shown the spatial distribution of thresholds below 50  $\mu$ A. The lowest thresholds for evoking these EPSPs were between 20 and 50  $\mu$ A. These results demonstrate that disynaptic EPSPs in dorsal neck motoneurones could be evoked at low threshold from the ipsilateral tegmentum but not from the tectum.

The most effective stimulation site for evoking these EPSPs corresponds well to the cuneiform nucleus which has projections to the reticular formation (Edwards, 1975). It is suggested that the tectal disynaptic EPSPs are evoked by direct activation of cell bodies in the cuneiform nucleus which project to reticulospinal neurones. This hypothesis is supported by interaction experiments which have demonstrated convergence from the tegmentum onto the same reticulospinal neurones which mediate the disynaptic contralateral tectal and pyramidal EPSPs to dorsal neck motoneurones (Alstermark *et al.* 1983, and unpublished observations).

Similar results as shown in Fig. 8 for A1 were found more rostrally at A2–A5. Disynaptic EPSPs could still be evoked at A6–A8 but mainly from a restricted region at depths +1 to –2 at laterality 1.5 to 3. Tracking rostrally at A9–A11.5 revealed no excitation. It is not known if the EPSPs evoked at A6–A8 are evoked by antidromic activation of tectal neurones with ascending collaterals.

#### DISCUSSION

The results of this study confirm the original observations by Anderson *et al.* (1971) that disynaptic EPSPs can be evoked from the contralateral tectum in SPL and BCC motoneurones via reticulospinal neurones. The tecto-reticular neurones could be synaptically activated from the dorsal tectal layers, which resulted in EPSPs of longer latencies compatible with a trisynaptic linkage. Anderson *et al.* (1971) found no systematic differences when they stimulated at various positions rostrocaudally in the caudal three-quarters of the superior colliculus. However, although we also observed that disynaptic EPSPs could be evoked throughout the ventral part of the tectum, we found that the trisynaptic EPSPs from the dorsal tectal layers could only be elicited from the caudal half of the superior colliculus. The disynaptic EPSPs evoked ventrally in the rostral part were due to stimulation of the ascending collaterals of the tectofugal neurones (*cf.* below). It is postulated that the tectofugal neurones which evoke disynaptic excitation in SPL and BCC motoneurones are mainly located in the caudal half of the superior colliculus. Results from a recent anatomical study have shown a higher density of tecto-reticular neurones in the caudal half of the superior colliculus (Olivier, Chat & Grantyn, 1991). A functional rostrocaudal organization in the superior colliculus has previously been described by Harris (1980) and Roucoux, Guitton & Crommelinck (1980). They found in alert cats that electrical stimulation of: (1) the anterior zone evoked retinotopic eye saccades and only slow head movements of small amplitude (2) the intermediate zone elicited goal-directed saccades and fast head movements of large amplitude and (3) the posterior zone produced goal-directed head movements but not saccades. It was proposed that the posterior zone is involved in the control of body-orienting movements (Roucoux *et al.* 1980).

The fact that disynaptic EPSPs could be evoked at low threshold from the contralateral side also at laterality 4.0 and ventral to the tectal layers raises the possibility that neurones in the underlying tegmentum could contribute. It has been demonstrated anatomically that neurones in this region of the cuneiform nucleus have a strong crossed projection via the ventral tectal bundle to the pontine and medullary reticular formation (Edwards, 1975).

The anatomical study by Grantyn & Grantyn (1982) of tectofugal neurones labelled intracellularly with horseradish peroxidase demonstrated that their axons bifurcate into one descending and one ascending branch. The latter branch had terminal ramifications in the tegmentum, central grey, nuclei of Cajal and Darkschewitsch, prerubral area and in the fields of Forel. The results of the present study thus confirm the projection to the fields of Forel and also suggest a projection to Zona incerta. In addition it was demonstrated that this projection was from bifurcating tectofugal neurones which act on reticulospinal neurones in a disynaptic excitatory pathway to dorsal neck motoneurones. The ascending projection from tectofugal neurones is interesting also with respect to eye motor control since it has been shown that the target neurones project to the frontal eye field (area 8) and the inferior parietal lobule (area 7; Harting, Huerta, Frankfurter, Strominger & Royce, 1980). Mono- and disynaptic excitatory connections from tectofugal neurones to vertical saccade-related neurones have recently been observed in the fields of Forel (Nakao, Shiraishi, Li & Oikawa, 1990). Furthermore, it has been shown by Isa, Iitouji, Nakao & Sasaki (1988*a*) and Isa, Iitouji & Sasaki (1988*b*) that excitatory neurones in the fields of Forel project monosynaptically or disynaptically via reticulospinal neurones to dorsal neck motoneurones. Thus activity in the ascending branch of the bifurcating tectofugal neurones may act both in a feedback and feed forward manner and could be of importance for co-ordinating eye and head movements.

A clear difference with respect to the control of forelimb motoneurones (Illert, Lundberg & Tanaka, 1977) was the lack of disynaptic excitation in SPL and BCC motoneurones from the contralateral red nucleus. Thus, the C3–C4 propriospinal neurones which mediate disynaptic rubral EPSPs in forelimb motoneurones (Illert *et al.* 1977) lack projections to dorsal neck motoneurones in the C3–C4 segments. This is analogous to the case of disynaptic pyramidal excitation which has been shown to be mediated via C3–C4 propriospinal neurones to forelimb motoneurones (Illert *et al.* 1977) and via reticulospinal neurones to dorsal neck motoneurones (Alstermark, Pinter & Sasaki, 1985). These electrophysiological findings are confirmed by anatomical results which show a lack of projection from the C3–C4 propriospinal neurones to the SPL and BCC motor nuclei (Alstermark, Isa & Tantisira, 1991).

From the ipsilateral side, the short latency excitation within a disynaptic range was evoked at low threshold from the tegmentum but not from the tectal layers, which is in contrast to the previous results of Anderson *et al.* (1971). The discrepancy might be due to differences in stimulation strength, since we could evoke disynaptic EPSPs from the ipsilateral deep tectal layers but at a threshold of 200  $\mu$ A. However, Anderson *et al.* (1971) do not give the thresholds for evoking the disynaptic EPSP from the ipsilateral tectum. In contrast to the situation on the contralateral side, the lack of low threshold excitation from the ipsilateral tectum strongly suggests that the disynaptic excitation evoked from the underlying tegmentum is due to activation of neurones in the cuneiform nucleus. Since it is known that there is a strong projection from the ipsilateral tegmentum in the cuneiform nucleus to nucleus gigantocellularis in the reticular formation (Edwards, 1975), it is postulated that the disynaptic EPSPs evoked from the tegmentum could be due to direct activation of tegmento-reticular neurones.

It has also been demonstrated by Edwards & De Olmos (1976) that many neurones in the tegmental field have ascending projection to several nuclei in the diencephalon, e.g. to the fields of Forel. It remains to be investigated if the disynaptic excitation in the SPL and BCC motoneurones which was evoked from the ipsilateral fields of Forel could partly be due to stimulation of ascending collaterals from bifurcating tegmento-reticular neurones. However, another explanation is offered by the findings of Isa *et al.* (1988*a, b*) that neurones in the fields of Forel have a descending projection to reticulospinal neurones in the nucleus gigantocellularis.

The authors wish to thank Professor Anders Lundberg for helpful discussions and Mrs Rauni Larsson for excellent technical assistance. This work was supported by the Swedish Medical Research Council (Project Nos. 94 and 6953). M.J.P. and S.S. held IBRO/UNESCO Fellowships.

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