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DESCENDING AND SEGMENTAL INHIBITION OF TRANSMISSION THROUGH THE SPINOCERVICAL TRACT

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SUMMARY

1. Micro-electrode recordings were made from axons of the spinocervical tract in unanaesthetized decerebrate-spinal cats.

2. The effects of stimulation of (1) descending systems at the level of the upper cervical spinal cord and (2) hind limb cutaneous nerves, on discharges of spinocervical tract neurones were examined.

3. Effects were obtained from bilateral spinal cord regions in the dorsolateral funiculi and the most medial and ventral parts of the ventral funiculi and also from the dorsal columns in the upper cervical region even though the columns had been transected at low thoracic and upper lumbar levels.

4. Stimulation of either descending or segmental systems inhibited spontaneous and evoked responses. Facilitation was not seen. The inhibition had a time course of up to 250 msec, with maximal action at 20–40 msec and was greatest for polysynaptic responses or those evoked from the smaller myelinated cutaneous axons.

5. It is suggested that the descending and segmental systems converge on to common inhibitory interneurones.

INTRODUCTION

Transmission through the spinocervical tract (SCT) is inhibited by impulses descending from several regions of the brain (Taub, 1964; Wall, 1967; Fetz, 1968; Brown & Franz, 1969; Brown, 1971). Taub (1964) showed that electrical stimulation of part of the mesencephalic tegmentum not only inhibited SCT transmission but also evoked a lumbar dorsal root

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potential which could occlude part of a segmentally evoked dorsal root potential and suggested that the supraspinal effect acted through presynaptic inhibitory mechanisms.

Inhibition of transmission through the SCT may also be produced by natural stimulation of areas of skin outside the excitatory receptive field of the SCT neurone under study and by electrical stimulation of peripheral nerves (Taub, 1964; Hongo, Jankowska & Lundberg, 1968; Brown & Franz, 1969). Hongo *et al.* also showed that part of this inhibition was post-synaptic in nature. That some of the inhibition might be due to presynaptic mechanisms was suggested by the experiments of Eccles, Kostyuk & Schmidt (1962) who studied the effects of electrical stimulation of cutaneous and muscle afferent nerve fibres on the mass discharge evoked in the ipsilateral dorsolateral funiculus by cutaneous nerve stimulation. They demonstrated that the later components of this discharge were inhibited but that the monosynaptic component was little, if at all, affected. The time course of the inhibition was suggestive of presynaptic inhibition. Since Lundberg & Oscarsson (1961) had previously shown that most of the mass discharge in the ipsilateral dorsolateral funiculus produced by cutaneous nerve stimulation is due to activity in the SCT, it may be assumed that the effects described by Eccles *et al.* were produced predominantly on the discharges of SCT cells.

The present experiments were performed (1) to provide more direct evidence, at the single unit level, of the inhibitory actions on transmission through the SCT evoked from supraspinal and segmental systems, and (2) to determine the locations within the spinal cord of the descending systems involved in this inhibition.

Preliminary accounts of some of the results have been published (Brown & Kirk, 1972; Brown, Kirk & Martin, 1972).

METHODS

The experiments were performed on unanaesthetized decerebrate cats made spinal at the level of the first cervical segment and paralysed with gallamine triethiodide. The decerebration was performed under ether anaesthesia. The maintenance of the preparation and most of the electrophysiological methods have been described in detail previously (Brown & Franz, 1969; Brown, 1971). Briefly, microelectrode recordings were made from identified single axons of the spinocervical tract which responded to electrical stimulation of either the sural (SU) or medial plantar (MP) nerves in the ipsilateral hind limb. The contralateral SU and MP nerves were also available for stimulation. All peripheral nerves were left in continuity to allow examination of receptive fields. Ingoing afferent volleys were monitored at the appropriate dorsal root entrance zones with a monopolar silver-ball electrode.

Stimulation and location of the descending systems. Two approaches were used to define the locations and actions of the descending systems. In the first series of

seven experiments the cervical spinal cord was divided into fascicles. The dorsal columns were removed from the level of the spinal transection (at C 1) to the level of the fourth cervical segment and the remainder of this length of the spinal cord divided longitudinally, after the manner of Rudin & Eisenman (1951) and Laporte, Lundberg & Oscarsson (1956), by splitting it into right and left halves and then subdividing each half into approximately equal dorsal and ventral parts. Each of the four fascicles remained in continuity with the caudal part of the spinal cord and was placed on a pair of silver–silver chloride stimulating electrodes with the cathode caudal. Stimuli were trains of 4–7 square-wave shocks of 0·2 msec duration at 100–400 Hz. At the end of each experiment the cervical cord was bathed in 10 % formol-saline and subsequently removed for microscopical examination of the extent of each fascicle.

Since stimulation of each of the four fascicles produced inhibition of transmission through the SCT (see Results) and because more precise localization of the stimulus was required, a tungsten micro-electrode was used as a stimulating cathode in the second series of five experiments. The micro-electrode had a resistance of approximately 30 KΩ and the stimuli delivered through it were less than 1·5 V in amplitude. The anode was in the dorsal cervical muscles. A grid of stimulation sites was made transversely in the spinal cord at C 2–4 by moving the micro-electrode in 0·5 mm steps down dorso-ventral tracks 0·5 mm apart. At each position a conditioning tetanus of 4–7 shocks, 0·2 msec in duration at 200–300 Hz, was delivered 40 msec before a test shock to a peripheral nerve which excited the neurone under study. The 40 msec conditioning-testing interval was chosen because the first series of experiments had shown that maximal inhibition occurred at 20–40 msec. The number of impulses evoked by each test stimulus was counted. At least five recordings were made at each grid position. The degree of inhibition of each point was expressed as the mean percentage reduction from the mean of at least five control responses. The control responses were recorded every five steps in the grid. In one experiment of this type, however, with grids at C 2 and C 4 the mass discharge evoked in the dissected dorsolateral funiculus at L 2–3, by stimulation of the ipsilateral medial plantar nerve, was used as the test response. The inhibition observed was similar to that seen in the single unit reponses even though part of the dorsolateral funiculus at L 2 had been cut.

In all experiments of the second series, the dorsal columns were removed bilaterally at T 13–L 1 to prevent direct excitation of the SCT from collateral branches of the dorsal column axons and also to prevent inhibitory effects mediated via this route. At the end of each experiment the preparation was perfused with normal saline and then 10 % formol-saline. After fixation, 100 μm frozen sections of the cord were cut and stained with cresyl violet. Reconstructions were made to show the electrode tracks in the cervical cord and the extent of the thoracolumbar dorsal column lesions.

RESULTS

Descending inhibitory pathways and their actions on transmission through the spinocervical tract

Neurones in the dorsal horn, including the cells of origin of the SCT, are under the control of descending activity which is tonic in the decerebrate cat and which can be reversibly blocked by cooling the cord rostral to the recorded neurones (Wall, 1967; Brown, 1971). When stimulation of the cervical spinal cord affects transmission within lumbar segments,

however, it does not necessarily follow that the effects observed are due to activation of descending pathways even when the cord has been transected rostral to the site of stimulation. Antidromic activation of the axons of an ascending system will affect transmission at the lumbar level if the ascending axons have collateral branches with connexions to the system under study. One such ascending pathway is the dorsal column, most of the axons of which are branches of fibres entering the spinal cord in the dorsal roots and which also have connexions to the SCT. In the present experiments the dorsal columns were sectioned at the thoracolumbar junction. This was done to prevent effects on the SCT from antidromic activation of dorsal column fibres excited by stimulation of the cervical spinal cord. Evidence for collateral effects evoked by antidromic excitation of ascending pathways is difficult to obtain. Ascending systems, except the dorsal columns, which inhibit transmission through the SCT by means of collateral branches have so far not been described. In recording our results we have, therefore, assumed that the effects produced by stimulation of the cervical cord in high-spinal cats are due to orthodromic activation of descending pathways.

Location of the descending pathways

In the first series of experiments stimulation of each of the four fascicles into which the cervical cord had been divided produced inhibition of SCT cell discharges evoked from ipsilateral hind limb cutaneous nerves. The inhibition elicited from the ipsilateral dorsolateral fascicle, while similar to that produced from the other fascicles, appeared against a background of antidromic excitation evoked by stimulation of the SCT axons near their termination in the lateral cervical nucleus. This antidromic excitation made it difficult to evaluate short latency effects. It was obvious, however, that the inhibitory systems were bilateral and in both the dorsolateral and ventral funiculi of the cervical cord.

In one experiment, involving stimulation of fascicles, various lesions were made in the first lumbar segment of the spinal cord to determine the approximate locations of the descending systems at this level. Section of the ipsilateral dorsolateral funiculus abolished the effects from the ipsilateral dorsolateral cervical fascicle but had no apparent action on the inhibition which followed stimulation of the other three fascicles. Ipsilateral lumbar hemisection removed the effects from the ventral ipsilateral cervical fascicle in addition to the dorsolateral one but had no apparent action on contralaterally evoked inhibition. Finally, section of most of the contralateral lumbar cord, at a level in L 1 different from the previous lesions, removed the effects from the contralateral fascicles. These findings suggests that the descending pathways retain their positions to at least the level of the first lumbar segment.

A detailed investigation of the locations of the descending pathways was made using a tungsten micro-electrode as a stimulating cathode in

the second series of experiments. Fig. 1 shows a reconstruction of a stimulation grid at caudal C 2. Each stimulation site is marked by a symbol indicating the percentage reduction in the number of impulses in the test response after delivery of the conditioning tetanus 40 msec earlier. It was not possible to produce a complete grid for any one SCT neurone and in the experiment illustrated in Fig. 1 seven units were needed to produce the grid but changing from one unit to another did not alter the amount of inhibition observed. Inhibition was obtained from

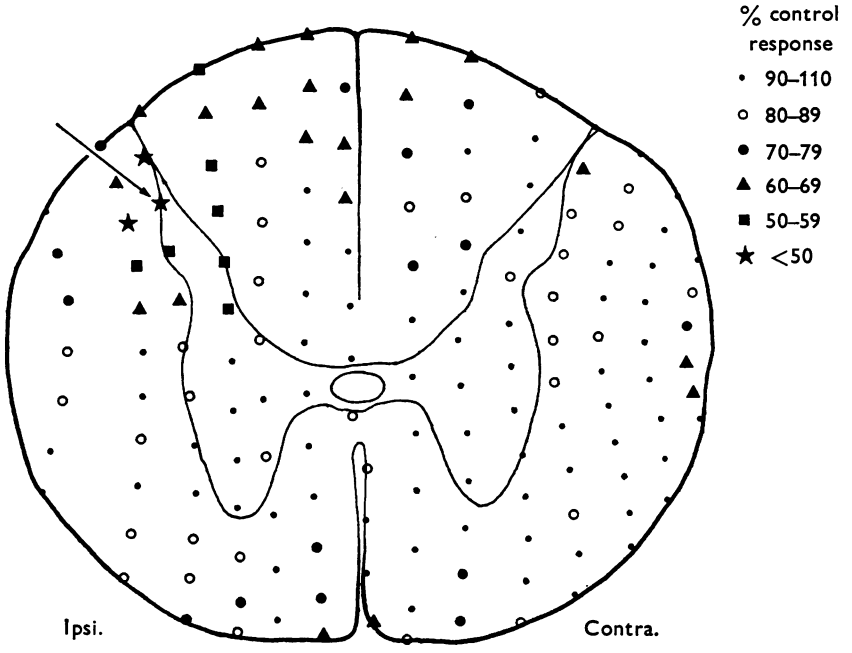

Fig. 1. Reconstruction of a grid of stimulating points at a caudal level in the second cervical segment. Each symbol is at the location of the stimulating micro-electrode tip through which a short (20 msec) tetanus at 200–300 Hz was delivered 40 msec before a testing volley to an ipsilateral cutaneous nerve. The symbols indicate the strength of the test response (the mean number of impulses evoked) in terms of the control values. Inhibition of the test response was produced from bilateral areas in the dorsolateral and ventromedial parts of the cord, the dorsolateral area on the contralateral side having two component parts separated by a completely negative track of stimulation sites. Inhibition was also elicited from the dorsal columns on both sides even though the dorsal columns had been transected at the first lumbar segment. A total of seven SCT units were needed to produce the grid. The arrow indicates the only stimulation site from which antidromic excitation of a SCT axon could be elicited with the strength of stimulation employed and shows that the spread of stimulating current was not excessive.

several areas of the cord. These were in the dorsolateral funiculi, the most medial and ventral parts of the ventral funiculi and also in the dorsal columns. Similar results were found in all five cats in the series. In the experiment illustrated in Fig. 1 antidromic activation of SCT axons was produced from only one of the stimulation sites (marked by an arrow), just lateral to the apex of the dorsal horn on the ipsilateral side, in a position where SCT axons would be expected. The spread of the stimulating current was therefore severely limited.

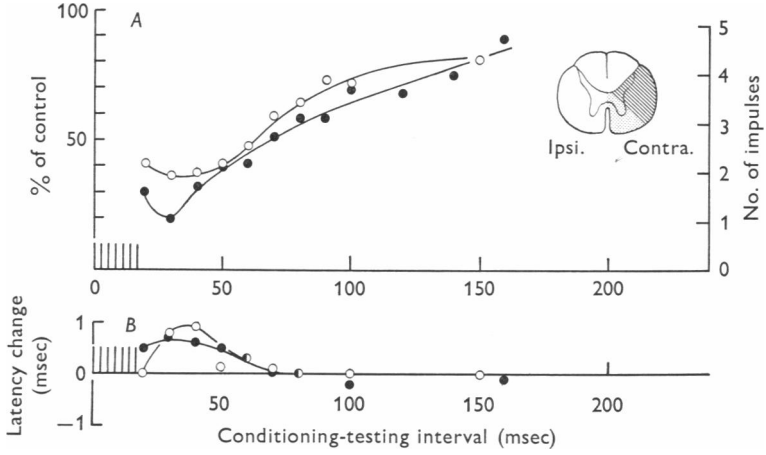

Fig. 2. Time course of descending inhibition of SCT cell discharges (monosynaptic input). The graphs show the responses of a SCT neurone evoked by electrical stimulation of the SU nerve at 1·25 times threshold when conditioned with a short tetanus to either dorsolateral (●) or ventral (○) fascicles dissected from the contralateral upper cervical cord. The extent of the fascicles is shown in the inset in *A*. In *A* the number of impulses and the percentage of the control values are plotted against the conditioning-testing interval. In *B* the change in latency of the first impulse evoked by the testing shock is plotted against the conditioning-testing interval. The maximum latency change is just under 1 msec. Each point represents the mean of at least five observations. The vertical lines on the abscissae represent the train of conditioning shocks.

In Fig. 1 the contralateral dorsolateral area from which inhibition was obtained appears to consist of two parts, one dorsal and medial near the apex of the dorsal horn and the other more ventral and lateral. It was also seen in other experiments, on both the ipsilateral and contralateral sides, but less clearly than in the experiment illustrated. The ventral areas were consistently in the most medial and ventral parts of the ventral funiculi. The inhibition produced from the dorsal columns was elicited in spite of the fact that the dorsal columns had been removed at T 13–L 1.

Actions of the descending systems

Stimulation of the dorsolateral and ventral funiculi on either side of the cervical cord produced inhibition of both spontaneous and evoked discharges of SCT cells. Facilitation was never seen. Coincident with the

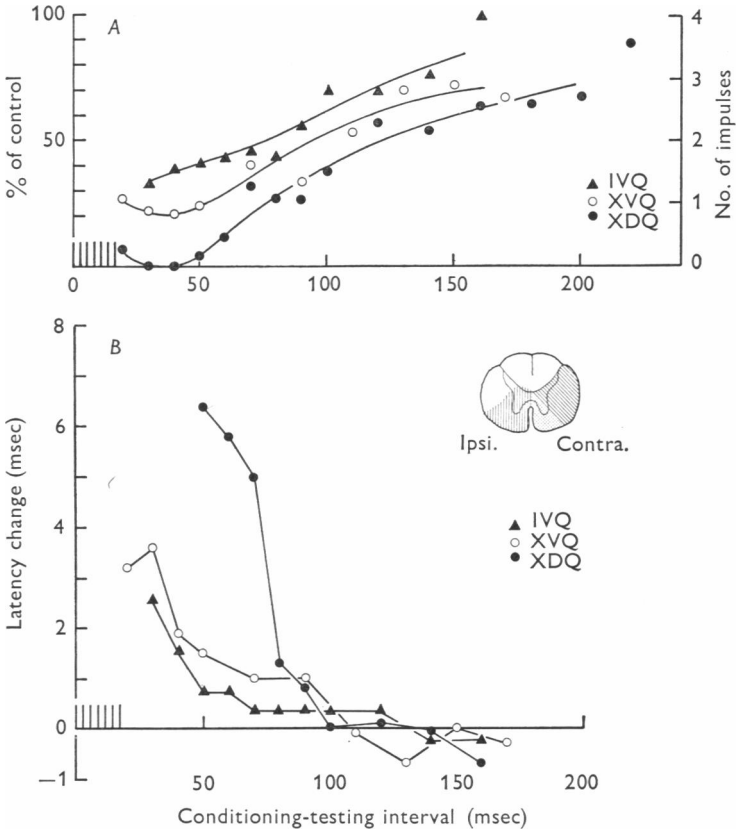

Fig. 3. Time course of descending inhibition of SCT cell discharges (polysynaptic input). This is similar to Fig. 2 except that the central latency of the unit (about 5 msec) indicates a polysynaptic connexion to the tract cell. The ipsilateral ventral cervical cord was stimulated (▲) in addition to the contralateral ventral (○) and dorsolateral (●) fascicles. Marked changes in the latency of the first evoked impulse were produced by the conditioning stimuli.

inhibition of SCT cell discharge, P waves were evoked on the lumbar cord dorsum. This suggests a presynaptic mechanism for the inhibition.

Time course of the inhibition. Short tetanic stimulation of cervical cord fascicles was used to condition test responses evoked by electrical stimu-

lation of cutaneous nerves. Similar curves were obtained for units with monosynaptic (Fig. 2*A*) and polysynaptic (Fig. 3*A*) linkages when the inhibition was expressed as the mean number of impulses evoked by the testing stimulus. The central delay in conduction for the unit shown in Fig. 2, measured from the arrival of the afferent volley at the dorsal root entrance zone to the first evoked impulse recorded at L 4–5, was 1·0 msec indicating a monosynaptic linkage, whereas that for the unit shown in Fig. 3 was nearly 5·0 msec suggesting that more than one synapse was interpolated on the afferent pathway. Both of these units responded to hair movement and to pressure on the skin of the receptive field. The inhibitory curves for units responding to hair movement alone and for units responding to both hair movement and skin pressure (Types I, II and III of Brown, 1971) were similar. For all units inhibition was maximal at conditioning-testing intervals of 20–40 msec and lasted for 150–250 msec.

The inhibition produced by activation of the descending systems was particularly effective against the discharges evoked by the smaller myelinated afferent fibres (non-myelinated afferent fibres would not be excited by the electrical stimuli used in the present experiments) and against weak excitatory actions from the large myelinated cutaneous axons. This is shown in Fig. 4 where stimulation of the contralateral ventral cervical cord produced severe inhibition of the responses evoked by peripheral nerve stimulation at 1·8 times threshold (1·8 T). When the peripheral stimulus was increased to 5 T then the early response (0–25 msec) was unaffected by the conditioning but the late response (25–100 msec), which appeared with the raised stimulus strength, was markedly inhibited.

While there were no differences in the time courses of inhibition between mono- and polysynaptically evoked SCT cell discharges when the total number of impulses were used to express the test response (there were, of course, differences in the *degree* of inhibition produced in different units and between the different parts of any one response, as shown in Fig. 4) marked differences were seen when the latency of the first evoked impulse was taken as the test response. The descending systems had little or no action on the latency of monosynaptic responses, any change in latency produced at optimum conditioning-testing intervals being less than 1·0 msec (Fig. 2*B*). For polysynaptically evoked responses (central latencies longer than 2·0 msec) the latency of the first impulse was increased by between 2·0 and 6·4 msec at optimum conditioning-testing intervals (Fig. 3*B*). Comparison of the upper and lower graphs in Figs. 2 and 3 shows that the time courses of the latency increases were similar to those of the reductions in the total number of impulses transmitted.

Actions on spontaneous discharges, naturally evoked discharges and on receptive fields. Stimulation of the descending systems inhibited both spontaneous and naturally evoked discharges of SCT cells. Fig. 5 shows the effects of stimulating the contralateral dorsolateral cervical cord on the spontaneous discharge and on that evoked by squeezing the skin of

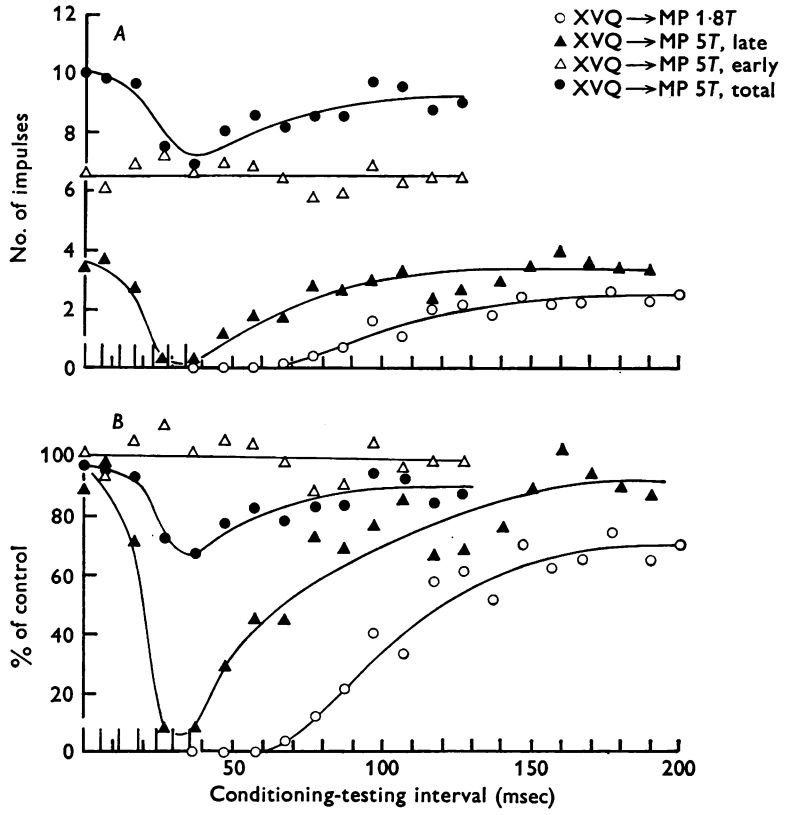

Fig. 4. Effects of descending inhibition on different components of an evoked discharge in the SCT. Stimulation of the contralateral ventral quadrant of the spinal cord produced marked inhibition of the discharge evoked by relatively weak (1·8 times threshold, (○)) stimulation of the MP nerve. When the testing stimulus strength was increased to 5 times threshold there was no inhibition of the early (first 25 msec) discharge (△), which covered the time of occurrence of the discharge evoked by the weaker stimulation, but the late discharge (25–100 msec), which appeared with the stronger stimulation, was severely inhibited (▲). This action on the discharge evoked by weak stimulation and the late discharge to stronger stimulation is emphasized in the lower graph where the responses are directly compared with reference to the control values. Each point is the mean of at least five individual responses.

the receptive field with a small toothed clip. Inhibition of the evoked response was particularly marked, and in both instances was more potent during the first few seconds of cord stimulation, there being some recovery during the later part of the period of stimulation. In general,

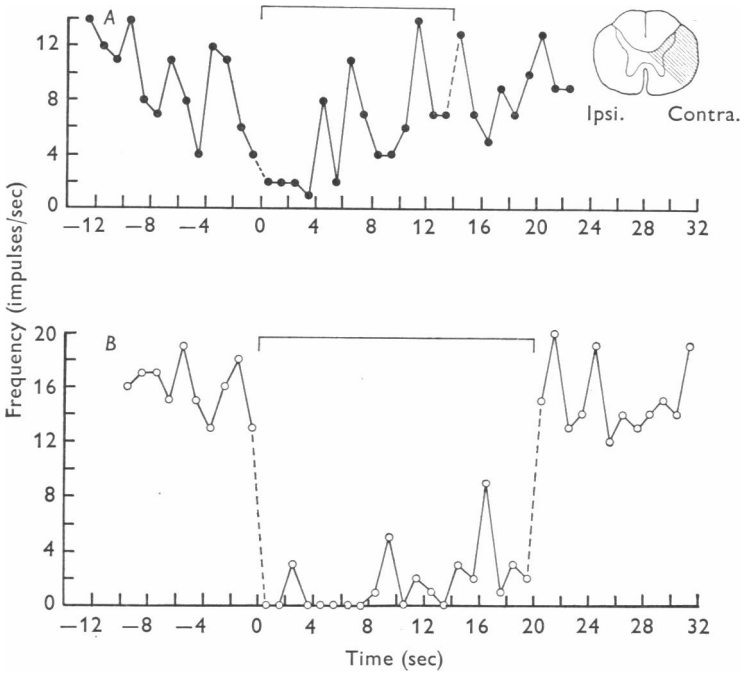

Fig. 5. Effects of the descending inhibition on spontaneous and naturally evoked discharges of a SCT cell. In *A* stimulation of the contralateral dorsolateral cord at about 300 Hz produced an initial reduction in the rate of spontaneous activity of the unit which gradually recovered to pre-stimulation rates during continued stimulation. Similar stimulation in *B* produced a severe depression of the rate of discharge when the unit was responding to a small toothed clip on the skin of the excitatory receptive field and the effects lasted throughout the period of stimulation. The rates of discharge were calculated over periods of 1 sec. The bars above each graph show the period of stimulation of the contralateral dorsolateral cervical fascicle shown in the inset in *A*.

the spontaneous activity was more resistant to the effects of the descending systems than the activity evoked by pressure or pinch of the skin and underlying tissues.

The sizes of the receptive fields of twelve units were determined both without and with one or more of the cervical cord regions being stimulated in turn. The fields were examined by moving hairs and by pressing on the skin with hand-held probes. Only one unit showed any obvious change

in the size of its field during stimulation of descending systems. This unit had a receptive field to hair movement and pressure on the outer aspect of the thigh, leg and foot. On stimulating the contralateral ventral fascicle the field shrank away from the foot leaving only the thigh and leg area

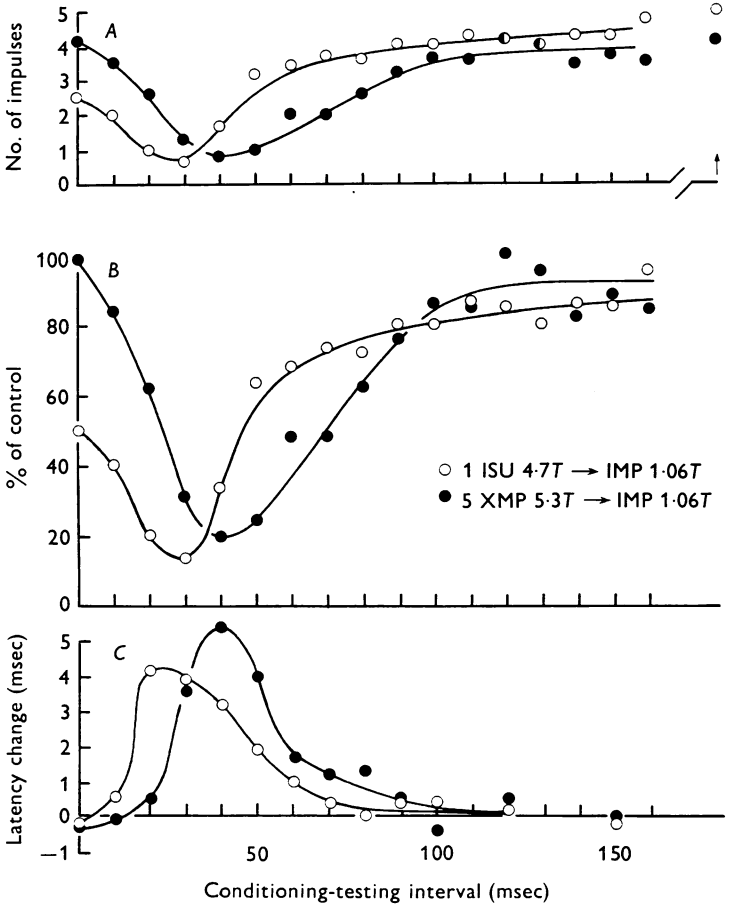

Fig. 6. Ipsilateral and contralateral inhibition of SCT discharges. *A* and *B* show the time course of the reduction in the number of impulses in the discharge of a SCT unit evoked by a test stimulus of 1·06 times threshold to the ipsilateral MP nerve when the conditioning stimuli were 5 shocks at 300 Hz to the contralateral MP nerve at 5·3 times threshold (●) or 1 shock to the ipsilateral SU nerve at 4·7 times threshold (○). The conditioning shock to the ipsilateral SU nerve did not evoke a discharge in the tract cell. The arrow in *A* indicates the control values for the test responses. In *C* the latency change of the first impulse evoked by the testing shock is plotted against the conditioning-testing interval for the same series shown in *A* and *B*. The central latency of the first evoked impulse was greater than 2 msec indicating a polysynaptic linkage in the excitatory pathway. Each point is the mean of at least five observations.

responsive. In the other eleven units the areas of skin from which responses could be obtained to hair movement were, as far as could be determined, not changed by stimulation of the descending systems. The situation with regard to the pressure sensitive component was more difficult to evaluate. When the descending systems were not being stimulated the pressure sensitive fields were coextensive with the areas responding to hair movement. When descending systems were stimulated then the units became much less responsive to pressure. It was then usually not possible to determine the extent of the field with any certainty since the heavy pressure required to produce a response in the unit could have excited receptors over a wide area of skin and underlying tissue.

Segmental inhibitory actions on transmission through the spinocervical tract

Segmental inhibitory mechanisms were examined by conditioning test responses evoked in SCT units with volleys of impulses in either contralateral hind limb cutaneous nerves or in ipsilateral nerves which did not excite the tract cell under study. The inhibitory actions were essentially the same as those evoked from the descending systems and, again, facilitatory effects were not seen. Figs. 6 and 7 show the effects of the inhibition on both the numbers of impulses evoked and the latency of the first impulse for both mono- and polysynaptic responses in SCT cells. The inhibition had a time course of up to 200 msec with maximal action at 20–50 msec. It was most effective against weak excitation produced by stimulation of large cutaneous axons (Fig. 6 and ○ in Fig. 7) or against the discharge produced by stimulating smaller myelinated cutaneous axons (■ in Fig. 7). As with the actions of the descending systems, large latency increases (up to 6 msec) were produced at optimal conditioning-testing intervals for the first evoked impulse in polysynaptically evoked discharges, whereas for monosynaptically evoked discharges the latency was either unaffected or increased by less than 1 msec. The unit illustrated in Fig. 7 had a polysynaptic response to stimulation of the sural nerve at 1·29 times threshold (1·29T) and there was the usual latency increase for the first evoked impulse, in this instance of 3·2 msec at a conditioning-testing interval of 50 msec. When the test shock was increased the latency of the first impulse fell to 1·0 msec indicating that the cell was now being excited monosynaptically and the conditioning stimulus was no longer affecting the latency. The strength of stimulation necessary to evoke the monosynaptic response was not determined but could have been as low as 1·3–1·4T.

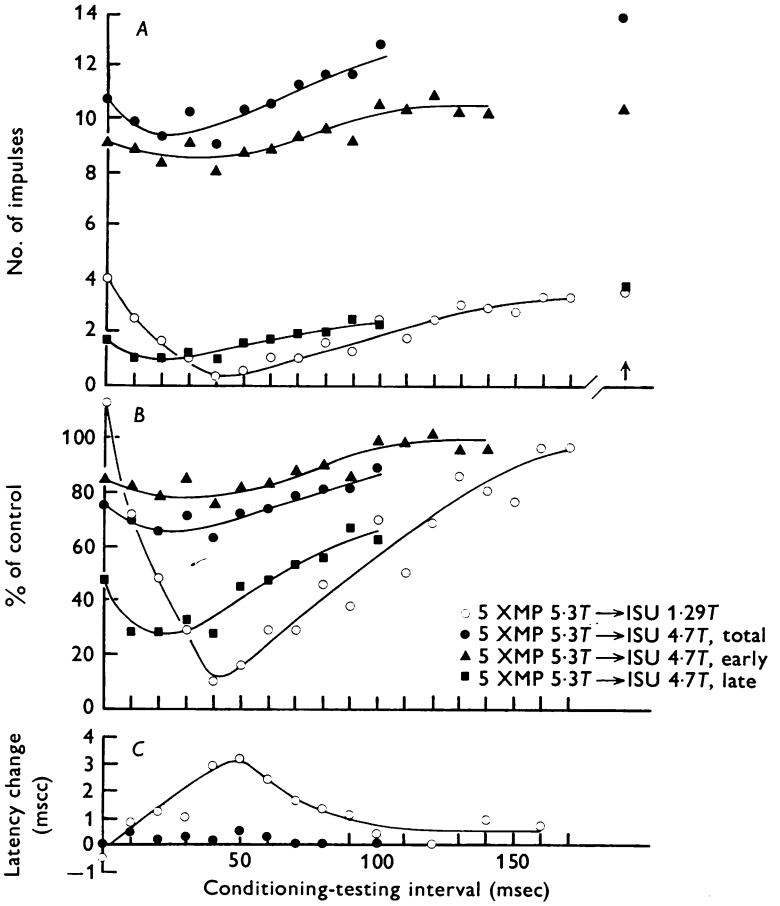

Fig. 7. Segmental inhibition of mono- and polysynaptic SCT discharges. The test responses were evoked by electrical stimulation of the ipsilateral SU nerve at either 1·29 (○) or 4·7 (● ▲ ■) times threshold. The conditioning stimulus was 5 shocks at 300 Hz to the contralateral MP nerve at 5·3 times threshold. *A* and *B* show the time course of the reduction in the number of impulses evoked by the testing stimuli. The most marked inhibition was produced either when the testing stimulus was weak (○) or on the late (25–100 msec) components of the discharge when the testing stimulus was strong (■). The early component (up to 25 msec) was not severely affected when the testing stimulus was strong (▲). The arrow in *A* indicates the control values for the test response. In *C* the latency change of the first impulse evoked by the test response is plotted against the conditioning-testing interval. With a testing stimulus of 1·29 times threshold (○) the central latency was 3·0 msec indicating a polysynaptic response and there was a corresponding latency change of up to 3·2 msec at conditioning-testing intervals of 50 msec. When the testing shock was increased (●) the central latency fell to 1·0 msec indicating a monosynaptic linkage and the conditioning stimulus now had no effect on the latency. Each point is the mean of at least five observations.

DISCUSSION

The present experiments have confirmed that there are several bilateral descending pathways which can inhibit transmission through the SCT and have established that in the upper cervical cord they are in each dorsolateral funiculus and each ventral funiculus. The results suggest that in the dorsolateral funiculus there may be two descending systems rather than one (see Fig. 1), one in its medial and dorsal part and the other located more ventrally and laterally. In the ventral funiculus the descending systems are located in the most medial and ventral parts. The positions of the pathways are in accord with expectations from the results of Taub (1964) and Fetz (1968) and they may include all or some of the following; corticospinal, rubrospinal, vestibulospinal and reticulospinal tracts. Whether all, or only some, of the descending pathways are responsible for the tonic inhibition observed in the decerebrate cat (Wall, 1967; Brown & Franz, 1969; Brown, 1971) remains to be determined, but cortico- and rubrospinal pathways would not be functioning in intercollicular-decerebrate preparations.

In addition to the pathways in the dorsolateral and ventral funiculi, it has been shown that stimulation of the dorsal columns at C 2–4 in high-spinal preparations with the dorsal columns interrupted at T 13–L 1 also inhibits transmission through the SCT. We think it most likely that this effect is due to excitation of propriospinal pathways by collateral branches of dorsal root fibres which enter at spinal segments rostral to the thoracolumbar region and have collateral axons which ascend in the dorsal columns. It is possible, however, that propriospinal fibres or axons descending short distances in the dorsal columns were involved. Erulkar, Sprague, Whitsel, Dogan & Jannetta (1966) have described vestibulospinal fibres in the upper cervical dorsal columns.

The inhibition of transmission through the SCT produced by activity in the descending systems has the following properties: (1) a long duration (up to 250 msec after short tetanic stimulation), with maximal effects at 20–40 msec, (2) a more pronounced action on polysynaptic responses and those evoked from the smaller cutaneous nerve fibres, particularly those excited by heavy pressure and pinch of the skin. These small fibres presumably include both small myelinated axons and non-myelinated (C) fibres, and (3) apparently only weak effects on monosynaptic responses evoked from large-diameter myelinated fibres. As indicated by the results of Taub (1964) the long duration of the inhibition suggests a presynaptic mechanism. The fact that in the present study stimulation of the descending systems usually evoked P waves on the cord dorsum supports this suggestion. Intracellular recording from SCT cells will be

necessary to establish whether or not there is a post-synaptic component to the inhibition. The present results support the previous suggestion (Brown, 1971) that the descending systems inhibit polysynaptic inputs to SCT cells but leave monosynaptic inputs relatively unaffected.

The descending systems are very effective in delaying the discharge of SCT cells excited along polysynaptic pathways. The delays of up to 6 msec observed in the present study were not solely due to the artificial high frequency tetanic stimulation of the descending systems. In a previous study (Brown, 1971) changes in the latency of SCT cell discharges of up to 7 msec were observed on blocking the tonic activity of descending systems which is present in the decerebrate cat. Delays of this order of magnitude (5 msec or more) are greater than the time taken for impulses to travel the length of the cord in the SCT in the majority of SCT axons. If the SCT is involved in alerting the animal, as suggested by Taub (1964), or with timing of the occurrence of stimuli, then the latency changes produced by the descending systems may be very significant. The effect would be to delay the polysynaptic actions but allow the monosynaptically evoked discharges to proceed unaffected. One function of the descending systems could therefore be to focus the 'attention' of the central nervous system on to the monosynaptically produced discharges, in particular to compare the times of arrival of these discharges at some central destination.

Taub (1964) observed consistent reductions in excitatory receptive field sizes during supraspinal stimulation in unanaesthetized decerebrate cats. For twelve units that we examined carefully only one showed any obvious receptive field constriction. The reasons for the differences between the two sets of results are not immediately obvious but when determining the overall size of the field we limited ourselves to the field responsive to hair movement, since we found it very difficult to evaluate the area from which responses to heavy pressure could be elicited (see Results). In a previous study (Brown, 1971) where the tonic activity in descending systems was reversibly blocked by cooling the spinal cord, similar difficulties were experienced in showing changes in the sizes of receptive fields. Wall (1967) could also find no change in sizes of fields for cells in lamina IV of the dorsal horn, some of which give rise to SCT axons.

The inhibitory actions evoked from hind limb cutaneous nerves appeared to be the same as those evoked from the cervical spinal cord. Eccles *et al.* (1962) have suggested that the activity of neurones with axons in the dorsolateral funiculus might be influenced by presynaptic inhibition. Eccles *et al.* recorded the mass discharge from the lumbar dorsolateral funiculus in response to ipsilateral cutaneous nerve stimulation and found that the later components of the discharge were reduced

by stimulation of cutaneous and muscle afferent fibres from the same limb. However, the conditioning volleys used in their experiments evoked a discharge in the dorsolateral tract and the inhibition could therefore be attributed either to post-activation depression or to recurrent inhibition in polysynaptic pathways. The possibility of post-activation depression does not arise in the present study in which contralateral nerves were used for conditioning since no discharge or excitatory post-synaptic potentials are evoked in SCT cells from contralateral nerves (Hongo *et al.* 1968). The observations of Eccles *et al.* that the polysynaptically evoked (that is, later) impulses are the ones most strongly affected by segmental inhibition are also confirmed.

We could find no qualitative differences between the actions of the various descending systems nor between the descending and segmental systems. This leads to the conclusion that all of these systems might converge on to common inhibitory interneurones. Support for this conclusion comes from the observation (A. G. Brown & H. F. Martin III, unpublished) that the inhibition produced from the descending and segmental inputs will occlude with one another.

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REFERENCES

BROWN, A. G. (1971). Effects of descending impulses on transmission through the spinocervical tract. *J. Physiol.* **219**, 103–125.

BROWN, A. G. & FRANZ, D. N. (1969). Responses of spinocervical tract neurones to natural stimulation of identified cutaneous receptors. *Expl Brain Res.* **7**, 231–249.

BROWN, A. G. & KIRK, E. J. (1972). Ipsilateral and contralateral inhibitory actions on transmission through the spinocervical tract. *Brain Res.* **43**, 264–267.

BROWN, A. G., KIRK, E. J. & MARTIN, III, H. F. (1972). The actions and locations in the spinal cord of descending pathways that inhibit transmission through the spinocervical tract. *J. Physiol.* **223**, 27–28*P*.

ECCLES, J. C., KOSTYUK, P. G. & SCHMIDT, R. F. (1962). Presynaptic inhibition of the central actions of flexor reflex afferents. *J. Physiol.* **161**, 258–281.

ERULKAR, S. D., SPRAGUE, J. M., WHITSEL, B. L., DOGAN, S. & JANETTA, P. J. (1966). Organisation of the vestibular projection to the spinal cord of the cat. *J. Neurophysiol.* **29**, 626–664.

FETZ, E. E. (1968). Pyramidal tract effects on interneurones in the cat lumbar dorsal horn. *J. Neurophysiol.* **31**, 69–80.

HONGO, T., JANKOWSKA, ELŻBIETA & LUNDBERG, A. (1968). Post-synaptic excitation and inhibition from primary afferents in neurones of the spinocervical tract. *J. Physiol.* **199**, 569–592.

LAPORTE, Y., LUNDBERG, A. & OSCARSSON, O. (1956). Functional organization of the dorsal spinocerebellar tract in the cat. I. Recording of mass discharge in dissected Flechsig's fasciculus. *Acta physiol. scand.* **36**, 175–187.

LUNDBERG, A. & OSCARSSON, O. (1961). Three ascending spinal pathways in the dorsal part of the lateral funiculus. *Acta physiol. scand.* **51**, 1–16.

RUDIN, D. O. & EISENMAN, G. (1951). A method for dissection and electrical study *in vitro* of mammalian central nervous tissue. *Science, N.Y.* **114**, 300–302.

TAUB, A. (1964). Local, segmental and supraspinal interaction with a dorsolateral spinal cutaneous afferent system. *Expl Neurol.* **10**, 357–374.

WALL, P. D. (1967). The laminar organization of dorsal horn and effects of descending impulses. *J. Physiol.* **188**, 403–423.