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ACTIVATION OF DESCENDING CONTROL OF THE SPINOCERVICAL TRACT BY IMPULSES ASCENDING THE DORSAL COLUMNS AND RELAYING THROUGH THE DORSAL COLUMN NUCLEI

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SUMMARY

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

2. Orthodromic activation of the dorsal columns and dorsal column nuclei was used to condition responses evoked in spinocervical tract neurones from cutaneous nerves. Such conditioning produced inhibition of transmission through the tract. The inhibition had a time course of 200 msec or more with maximal action at 30–70 msec and was most effective against polysynaptic responses.

3. After removal of the cerebellum or section of the cerebellar peduncles the degree of inhibition was reduced but inhibition could still be evoked by activation of the dorsal columns and dorsal column nuclei.

4. Transection of the brain stem just rostral to the dorsal column nuclei removed the inhibitory effects although segmental inhibition was not affected.

5. It is concluded that impulses ascending the dorsal columns and relaying through the dorsal column nuclei can lead to activation of descending control of the spinocervical tract. Parts of the pathways involved include the cerebellum and the brain stem. It is unlikely that the cells in the dorsal column nuclei which have descending axons are concerned with the control of transmission through the spinocervical tract.

INTRODUCTION

Activity in several neuronal systems which descend from the brain inhibits transmission of information, about stimuli to the skin and subcutaneous tissues, through the spinocervical tract (Taub, 1964; Wall,

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1967; Fetz, 1968; Brown & Franz, 1969; Brown, 1971; Brown, Kirk & Martin, 1973). The origins of these descending pathways are not known in any detail nor is it known how or by which ascending systems they are activated.

The present experiments were started because of a report by Dart (1971) that some cells in the dorsal column nuclei of the cat have axons which *descend* the spinal cord. These axons are situated in the dorsolateral funiculus at upper cervical levels and Dart suggested that they might project to spinocervical tract neurones. Inhibitory effects on spinocervical tract transmission can certainly be obtained from the cervical dorsolateral funiculi (Brown *et al.* 1973) and the original aim of the experiments was to test Dart's suggestion. A consideration of the experimental design, however, led us to extend the aims so that we could examine whether or not activity ascending the dorsal column system would lead to alteration of transmission through the spinocervical tract. A preliminary report of the results has been published (Brown & Martin, 1972).

METHODS

Unanaesthetized decerebrate cats paralysed with gallamine triethiodide were used. The intercollicular decerebration was performed under anaesthesia with halothane in nitrous oxide and oxygen which was discontinued as soon as the decerebration was complete. The sural and medial plantar nerves in both hind limbs were exposed through small skin incisions, freed from connective tissue but left in continuity, for stimulation through pairs of silver-silver chloride electrodes (ISU, XSU, IMP, XMP in Fig. 1). Part of the occipital bone was removed in order to expose the dorsal column nuclei and laminectomies were performed at C1–C4 and L2–L7.

The experimental arrangement is shown in Fig. 1. Recordings were made from single axons of the spinocervical tract with a tungsten micro-electrode at L4–5 (R_{ME}), the axons being shown to belong to the tract by stimulation through the electrodes on the dorsolateral funiculus above and below the lateral cervical nucleus (SII and SI respectively; see Brown & Franz, 1969; Brown, 1971). Afferent volleys from the cutaneous nerves and cord dorsum potentials were recorded at the L7–S1 dorsal root entrance zones with a monopolar silver ball electrode (R_{CDP}). The dorsal columns were transected, using watchmakers' forceps under microscopic observation, at rostral C4 and a pair of stimulating electrodes (silver or platinum ball electrodes) placed on their dorsal surface at C3 for eliciting ascending activity (S_{DC}). A similar, movable, pair of electrodes was placed on the exposed surface of the medulla to stimulate the dorsal column nuclei and adjacent regions (S_{DCN}). All electrical stimuli were 0·2 msec square wave shocks. Stimuli to the dorsal columns and dorsal column nuclei were either single shocks or brief tetani of 4–8 shocks at 200–400 a second.

During the course of the experiments various lesions were made in the brain. These included removal of a small part of the cerebellum overlying the rostral parts of the dorsal column nuclei to facilitate placement of the stimulating electrodes on them, section of the cerebellar peduncles (one experiment), removal of the cerebellum by suction and transection of the hind brain about 3 mm rostral to the obex.

At the end of each experiment the preparations were perfused with normal saline followed by 10% formol-saline. After fixation the brains were examined to determine whether decerebellation had been complete and 50 μm frozen sections were cut, stained with cresyl violet and examined to determine the extents of the lesions of the brain stem and cervical dorsal columns.

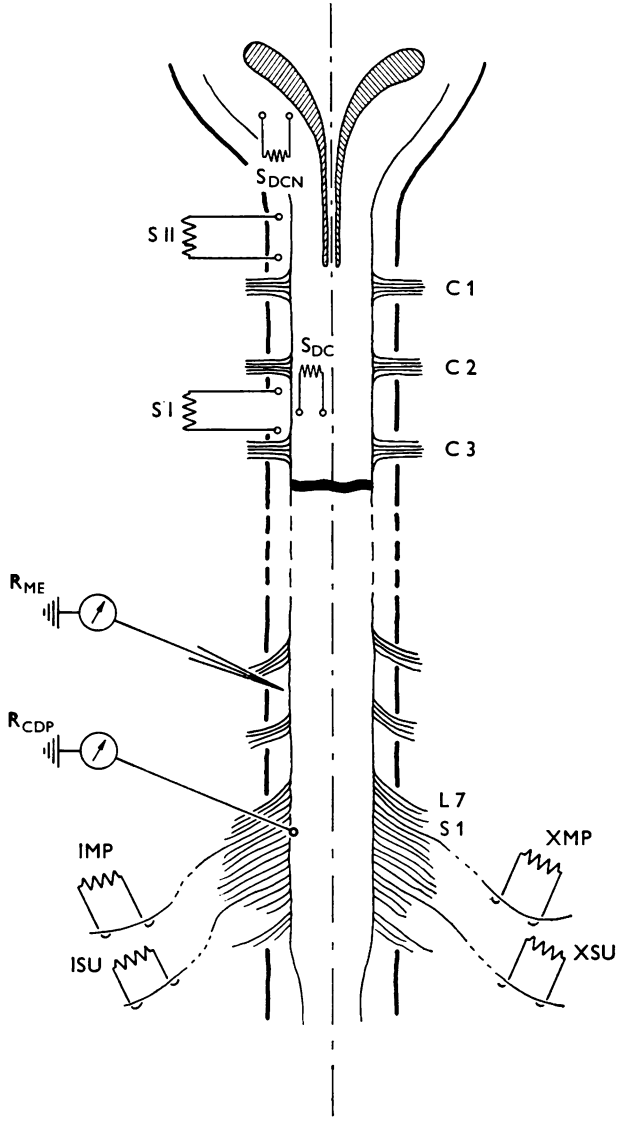

Fig. 1. Schematic representation of the experimental design. For full details see the text.

RESULTS

The approach adopted in the present experiments was to examine the effects of stimulation of the dorsal column nuclei and the dorsal columns (orthodromic activation) on the responses of spinocervical tract cells, first in the decerebrate preparations, then after removal of the cerebellum and then after transection of the brain stem just rostral to the dorsal column nuclei. In one experiment lesions were made in the cerebellar peduncles

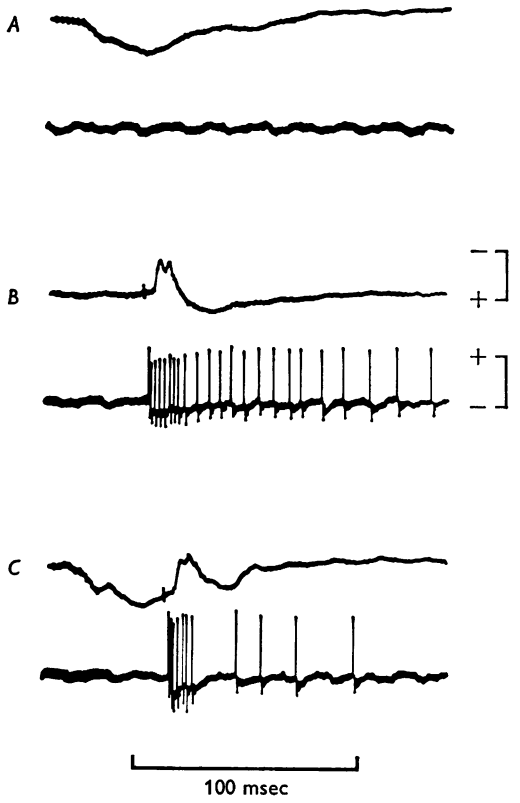

Fig. 2. Cord dorsum P waves and associated inhibition of the discharge of a spinocervical tract neurone produced by electrical stimulation of the dorsal column nuclei. Each pair of records shows the cord dorsum potential (upper trace) and the response of a spinocervical tract unit (lower trace). In *A* a short tetanus was given to the dorsal column nuclei at the start of the record and produced a P wave on the lumbar cord dorsum. There was no excitation of the tract cell. In *B* a single shock to the ipsilateral medial plantar nerve elicited the ingoing volley and associated N and P waves on the cord dorsum together with a discharge of the spinocervical tract neurone. In *C* the conditioning stimulus to the dorsal column nuclei precedes the testing shock to the cutaneous nerve by 40 msec and inhibits the unitary discharge.

instead of removing the cerebellum completely and this produced similar effects to cerebellectomy. The results will be presented in sections corresponding to the states of the preparations.

In each experiment the effectiveness of segmental inhibition was assessed before and after each lesion by conditioning responses of spinocervical tract neurones with volleys of impulses in contralateral cutaneous nerves (Brown *et al.* 1973). This was necessary in order to see if there were any long-term trends in inhibitory mechanisms throughout the experiment and particularly to ensure that the trauma of making the various lesions had not interfered with inhibitory mechanisms. In our experience the presence of segmental inhibition of transmission through the spinocervical tract is a very sensitive indicator of the general condition of the preparation and is more reliable than the level of the arterial blood pressure or the local blood flow to the spinal cord assessed visually. The experiments were terminated if the level of segmental inhibition, elicited by constant strength of stimulation of the contralateral nerves throughout the experiment, began to fall.

Decerebrate preparations

Inhibition of spinocervical tract discharges was produced by surface stimulation of the dorsal column nuclei. This is shown in Fig. 2 where it can be seen that P waves were evoked on the lumbar cord dorsum by the stimulation to the dorsal column nuclei. For sixteen units the best position of the stimulating cathode for producing the most pronounced inhibition was determined. The best position was always over the ipsilateral dorsal column nuclei, usually on the surface of the gracile nucleus or the junction of the gracile and cuneate nuclei and at the level of the middle third or rostral half of the nuclei. At the best points, stimulus strengths as low as 210 mV were sufficient to produce inhibition that could be seen on single oscilloscope sweeps at optimal conditioning-testing intervals (see below). When the cathode was moved away from the best position an increased strength of stimulation was needed to produce inhibition. Inhibition could also be produced by stimulating the contralateral dorsal column nuclei. Stimulation of the surface of the hind brain away from the dorsal column nuclei was ineffective unless the stimulus strength was increased about five or ten times above the minimum needed at the best position.

In one experiment three axons were recorded from which, although running with identified spinocervical tract axons and responding to cutaneous nerve stimulation, did not have a reduction in conduction velocity between C1 and C3. Thus these axons appeared to be ascending beyond the lateral cervical nucleus and would not belong to the spinocervical tract by our criteria. They were not inhibited by conditioning stimuli applied to the dorsal column nuclei, which indicates that there is some degree of selectivity in the control systems.

The time course of the inhibition elicited from the dorsal column nuclei is shown in Fig. 3 where it is compared with that produced by stimulating the contralateral medial plantar nerve. Both sets of conditioning stimuli produced inhibition with a long time course of 200 msec or more. The segmental inhibition had a maximal action at about 40 msec whereas the

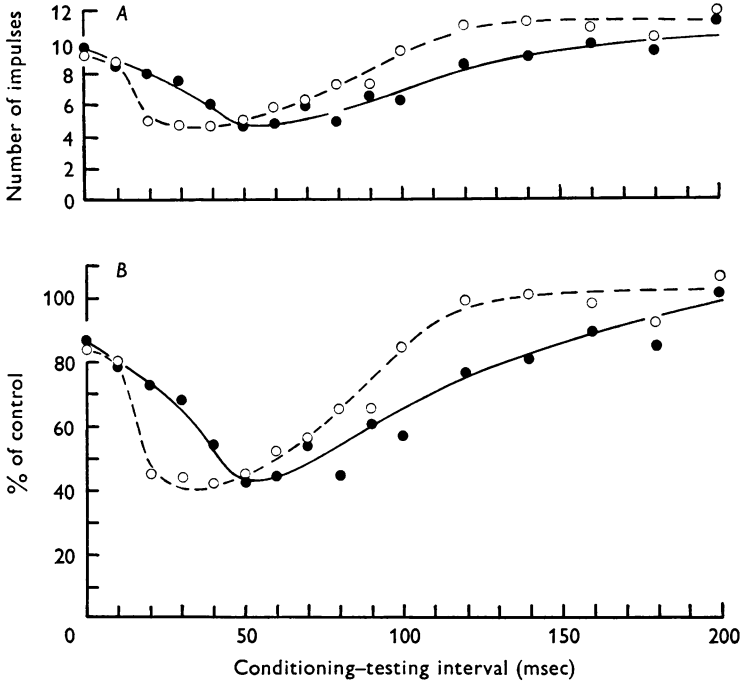

Fig. 3. Time courses of inhibition of spinocervical tract cell discharges elicited from the dorsal column nuclei and from a contralateral cutaneous nerve. The inhibition is expressed in terms of the number of impulses evoked (in *A*) and as the percentage of control (unconditioned) values (in *B*). Each point is the mean of at least five observations. Stimulation of both the contralateral medial plantar nerve (–○–) and the dorsal column nuclei (–●–) produced inhibition with a time course of 150–200 mec. Maximal action occurred earlier with the segmental inhibition which also had the shorter time course.

inhibition produced from the dorsal column nuclei was maximal at about 50 msec. For different units maximal inhibition to stimulation of the dorsal column nuclei occurred at 30–60 msec after the start of the conditioning tetanus.

When the latency of the first peripherally evoked impulse was taken as the test response, conditioning from the dorsal column nuclei produced increases in the latency of polysynaptically evoked responses (central

latency greater than 2·0 msec) which followed a similar time course to the inhibition of the number of impulses (Fig. 4). As shown in Fig. 4, however, there was little or no action on the latency of monosynaptically evoked responses (central latency less than 2·0 msec).

Although the experiments just described show that transmission through the spinocervical tract may be inhibited by stimulation of the dorsal column nuclei we thought it was possible that the effects were not due to excitation of cells in these nuclei. For example, the inhibition could have

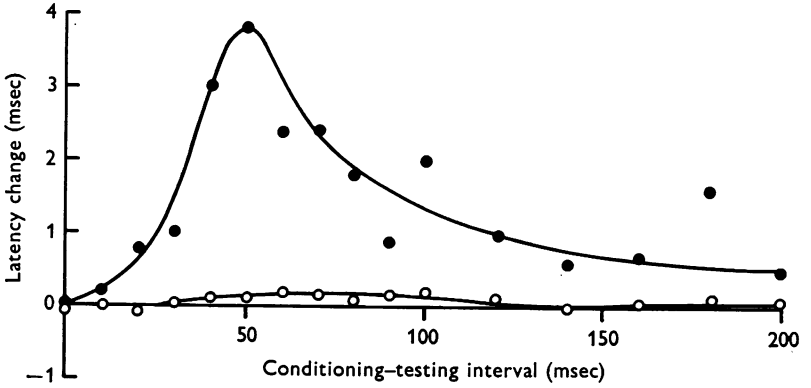

Fig. 4. Effects from the dorsal column nuclei on the latency of spinocervical tract cell discharges. In this graph the change in latency of the first impulse discharged on stimulation of a cutaneous nerve is plotted against the conditioning-testing interval when the conditioning stimulus was a short tetanus to the dorsal column nuclei. Unit 720501 (○) had a central latency of 0·7–0·8 msec indicating a monosynaptic linkage and the conditioning had virtually no action on the latency of the first impulse. Unit 720504 (●), on the other hand, had a central latency of 6·2 msec indicating a polysynaptic linkage and the conditioning stimulus produced increases in the latency of the first evoked impulse, with maximal effects at about 50 msec and a time course lasting for more than 200 msec. Each point is the mean of several observations.

been produced by excitation of axons descending to the nuclei, if these axons also had collateral branches which either descended to the lumbar cord and influenced transmission through the spinocervical tract or excited other neuronal systems which did. In order to control against these possibilities the cervical dorsal columns were stimulated rostral to a transection of the columns at C4. When this was done inhibitory effects were produced on spinocervical tract neurone responses. As shown in Fig. 5, when units were conditioned by stimulation of the dorsal columns and the dorsal column nuclei similar inhibitory curves were generated but the maximal effects from the columns occurred at about 10 msec later than the maximal effects from the nuclei. This difference would be due to

the time needed for the impulses to ascend the columns from C3 and be relayed through the nuclei. If the dorsal column stimulus had spread to the dorsolateral funiculus and excited the descending axons known to run in this region (Brown *et al.* 1973) then this should have produced maximal effects at 20–40 msec and not at the observed conditioning-testing intervals of 50–70 msec.

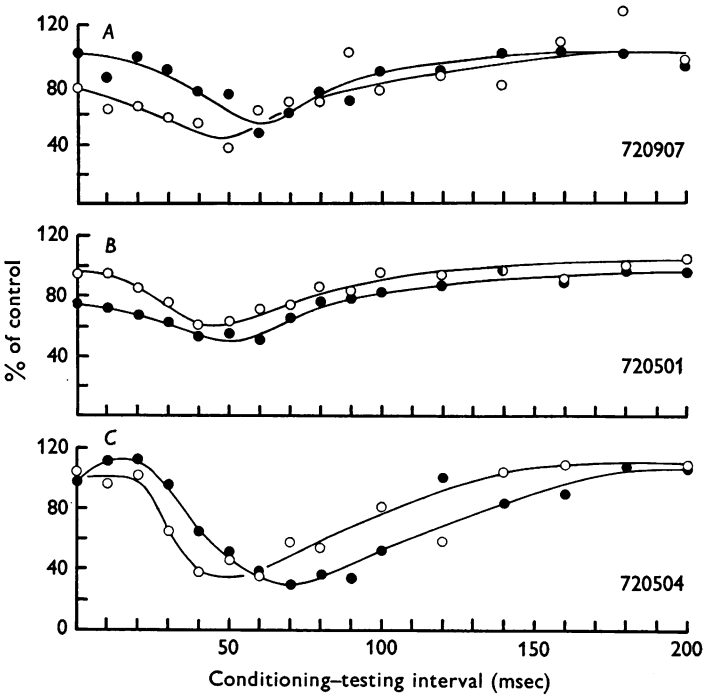

Fig. 5. Inhibition of spinocervical tract responses produced from the dorsal column nuclei and from the dorsal columns. Each graph shows the responses of a spinocervical tract cell, expressed as a % of the unconditioned response, plotted against the conditioning–testing intervals when the conditioning was given either to the dorsal column nuclei (○) or to the dorsal columns rostral to a section of the columns at C4 (●). Similar inhibitory curves were produced from both stimulation sites but the maximal effect occurred about 10 msec later for the dorsal column stimulus compared to the dorsal column nuclei stimulus. Each pair of curves is for the same unit, identified on the right of each graph, and all points represent the mean of at least five observations.

Decerebrate-decerebellate preparations

After removal of the cerebellum (or transection of most of the cerebellar peduncles in one cat) inhibitory effects on transmission through the spinocervical tract could still be obtained by stimulating the dorsal columns and

dorsal column nuclei. Just over one half of the units (fourteen of twenty-three) showed inhibition, that is, the test response was reduced to less than 90 % of control values at conditioning-testing intervals of 40–50 msec. The conditioning stimuli were of the same strength or up to 1·5 times greater than those used to condition the responses before cerebellectomy. There were no consistent differences between the types of spinocervical tract unit that were and those that were not inhibited from the dorsal column system after cerebellectomy. For the inhibited units the time course of

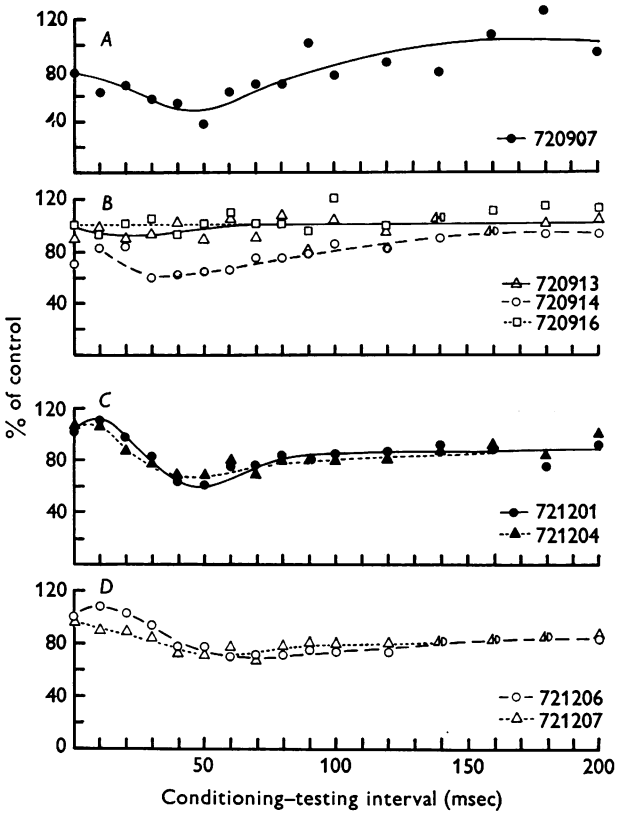

Fig. 6. Effects of cerebellectomy on the inhibition of spinocervical tract discharges produced by stimulation of the dorsal column nuclei. The graphs show inhibitory time courses in which the number of impulses discharged in spinocervical tract cells (expressed as % of control values) is plotted against the conditioning-testing interval when the conditioning stimulus was a short tetanus to the dorsal column nuclei and the testing stimulus was a single shock to a cutaneous nerve. *A* and *B* are from one experiment and *C* and *D* from another. *A* and *C* show the inhibition produced before cerebellectomy and *B* and *D* that after cerebellectomy. Cerebellectomy reduced or abolished the inhibition. The units are identified on the right hand sides of the graphs. Each point is the mean of at least five observations.

inhibition was similar to that obtained before cerebellar removal but the maximal amount of inhibition was only about one third of that produced by similar strengths of shock when the cerebellum was intact. This is illustrated in Fig. 6 which shows the time course of inhibition produced by stimulation of the dorsal column nuclei for different units before and after cerebellectomy in two experiments (see also Fig. 8).

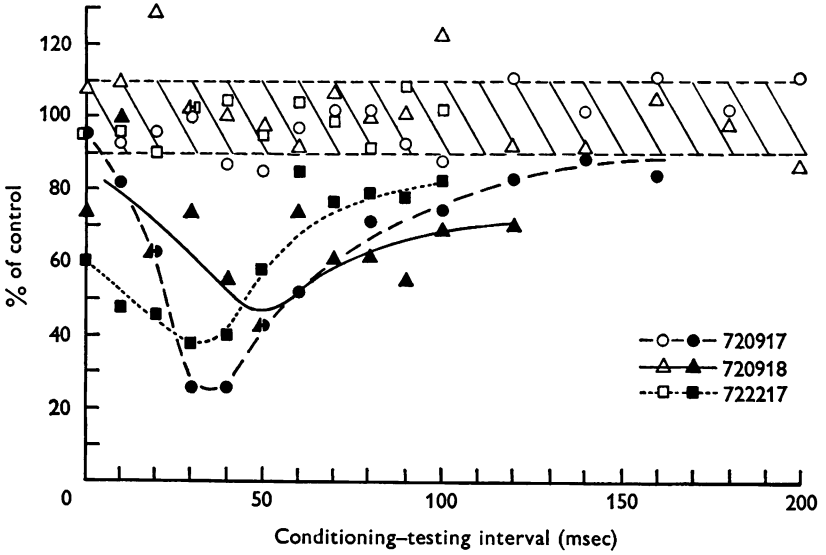

Fig. 7. Removal of inhibitory effects on the spinocervical tract from the dorsal column nuclei after transection of the brain stem. The brain stem was transected just rostral to the dorsal column nuclei. The conditioned responses of spinocervical tract units (number of impulses evoked by the testing stimulus expressed as a % of the unconditioned response) is plotted against the conditioning-testing interval for three units. The lack of inhibition elicited from the dorsal column nuclei (open symbols) contrasts with the marked inhibition produced from contralateral cutaneous nerves (filled symbols). The dashed horizontal lines enclosing the cross-hatching are at 110 and 90 % of the control values and very few clear symbols fall outside these limits showing the absence of any obvious inhibition elicited from the dorsal column nuclei.

Preparations with the brain stem transected

After the brain stem had been transected just above the rostral ends of the dorsal column nuclei, no inhibitory effects could be produced by stimulating the nuclei or the dorsal columns at stimulus strengths up to 1·5 times greater than the strengths which produced clear inhibition before this lesion. Fig. 7 shows the absence of effect from the dorsal column system and compares this with the inhibition produced from the contralateral medial plantar nerve.

The histograms of Fig. 8 summarize the results. The degree of inhibition produced from the dorsal column nuclei and from the contralateral medial plantar nerve are compared for each state of the preparation (decerebrate, decerebrate–decerebellate and after transection of the brain-stem). Fig. 8*A* shows the results from a single experiment in which the stimulus strengths to the dorsal column nuclei and the contralateral medial plantar nerve were kept constant throughout. The segmental inhibition remained the same but the inhibition elicited from the nuclei fell after each lesion until there was no significant inhibition in the preparation with the brain stem

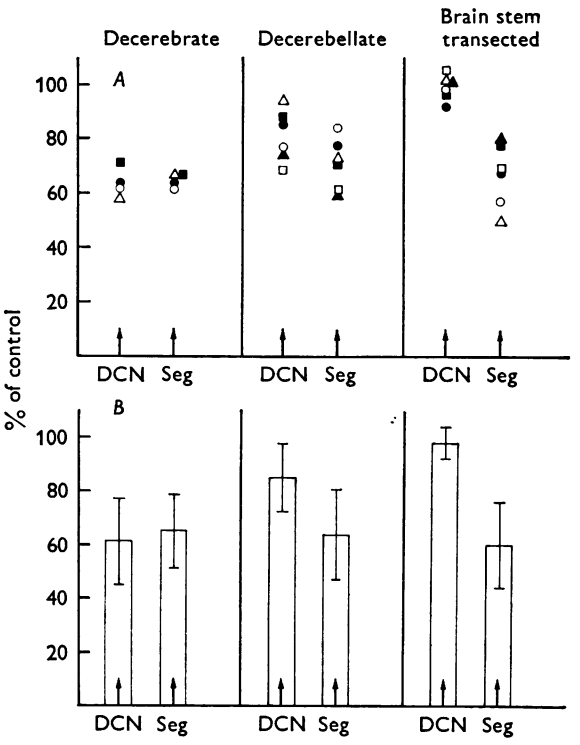

Fig. 8. Effects of cerebellectomy and then brain stem transection on the inhibition of spinocervical tract responses produced from the dorsal column nuclei. *A* shows the results of a single experiment and *B* the pooled results from fifty-two units recorded in five cats. Inhibition from the dorsal column nuclei (DCN) is progressively reduced by the lesions whereas there is no significant action on the segmental inhibition produced from contralateral cutaneous nerves (Seg). Conditioning-testing intervals were 50 msec in *A* and 40 or 50 msec in *B*. In *A*, each unit is represented by a pair of similar symbols and each point is the mean of at least five observations. In *B*, the vertical lines indicate ± 1 S.D. of the mean values. For further details see the text.

sectioned. In Fig. 8*B* the pooled results from fifty-two units recorded in five cats are presented. The strengths of stimulation of the dorsal column nuclei were either the same throughout an experiment or were increased after one or both lesions. Each measurement of the degree of inhibition was the mean of at least five individual observations at conditioning-testing intervals of 40–50 msec which is close to the time for maximal inhibition from the dorsal column nuclei and at a time when segmental inhibition is still marked. For the pooled results there was no significant difference after either lesion for the amounts of segmental inhibition. For inhibition produced from the dorsal column nuclei, cerebellectomy produced a significant lowering of the degree of inhibition (from 61·3% $\pm$ 15·97 to 84·9 $\pm$ 12·53, means $\pm$ S.D., $P < 0{\cdot}01$, Student's t test) and the brain stem section further lowered the degree of inhibition (to 97·7% $\pm$ 6·16) which was again significant ($P < 0{\cdot}01$) when compared to the values obtained in the decerebellate preparations.

DISCUSSION

Stimulation of the dorsal column nuclei led to inhibition of transmission through the spinocervical tract. Similar inhibitory actions were produced by orthodromic activation of the dorsal columns. This latter observation shows that the effects from the dorsal column nuclei were produced by exciting cells in the nuclei and not by activation of axonal branches of neurones which might project both to the nuclei and to other systems which control spinocervical tract transmission. Inhibition could be elicited by stimulation of the dorsal column nuclei on both sides but the sites at which the lowest strengths of shock produced inhibition were over the ipsilateral nuclei, usually in their rostral parts. It is concluded that activity ascending the dorsal columns and relaying through the dorsal column nuclei can lead to activation of descending systems which control transmission through the spinocervical tract. There is some selectivity in the system since no inhibition was observed in a number of units whose axons ran with the spinocervical tract at lumbar levels, which had similar response properties to spinocervical tract neurones, but which projected beyond the lateral cervical nucleus. These units presumably belonged to some other afferent system or systems.

The actions of the descending system or systems brought into operation by the dorsal column pathway are similar to those previously described when descending axons in the dorsolateral and ventromedial funiculi of the cord were stimulated (Brown *et al.* 1973). The inhibition has a long (200 msec or more) time course and is most effective on polysynaptically evoked discharges. A P wave may be evoked on the cord dorsum by

stimulation of the dorsal columns or dorsal column nuclei, as it was from the descending systems, and may be taken to indicate that part of the inhibition, at least, is presynaptic in nature. The inhibition apparently acts on all spinocervical tract units in the same way and there appear to be no differences in the effects on different types of spinocervical tract units. The only difference between the actions evoked from the dorsal column system and the descending systems stimulated at the cervical level was that the time to maximal effect was longer from the dorsal column system presumably because there is a supraspinal loop in that pathway (see below). There was also a difference in the time to maximal inhibition when the effects elicited from the dorsal columns were compared with those from the dorsal column nuclei, the former being some 10 msec longer. This would be due to the time taken for the impulses to ascend from C3 to the nuclei and for synaptic transmission through them.

After the cerebellum had been removed, stimulation of the dorsal columns and the dorsal column nuclei, at similar strengths to those used before cerebellectomy, still produced some degree of inhibition of transmission through the spinocervical tract in rather more than half the units examined. In these units the amount of inhibition was, however, significantly reduced in comparison with the amounts observed in other units before cerebellectomy. This suggests that part of the inhibitory pathway involved passes through the cerebellum. It is known that there are projections from both the gracile and cuneate nuclei to the cerebellar cortex (Gordon & Seed, 1961; Holmqvist, Oscarsson & Rosén, 1963; Oscarsson, 1969; Larson, Miller & Oscarsson, 1969) and it is perhaps significant that the parts of the dorsal column nuclei from which the lowest strengths of stimulation evoked inhibition were in the rostral halves. It is from the rostral parts of the nuclei that the projections to the cerebellum (and to the brain stem, see below) arise.

The inhibition of spinocervical tract transmission, elicited from the dorsal column system, that remained after cerebellectomy was abolished by transection of the brain stem just rostral to the dorsal column nuclei. Part of the pathway involved therefore passes through the brain stem. Neurones in the rostral parts of the dorsal column nuclei have been shown, by both anatomical and electrophysiological methods, to project to various parts of the brain stem (Busch, 1961; Kuypers & Tuerk, 1964; Gordon & Jukes, 1964) and some of these neurones may be involved in the inhibitory pathway described in the present paper. The results of successive removal of the cerebellum and transection of the brain stem lead to the conclusion that there are at least two pathways by which the dorsal column system may influence the spinocervical tract, one through the cerebellum and the other through the brain stem. The two pathways may, of course, converge

at brain stem level to activate a single set of neurones with axons that pass down the spinal cord.

Dart (1971) has suggested that the axons which *descend* the spinal cord from cells in the dorsal column nuclei might project to the spinocervical tract. No actions from the dorsal column nuclei on transmission through the tract could be observed after brain stem section even though segmental inhibitory actions were not affected. It was important to have the control of segmental inhibition since there were large increases in blood pressure while the brain stem section was being made and afterwards the blood pressure fell, usually to 70–80 mmHg (systolic). Segmental inhibitory mechanisms are very sensitive to the general condition of the preparation and only those animals which maintained a good level of segmental inhibition were used in the present study. It is concluded that the cells in the dorsal column nuclei which have descending axons do not control transmission through the spinocervical tract unless their axons run first of all rostrally into the brain stem before turning and running caudally to enter the dorsolateral funiculus, in which case they would have been damaged by the lesions we made.

The present results emphasize the close relationship between the dorsal column and spinocervical systems. The dorsal column nuclei receive ascending inputs not only from the dorsal columns themselves but also from the ipsilateral dorsolateral funiculus, possibly as collateral branches of the spinocervical tract (Tomasulo & Emmers, 1970; Dart & Gordon, 1970, 1973). It is now established that activity ascending the dorsal columns and relaying through the dorsal column nuclei can lead to activation of descending systems which control transmission through the spinocervical tract. As recently pointed out (Brown, 1973; Gordon, 1973), such cross-connexions create a practical difficulty in designing electrophysiological or behavioural experiments to investigate the functional components of these systems. Furthermore, the classical views of the functions of the dorsal column system which emphasize its role in the fine discriminatory aspects of mechanoreception (cf. Mountcastle & Darian-Smith, 1968) are shown to be too restrictive. As the evidence accumulates on the fibre composition of the dorsal columns (see Brown, 1973), on the input to and the projections of different cells in the dorsal column nuclei, together with their selective control from other regions of the brain, the concept of 'a dorsal column system' becomes more and more untenable. The present results have shown that the dorsal column system controls the flow of information through other somatosensory pathways (see Wall, 1970) and we should, perhaps, consider the dorsal columns and the dorsal column nuclei as a set of systems each with different, and perhaps more or less independent, functions, rather than as a single system.

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