J. Physiol. (1958) 141, 489–499

SPINAL TRACTS AND SUPRASPINAL CENTRES INFLUENCING VISCEROMOTOR AND ALLIED REFLEXES IN CATS*

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(*Received* 1 *January* 1958)

Stimulating the abdominal viscera may evoke movements of the limbs and trunk muscles (Miller, 1924; Lewis & Kellgren, 1939; Downman & McSwiney, 1946; von Euler & Sjöstrand, 1947). These visceromotor reflexes may be recorded as compact reflex volleys in the intercostal and lumbar nerves following single-shock stimulation of the central cut end of a splanchnic nerve (Downman, 1955). Using the single-volley analysis it has been shown that the splanchnic-to-intercostal, and also the allied intercostal-to-intercostal, reflexes have different properties in the decerebrate and the spinal cat (Downman, 1955). In the decerebrate these polysynaptic reflexes are smaller, have limited irradiation along the cord, but mutually facilitate each other. Transecting the cervical cord causes the responses to become at once larger and to irradiate far along the cord, but to inhibit each other. In this investigation an attempt has been made to define the spinal paths and brain-stem mechanisms concerned in maintaining the decerebrate–spinal differences in the thoracic arcs. Basically the method has been to determine which tracts must be cut to cause increase in size of the reflexes (release) and change from mutual facilitation to inhibition in a two-volley test (change-over).

METHODS

Adult cats were decerebrated under ether anaesthesia after preliminary tracheotomy and bilateral ligature of the common carotid arteries. The cerebrum was removed piecemeal through a trephine opening in the skull, the spatula being slid downwards on the tentorium cerebelli to cut the brain stem at the intercollicular level. Temporary manual compression of the vertebral arteries in the neck controlled the bleeding from the brain stem. The greater splanchnic nerve on the left side was exposed retroperitoneally and cut distal to the coeliac ganglion. Three of the lower intercostal

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* This report includes work submitted by A. Hussain in part requirements for the degree of Ph.D. in the University of London.

nerves were dissected free over a length of about 3 cm lateral to the posterior angle of the rib, cutting small side branches but leaving the dorsal ramus intact. The ventral ramus was cut distally in its freed length, the crushed central end being later suspended by a small cotton loop on a stainless steel wire recording electrode. After these operations the animal was usually rested 2–3 hr to excrete the ether. The splanchnic and the upper and the lower of the intercostal nerves could be stimulated with single shocks, delivered from a square pulse generator driven by the oscilloscope time base. Resultant reflex activity was recorded off the intermediate intercostal nerve, using a conventional RC-coupled amplifier and oscilloscope.

For more extensive exposures of the remaining brain stem, and for removal of the cerebellum, the cranial bone was removed with a dental drill and bone nibblers. Bleeding was controlled by plugging the bone edges with a kaolin paste, and by cautious diathermy. Retrograde air embolism into the bone sinuses was avoided by keeping the head low. Removal of nervous tissue was done with a sucker. Cuts into the brain stem were made with a sucker or with a fine scalpel. During recording, the cats were paralysed with tubocurarine up to 1 mg/kg or decamethonium iodide up to 100 μg/kg, repeated intravenously or intramuscularly as needed, and were given positive-pressure artificial ventilation.

Partial and complete transections of the spinal cord were made with a fine knife after exposing the cord by laminectomy and opening the dura, usually at C 2–3 level. Usually a partial lesion was followed by complete transection about 1 cm more caudally, to compare the fully spinal animal. The extent of the cuts into the spinal cord, and of other brain-stem lesions, was seen on serial sections of formol-fixed material, stained by the method of Loyez (1910) or of Weil (1946). The full extent of the lesions was subsequently mapped by superimposing camera lucida drawings of the sections. Particular attention was paid to the extent of haemorrhage.

RESULTS

Spinal cord sections

Fig. 1 is an example of a cut across the dorsal half of the spinal cord, severing the dorsal and dorso-lateral columns. In this and subsequent figures the size of the response has been measured as the peak height of the volley, from enlargements of the photographic record. The conditioned test response is then expressed as a percentage of the height of the test response alone. In previous work (Downman, 1955) the area of recorded response was used as the best index of magnitude of the reflex discharge. In this investigation peak height was taken to be an adequate index since the differences brought about by the cord lesions were so conspicuous that the method of assessment did not affect the conclusions. It may be noted that the dorsal root reflex makes no significant contribution to the recorded reflex volley (Downman, 1955). In Fig. 1, before the cord section, i.e. in the decerebrated cat, a submaximal reflex volley evoked in 11th intercostal nerve on stimulating 12th intercostal nerve was of a size represented by the vertical line, ●. A conditioning maximum reflex response of splanchnic origin facilitated a later testing submaximal response of intercostal origin, shown by the graph ●. After making the cut into the cord both splanchnic- and intercostally-evoked volleys increased in size; the height of the intercostally-evoked response is indicated by the line ○. Now the two-volley test curve followed the course indicated by the graph ○. Later complete section of the cord caused no more release, height of intercostally-evoked response (shown by the line *Sp*) being unchanged, and the two-volley test curve was also unchanged. It is concluded, from this result, that full release and change-over follows section of some tracts in the dorsal half of the cord. Since the picture was not altered by subsequently cutting the ventral half of the cord also, it is concluded that the tracts therein are not themselves actively causing the changes in cord activity in the absence of the dorsal paths.

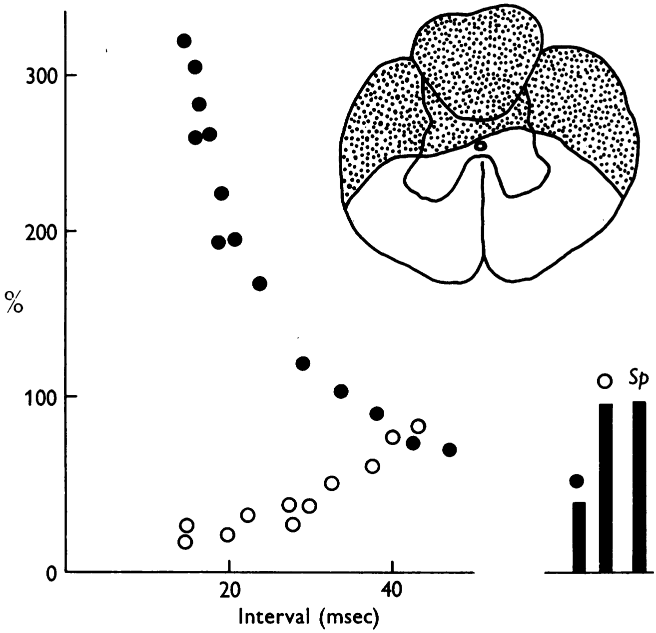

Fig. 1. Dorsal hemisection of spinal cord, shown dotted, in C6 segment in decerebrated cat. In the graph size of a conditioned test intercostal-12-to-intercostal-11 submaximal reflex volley is expressed as a percentage of its unconditioned size. The conditioning volley was a maximal centripetal volley in the ipsilateral splanchnic nerve at the volley intervals shown as abscissa. In the decerebrate before hemisection, ●, conditioning splanchnic volley increasingly facilitates test volley at shorter intervals. After hemisection, ○, conditioning volley inhibits test volley over same time course. Inset right, shows height in arbitrary units of test response alone, in the decerebrate, ●; after hemisection, ○; after later complete spinal transection, *Sp*. Strength of single-shock stimuli unchanged throughout.

By making various cuts in the cord it was found that the results could be grouped into those cuts which caused change-over and those which did not. The former also caused full release of the reflexes of both intercostal and splanchnic origin. The effective cut had to include the dorsal third of the lateral funiculus (Fig. 2) of the same side. In contrast, cutting other regions of the cord caused no change-over (Fig. 2). Cuts into any part of the cord caused some release of the reflexes, but not more than about 30% of the full release found on subsequent complete transection.

Relation to decerebrate rigidity. In two cats the reflex discharges were recorded before and after a cut into the dorsal third of the ipsilateral dorsolateral funiculus, with the animal paralysed with decamethonium iodide. These tests confirmed that the cuts caused release and change-over. Then the animals were left to recover from the decamethonium paralysis. As this wore off, good decerebrate rigidity returned. The spinal pathways which maintain the decerebrate status of the visceromotor and allied reflexes are not the same as those maintaining decerebrate rigidity.

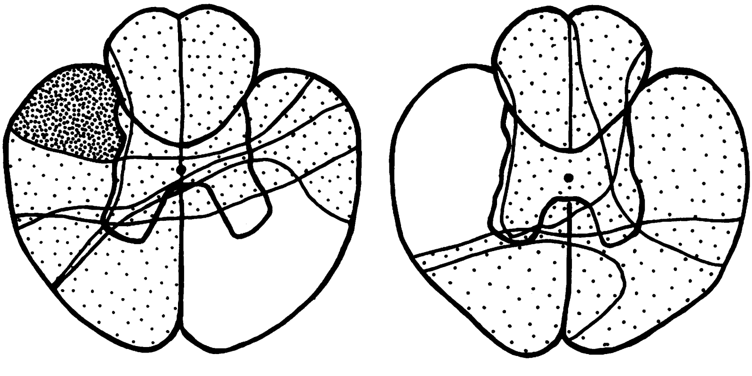
A Effective B Ineffective

Fig. 2. Composite diagrams of cord sections made in different cats. *A*, shows lesions (dotted) which were followed by release and change-over of the thoracic reflexes described; the heavily dotted region is common to all the lesions, and a lesion restricted to this region was effective. *B*, lesions (dotted) which did not cause full release and change-over.

Ascending or descending pathway? The effective cuts lie in a region of the cord containing both ascending and descending tracts. It has been noted before (Downman, 1955) that transecting the cord in mid-thoracic region does not cause any release or change-over in the headward segments, even in the next segment above the cut. Hence the results cannot be ascribed to loss of ascending impulses originating in levels of the cord below the segment under investigation, such as is responsible for the Schiff–Sherrington phenomenon (Ruch, 1936). Combining total transection of the cord with division on the chest wall of all the ipsilateral intercostal nerves lying rostral does not alter these reflex arcs; loss of the major part of the ipsilateral input from other levels does not seem to be a critical factor. Finally, making a cut into the ipsilateral dorsolateral column in the segment above that used in recording causes release and change-over as effectively as a lesion made higher up. If the inhibition depends on a tonically active ascending path, this path would have to originate in the segment itself. In other experiments it was found that cutting the dorsal roots of the recording intercostal nerve did not alter the responses in decerebrate cats. These findings do not support the hypothesis that the effective cord lesions break an ascending path which begins in ipsilateral dorsal roots below, within, or above the segment tested. The findings do not entirely disprove the possibility of a localized ascending path which is activated by general cord activity maintained by other uncut inputs.

Whether an ascending path is involved or not, it is still necessary to postulate a descending path in the dorsolateral column. Since a cut in this region causes full release and change-over, the majority, if not all, of the descending fibres lie therein. There may be a thinner scatter of fibres in other regions of the cord whose section gives some release without change-over. The present results cannot settle the point. The relation between release and change-over is unknown.

Conclusion. The decerebrate status of the visceromotor and allied reflexes depends on a descending tract in the dorsal third of the lateral funiculus of the same side of the cord. When this tract is cut, the reflexes are released and facilitation in the two-volley test is changed to inhibition over the same time course.

Supraspinal influences

Anaemic decerebration. In three examples of the Sherrington decerebrate cat, as used throughout these experiments, anaemia of the upper brain stem was caused by tying the basilar artery through a hole drilled in the basis cranii (Pollock & Davis, 1923). This caused no release nor change-over. The head was perfused from the aorta with 10% indian ink in reconstituted dried plasma (M. J. Blunt, personal communication). After immersion during the night in 10% formol-saline, the cerebellum and brain stem were removed and cleared by Spalteholz method (Cowdry, 1948). Thick frozen sections were cut in the sagittal plane. It was found that the medulla and lower pons and lower half of the cerebellum retained a blood supply. The centres above the mid pons and the anterior lobe of the cerebellum are not essential in sustaining the thoracic arcs.

Cerebellar lesions. In Sherrington-decerebrate cats the whole dorsal surface of the cerebellum was exposed by removing the overlying bone and tentorium. The size of the reflexes and the form of the facilitation curve in the two-volley test were recorded. Sucking away the anterior lobe of the cerebellum caused no change in the responses. Subsequent removal of the whole cerebellum was also without effect (Fig. 4). These findings confirm and extend the results of anaemic decerebration, and show that loss of cerebellar function was not a critical factor.

Vestibular nuclei. Fulton, Liddell & Rioch (1930*a*, *b*) have related the vestibular nuclei to decerebrate rigidity in the cat. Although the consequences of spinal tractotomies did not suggest that vestibulospinal paths are concerned in controlling the visceromotor arcs, it was considered advisable to test the effects of vestibular nuclear destructions. This was done in cats in which the floor of the medulla had been exposed by complete removal of the cerebellum, as described above. Dividing both VIII nerves intracranially caused no release or change-over. Similarly, removing the vestibular nuclei with a sucker, either ipsilateral or bilateral, caused no change (Fig. 3). Subsequent histological examination showed that the destruction encompassed the main bulk of the vestibular nuclei, including Deiters' nuclei. From comparison with published maps of the cat brain stem (Winkler & Potter, 1914) it is estimated that the greater part, probably 90%, of the vestibular nuclei was destroyed. These findings confirm that the vestibular nuclei are not responsible for the decerebrate status of the visceromotor and allied reflexes.

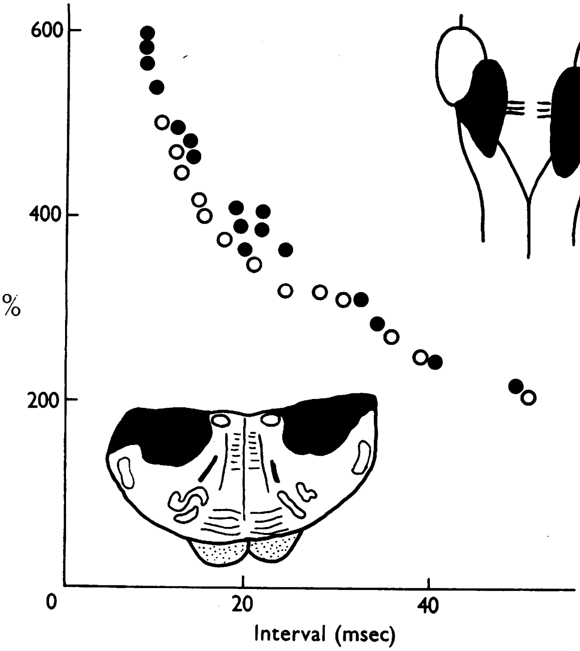

Fig. 3. Graph shows facilitation of reflex motor volley in 11th intercostal nerve, evoked by centripetal volley in 12th intercostal nerve, by preceding centripetal volley in splanchnic nerve. Decerebrate cat, cerebellum removed, ●. After extensive bilateral destruction of vestibular nuclear region, shown in inset diagrams of medulla from above and in section, ○. Height of conditioned test response plotted as percentage of unconditioned response. Submaximal single shock stimulation of nerves. Abscissa shows volley intervals in msec.

Cuts into the pons and medulla. Deep cuts were made into the medulla after exposing the floor of the medulla by removal of the cerebellum (Fig. 4). Deep transverse cuts into the pons cutting across the central mass of reticular substance were without effect. It was found that wide deep cuts had little effect at levels above the obex. Deep cuts into the lower medulla, at the level of the middle of the cuneate tubercles, caused both full release and change-over. More laterally placed lesions, which would have cut the descending paths from the lateral vestibular (Deiters') nuclei, were without effect. These results show that the decerebrate status of the visceromotor and allied arcs depend upon the action of a portion of the medial substance of the medulla.

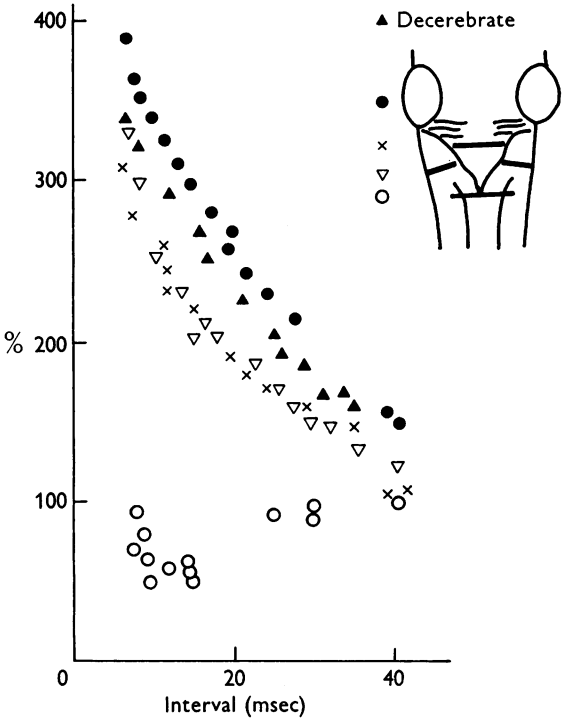

Fig. 4. Graph shows the facilitation of the reflex motor volley in 11th intercostal nerve, evoked by centripetal volley in 12th intercostal nerve, by preceding centripetal volley in splanchnic nerve. Decerebrate cat, ▲; after total removal of cerebellum, ●; deep cut into upper medulla, × ; deep cuts into lateral medulla below vestibular nuclei, ▽. These lesions did not cause release or change-over. Subsequent deep cut into mid-line lower medulla, ○, was effective. Cuts made serially in same preparation in order given. Conditioned test response plotted as percentage of test response alone; submaximal single shock stimulation of nerves.

DISCUSSION

Severing the spinal cord in the decerebrated cat increases some spinal reflex activities, whereas others are depressed so deeply as to merit the term 'spinal shock'. Flexor and extensor arcs show such contrasting change. Sherrington (1910), Sherrington & Sowton (1915), Forbes & Baird (1929), and McCouch, Snape & Stewart (1935) recorded release of the flexor arcs. Flexor reflexes increase in amplitude and have a lower threshold. Other changed activities include increase of the N_1 potential recorded on the dorsum of the cord on cutaneous afferent stimulation (Lindblom & Ottosson, 1952); lowering of threshold of both cord potential and of flexor reflex to that of the nerve (Stewart, Hughes & McCouch, 1940); reappearance of the galvanic skin response (Wang & Brown, 1956); increased size, fall of threshold, and wider irradiation of the splanchnic-to-intercostal and intercostal-to-intercostal reflexes (Downman, 1955); loss of facilitation to repeated afferent volleys in flexor arcs (Liddell, Matthes, Oldberg & Ruch, 1932*b*); change-over from facilitation to inhibition of the second test volley in two-volley testing of the specified thoracic arcs (Downman, 1955); appearance of visceromotor reflexes elicitable by direct visceral stimulation (Downman & McSwiney, 1946). The release of function following chordotomy suggests that certain reflex arcs are kept in restraint in the decerebrate cat by the activity of some region of the brain stem, as proposed by Fulton (1926). The present findings could be explained by the existence of such a tonically active pathway to the thoracic as well as to limb flexor arcs. This path lies within the dorsolateral white column. A cut here causes the maximum release of the visceromotor and allied reflexes. Liddell *et al.* (1932*b*) found that an ipsilateral cord lesion released the flexor reflex, a contralateral lesion being effective only if it crossed the mid line; dorsolateral column and anteromedial lesions were effective. In the present work section in any region of the cord other than the dorsolateral column might cause some partial release, but never as great and not accompanied by change-over in the two-volley test. It is not clear whether this is due to spreading damage affecting a localized path, or to cutting other widespread descending fibres. It is notable that cuts including the anteromedial columns did not cause marked release. The lack of release following destruction of various parts of the brain above the spinal cord shows that corticospinal, rubrospinal, tectospinal and cerebellar influences do not sustain the decerebrate–spinal differences. The active centres lie within the medial region of the medulla.

Liddell and his colleagues (Ballif, Fulton & Liddell, 1925; Fulton *et al.* 1930*a*, *b*; Liddell, 1934, 1936) have shown that chordotomy changes extensor reflexes. Threshold, duration and ease of inhibition increase. This depends on section of the anteromedial cord fibres. Destruction of ipsilateral vestibular nuclei, especially Deiters' nucleus, caused loss of rigidity and a spinal-type knee jerk. The work showed that the vestibular nuclei, through their vestibulospinal paths, are a main but not sole factor in maintaining rigidity and the decerebrate–spinal differences in extensor arcs. Our own tests show that the vestibulospinal tracts and vestibular nuclei are not of importance in imposing the decerebrate–spinal differences in the specified thoracic arcs. These arcs again behave more like flexor than extensor arcs. Cutting N. VIII in the acute decerebrate caused no change in thoracic arcs. In contrast, Liddell, Matthes, Oldberg & Ruch (1932*a*) reported that in the cat decerebrated within a week of N. VIII section there was some release of ipsilateral flexors, but more release of the contralateral; flexor threshold was lower after chordotomy than after N. VIII section.

In the specific thoracic reflex arcs the decerebrate–spinal differences are maintained by structures in the medial upper medulla. This conclusion may be related to Torvik & Brodal's report (1957) on the origin of reticulo-spinal paths from the medial medulla and pons, but one notes that the effective spinal cord lesion appears to be more dorsal and compact than the main distribution of the descending medullary fibres of Torvik & Brodal. Also the pathway related to the thoracic arcs has ipsilateral origin, whereas the reticulo-spinal fibres of medullary origin have bilateral origin (Torvik & Brodal, 1957). This dorsolateral lesion would, however, probably cut the lateral reticulo-spinal pathway described by Papez (1926).

The fibres whose section causes release of the reflexes cannot be distinguished from those whose section causes the change-over from facilitation to inhibition in the two-volley test. If they prove to be the same, then the change-over may be a consequence of release from an inhibition somewhere in the arc. Liddell *et al.* (1932*b*) have also reported loss of facilitation of a flexor reflex with repeated stimuli after chordotomy in the decerebrate cat.

That the release and change-over of the reflexes is due to dividing an ascending, rather than a descending, pathway merits consideration. However, it has been described above that cutting the cord does not cause cephalad release, in spite of the section of a large number of ascending paths. Making the dorsolateral cord lesion one or two segments above the segment of recording is as effective as a higher lesion. Hence, if an ascending path is involved it would have to be driven by the thoracic segment under investigation. Cutting the dorsal roots of this segment does not alter the reflexes. The evidence is against an ascending pathway from the cord itself being a major factor in sustaining the tonic inhibition. In any case, it is still necessary to postulate a descending pathway from the medulla. Since cutting regions of the cord other than the ipsilateral dorsolateral segment is much less effective than section of this segment alone, it is clear that the descending path is most concentrated in, if not limited to, this region. This path can be cut without altering the decerebrate rigidity of the limbs.

SUMMARY

1. Splanchnic-to-intercostal and intercostal-to-intercostal polysynaptic reflexes have been recorded in decerebrated cats.

2. Spinal cord transection causes release of the reflexes from a tonic inhibition. This is accompanied by change-over from facilitation to inhibition in two-volley tests.

3. The tonic inhibitory path lies in the ipsilateral dorsolateral segment of the cord.

4. The inhibition is sustained by the medial medulla.

5. The decerebrate status of these thoracic arcs persists after anaemic destruction of remaining brain stem above the pons, including the red nucleus; after partial or total removal of cerebellum; after section of N. VIII unilaterally or bilaterally; after destruction of vestibular nuclei unilaterally or bilaterally; and after cutting other segments of the cord, including the vestibulospinal paths.

6. A dorsolateral column lesion in the cord causes release and change-over of these reflexes without change of decerebrate rigidity.

This work was aided by grants for apparatus from the Central Research Fund of the University of London and the Government Grants Committee of the Royal Society. The authors are indebted to Dr P. P. Scott and Dr M. H. Evans for advice; also to Mrs J. Thomas for photographic assistance.

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