STUDIES OF THE SPINAL CORD

PART II. TOPOGRAPHIC LOCALIZATION WITHIN THE VENTRAL SPINO-CEREBELLAR TRACT IN THE MACAQUE

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THREE FIGURES

While studying the topographic localization within the dorsal spino-cerebellar tract, the author (Yoss, '52) became aware of a rather surprising lack of mention in the literature of a pattern of localization within the ventral spino-cerebellar system. There are, it is true, many vague, and sometimes conflicting, references to the location in the cord or to the course of ascent or termination of this tract within the cerebellum. The greatest problem in the study of this fiber bundle is the apparent difficulty in differentiating between it and the closely allied systems — the more frequently studied lateral spino-thalamic tract and the less well-known spino-tectal and spino-bulbar fascicles. In the spinal cord the differences between these various systems are not apparent in all cases and it is not possible to determine with any great accuracy which of the large group of degenerated fibers in the ventral white column and the ventral portion of the lateral white column are destined to reach the cerebellum and which continue on through the brain stem to terminate in the dorsal thalamus or tectum. However, when this ven-

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tral group of degenerated fibers is followed to the region of the upper pons a large bundle of degenerated fibers (in their normal state, heavily medullated) turn dorsad to enter the cerebellum. These fibers from the ventral and lateral white columns of the spinal cord are obviously those of the ventral spino-cerebellar tract arising from below (caudal to) the level of the spinal cord lesion. Many smaller degenerated fibers continue forward into the midbrain as a relatively compact bundle to end in the thalamus or the tectum as the lateral spino-thalamic tract or the spino-tectal tract, respectively. In one monkey with a spinal cord lesion which had definitely interrupted bilaterally the lateral spino-thalamic systems (clinical examination demonstrated an analgesia approximately one or two segments below the level of the lesion), no degenerated fibers passed forward to or through the midbrain All of the degenerated bundles from the ventral and the lateral white columns turned dorsad to end in the cerebellum. Evidently, in this monkey, the lateral spino-thalamic tract did not take the Marchi stain even though it was unquestionably sectioned and presumably degenerated. Therefore, in this case, the degenerated fibers in the cord which were differentially stained by the Marchi technique could be regarded as belonging to the ventral spino-cerebellar system.

With these above observations in mind, re-examination of the degenerated fibers in the cord enabled one to locate the site of the degenerated ventral spino-cerebellar fibers in many of the series. They could be followed during their ascent and a pattern of localization within this tract could be determined.

MATERIAL AND METHODS

Twelve monkeys (Macaca mulatta-11; Macacus cynomolgus-1) were used for this series of experiments. Some of these monkeys had experimentally produced vascular lesions at various levels of the lumbar or lower thoracic cord and had been used in other studies (Yoss, '50, '52). Others had spinal cord lesions produced by chordotomy at upper thoracic and cervical levels or by complete transection of the lower-most tip of the cord. All animals were examined during the two week postoperative period of survival. In all cases in which a complete lesion of the ventral spino-cerebellar tract was made at a given level, there was also a loss of sensibility to painful stimuli on the side of the body opposite to the lesion and below it. An accurate anesthetic level was difficult to determine because of the uncooperative nature of the macaque.

The spinal cords, along with the brain stems and cerebella, were stained at representative levels by the Swank and Davenport ('35) modification of the Marchi technique. The cerebella were sectioned in either a sagittal or a transverse plane, the former being more satisfactory for the study of spino-cerebellar terminations on the cerebellum. The brain stems were sectioned in the conventional transverse plane, with or without an attached cerebellum. Some of the spinal cord sections were prepared by the rapid Marchi method of Mara and Yoss ('52).

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CONSIDERATION OF THE LITERATURE

In 1879 Gowers described a large ascending fiber tract in the anterolateral part of the spinal cord which he believed mediated some sensation; however, he did not specify the type. Later (1886) he thought that there was little doubt that the path related to sensations of pain was in this anterolateral system. This bundle of fibers is often referred to as Gowers' tract. Some observers regard all of the ascending fibers in this region as components of Gowers' bundle (Spiller, '05; Bruce, '10; Cooper and Sherrington, '40; Ranson and Clark, '47; Chang and Ruch, '49; and others) but others limit the use of the term to those fibers of the system which terminate in the cerebellum, that is, to the ventral spino-cerebellar tract (Thiele and Horsley, '01; Riley, '43; and others). If the term is used in the broader sense it includes not only ascending fibers of the ventral spino-cerebellar tract but also those of the lateral spino-thalamic, spino-tectal and spino-bulbar systems and probably of other systems as well. Since Gowers' original description appears to have included all anterolateral ascending fibers, the term can be used in this broader sense. To avoid confusion, in the present paper the anterolateral group of ascending fibers will be referred to simply as the anterolateral fasciculus.

Löwenthal (1885) discovered the course of the ventral spino-cerebellar component of the larger ascending anterolateral bundle and proved its termination in the cerebellum. He severed the left lateral column of the spinal cord of the dog between the 5th and 6th cervical nerves. From a study of the resulting ascending degeneration, he was able to follow spino-cerebellar fibers to the medulla where they separated into two divisions, the dorsal and the ventral tracts. He traced the ventral part to the upper region of the pons where it reached the cerebellum by way of the superior cerebellar peduncle. This was the first clear account of the destination of the ventral spino-cerebellar system.

Mott (1892) studied the ascending degeneration in the spinal cord of monkeys. He considered the anterolateral bundle as consisting only of ventral spino-cerebellar fibers since he was able to completely section this tract without producing analgesia. Mott (1895) determined that the ventral spino-cerebellar tract arose from cells of the opposite half of the spinal cord; Auerbach (1890) had earlier obtained the same results.

Thiele and Horsley ('01) reported the results of degeneration following a spinal cord lesion in a young man at approximately the level of L3. They found that the outer fibers of the anterolateral fiber bundle are coarser than the inner and that these coarser fibers ascend to the cerebellum. Because of this larger size of the ventral spino-cerebellar fibers, a method of differentiation from other ascending anterolateral fascicles is available and so the course of the ventral spino-cerebellar tract, as a discrete system, can be studied. Thiele and Horsley also emphasized that several fiber systems make up the anterolateral fasciculus.

Collier and Buzzard ('03) were unable to differentiate between the degenerated ventral spino-cerebellar and the lateral spino-thalamic fibers in the cord or medulla oblongata of man but pointed out the obvious difference in the sizes of the fibers of the two tracts as upper pons levels are reached, where the smaller fibers of the lateral spino-thalamic and spino-tectal systems continue forward, and the larger degenerated fibers of the ventral spino-cerebellar tract shift dorsad to enter the cerebellum.

Spiller ('05) demonstrated that Gowers' tract (used in the broader sense to include the lateral spino-thalamic system) carries fibers mediating impulses set up by pain and temperature stimuli. Up to 1905 many observers had been of the opinion that the anterolateral fasciculus carried impulses set up by painful and temperature stimuli but evidence supporting this opinion was lacking. Spiller's evidence was based on his clinical examination of a case of tuberculoma of the human spinal cord in the region of the anterolateral bundle. This case was largely responsible for the surgical procedure, anterolateral chordotomy, originated by Spiller and Martin ('12) for the relief of intractable pain.

In 1907 Schäfer and A. Miriam Bruce investigated the ventral and the dorsal spino-cerebellar tracts in the monkey. They thought that both the dorsal and the ventral spino-cerebellar bundles belonged to a common system since they found that many of the fibers which, more caudally, were components of the ventral spino-cerebellar tract, gradually shifted dorsad, as they ascended the cord, to become a part of the dorsal spino-cerebellar system. They regarded this as a transference of fibers from Gowers' to Flechsig's tract, believing that, when the spino-cerebellar tracts separated from one an-other in the medulla, a large number of fibers which originally had belonged to Gowers' bundle entered the cerebellum by way of the restiform body.

A. Ninian Bruce ('10), following lesions in the spinal cord at various levels, traced degenerated fascicles of both the dorsal and the ventral spino-cerebellar tracts in the monkey. He noted a definite dorsal and lateral shift of ventral spino-cerebellar fibers as they ascended in the cord which might be regarded as suggesting a localization pattern in the tract, although these shifting fibers also included those belonging to other fiber systems. He was of the opinion that, in the beginning of their course toward the brain, some of the ventral spino-cerebellar fibers were situated as far medially as the anterior median fissure but such fibers soon moved laterad and dorsad as they ascended. He also noted (and his figures clearly show this) a dorsal shift of dorsal spino-cerebellar fibers but he interpreted this shift as a transference of ventral spino-cerebellar fibers to the dorsal spino-cerebellar tract. Bruce pointed out that, in the ventrolateral (anterolateral) ascending fiber system, there were larger fibers at the periphery of the bundle than more medially. These larger fibers were traced upward to the cerebellum. He also determined that the smaller and deeper fibers passed to portions of the central nervous system other than the cerebellum.

Beck ('27) was never able to obtain degeneration within the lateral spino-thalamic tract in cats following anterolateral section. He explained this as due to the fact that the lateral spino-thalamic fibers were medial to his cut but (since his cord sections were deep) it seems more probable that the lateral spino-thalamic fibers (as well as spino-tectal) were sectioned but failed to stain by the Marchi technique.

The work of Hyndman and Van Epps ('39) on the localization pattern in the human spino-thalamic tract is very interesting, since any such pattern of localization for one of the components of the anterolateral bundle may be similar to that for other components, including the ventral spino-cerebellar tract. These observers found (by careful postoperative examination) that at upper thoracic levels the fibers of the lateral spino-thalamic tract mediating impulses set up by painful stimuli from the lower extremities were situated most dorsal and most lateral in the bundle, those from the groin and abdomen were intermediate in position and those from the chest were most ventral and medial in the tract. Their investigation did not include the cervical region. According to their diagram, the bundle did not extend to the anterior median fissure. Since their study was based entirely on clinical observations made during and following selective sectioning of various portions of the lateral spino-thalamic system in 6 patients, no anatomic material was available for study. These surgeons realized that they had also sectioned part of the ventral spino-cerebellar system and reported no evidence of ataxia or incoordination following such section. They thought the anterolateral bundle (at least the portion mediating impulses aroused by painful stimuli) extended from about 2 mm anterior to the dentate (denticulate) ligament to a region approximately 2 or 3 mm medial to the anterior roots.

Walker ('40), unaware of the Hyndman and Van Epps work, carefully examined two patients (both before and after operations for intractable pain) who subsequently came to autopsy. After staining various spinal cord sections by the Marchi technique, Walker stated that he was able to follow the course of the spino-thalamic fibers from the apical and pericornual cells of the posterior horn across the anterior commissure to the anterolateral column. The fibers, immediately after crossing, congregated in the anterior columns but, as they ascended, they became more laterally situated. This gradual lateral and dorsal displacement was attributed by Walker to two facts: that, as higher cord levels are reached, there are more and more uncrossed pyramidal fibers in the anterior columns; and that, as higher levels are attained, there are more spino-tectal and spino-thalamic fibers being added to the tracts from the medial aspect. These two factors led gradually to a displacement, in a lateral and dorsal direction, of the fibers arising from lower segments. Walker found, then, that the longest fibers of the tract (those from the sacral cord) are located, in the cervical region, most dorsal and most lateral in the system; and that fibers arising from the cervical cord are situated in the most ventral and most medial region of the bundle. Fibers from the thoracic and the lumbar segments of the cord have an intermediate position. Thus, the sacral fibers which lie near the anterior columns in the lumbar region are essentially lateral to the pyramidal tract (actually to its most ventral portion) at cervical levels of the spinal cord. This pattern is similar to the physiologic pattern determined by Hyndman and Van Epps ('39). However, Walker made no mention of any components of the anterolateral bundle other than the spino-thalamic and spino-tectal tracts. He made no mention of the ventral spino-cerebellar tract or of any pattern which might be present in it.

In 1941 Weaver and Walker described the pattern of localization in the spino-thalamic tract of the monkey as essentially that described for man by Walker. These observers, also, in describing the components of the anterolateral bundle, completely overlooked the ventral spino-cerebellar tract but, since they were unable to separate the degeneration of the spino-thalamic, the spino-tectal, and the spino-bulbar tracts, they recognized that the pattern of localization described for the spino-thalamic system also applied to the spino-tectal and spino-bulbar fibers. Presumably they meant that this pattern would apply to any other components of the anterolateral bundle.

Rasmussen and Peyton ('41) reported that there is a lateral and dorsal shift of the entire group of anterolateral fibers as they ascend in the spinal cord. This observation was made on material prepared from the spinal cord and the brain of a patient who expired 19 days after an anterolateral chordotomy in the upper thoracic region. They pointed out the much larger cross-sectional area of the lateral spino-thalamic tract (and other anterolateral fascicular components) than had been generally recognized and also the greater ventromedial extent of this system. They placed the ventral spino-cerebellar fibers in the more lateral and superficial portion of the anterolateral bundle. They did not comment regarding any differences in size or arrangement of the fibers of these different components of the anterolateral group.

Gardner and Cuneo ('45) discussed the pattern of localization within the lateral spino-thalamic and associated tracts after studying the spinal cord and brain of a patient who expired three weeks after a bilateral anterolateral chordotomy. They confirmed, essentially, the laminar arrangement of ascending fibers of the anterolateral bundle as earlier described by Hyndman and Van Epps ('39), Walker ('40) and Weaver and Walker ('41) except that they recognized that a large portion of the degenerated fibers that they were following belonged to the ventral spino-cerebellar system. They were unable to differentiate between ventral spino-cerebellar fibers and other ascending anterolateral fiber tracts in the spinal cord. Gardner and Cuneo were of the opinion that lateral spino-thalamic fibers do not extend as near the midline as had been suggested by Hyndman and Van Epps and also thought that there was no such sharp segmental demarcation within the tract as had been indicated by Walker ('40).

Chang and Ruch ('49), studying the ventral spino-cerebellar tract in the spider monkey, arrived at the conclusion that this tract can be distinguished from other components of the anterolateral fasciculus by various means including the closer aggregation of its fibers and its ventrolateral position, which is maintained throughout the spinal cord. They placed the ventral spino-cerebellar tract in the most peripheral region of the anterolateral bundle, with some of its fibers intermingling with the spino-thalamic fibers.

Glees and Bailey ('51) studied the brains and spinal cords of two patients who had had central nervous system surgery for intractable pain and observed a lamination of the spinothalamic tract, which corresponded, to a large extent, with the scheme of Walker ('40). They were cognizant that other fibers accompanied the spino-thalamic system but their diagrams place the ventral spino-cerebellar tract in the region which has been allocated in the present study to the ventral portion of the dorsal spino-cerebellar system. Because of the size of the spino-thalamic fibers (4 to 6 μ) Glees and Bailey concluded that this tract is used for the rapid conduction of pain.

Morin, Schwartz and O'Leary ('51) studied extensively the spino-thalamic and related tracts in the cat and the monkey in order to explain further the failures occasionally seen from the different surgical procedures in which this tract is interrupted. These observers, using Marchi preparations of spinal cord and brain stem material, determined a pattern of somatotopic localization within Gowers' tract (used by them to in-include all anterolateral ascending fibers). Their pattern resembled closely the scheme of Walker ('40), except that these investigators believed that fibers of this ascending system which are most dorsal at cervical levels arose from thoracic segments.

TOPICAL ARRANGEMENT IN THE VENTRAL SPINO-CEREBELLAR TRACT

Twelve monkeys were used for this report with lesions fairly well distributed over various levels of the spinal cords. Only material with complete ventral spino-cerebellar tract involvement at appropriate cord segments will be reported in detail. Lesions were produced at the following levels: Ca 1, S3, L7, L3, L2, T12, T8, T7, T1, C7 and C5.

Since spinal cord lesions in the monkeys with transections in the upper caudal and lower sacral levels were at approximately the same levels, only the material from the animal with the lesion at S3 will be described. In this monkey, the ventrolateral group of fibers is described for the right side, for only on this side was the section complete, although the degenerated fibers were nearly as numerous on the left.

At the first sacral level (fig. 1 e) there are many scattered degenerated fibers extending from the ventral median fissure along the periphery of the cord through the ventral white column and the ventral half of the lateral white column. The fibers are fairly evenly concentrated in the ventral column and slightly less so in the lateral column. At L7 the ventral group of degenerated fibers appears to be more concentrated in the ventromedial portion of the ventral column but there are still many scattered fibers extending dorsolaterad into the lower half of the lateral white column; again at L6 they are more evenly scattered (fig. 1 d). When these degenerated fibers of the ventral column reach the level of L2 the bundle has shifted somewhat dorsolaterad with the greatest concentration of fibers in the more dorsolateral portion of the tract, and so, almost exclusively within the lateral white column (fig. 1 c). At L2 the area just lateral to the ventral median fissure is almost void of degenerated fibers. On reaching the 12th thoracic segment, there is a well concentrated bundle of degenerated fibers in the ventral half of the lateral column with no degeneration granules in the now much smaller ventral column. Thus, degenerated fibers have shifted dorsolaterad, absolutely and relatively, into the lateral column. On reaching mid-thoracic levels (T7; fig. 1 b), the bundle of degenerated fibers is still more compact but in the same relative position as in lower thoracic levels.

At T4 the bundle of degenerated fibers has become slightly more compact with, however, only the more ventral and medial of the fibers still shifting dorsolaterad. On reaching the cervical enlargement (C7; fig. 1 a) the degenerated fibers form a fairly well concentrated bundle, situated exclusively in the lateral white column. At this level, the dorsalmost component of these fibers extends slightly above a coronal plane passing through the central canal. As the size of the ventral gray columns diminishes (C5 and C3) there is a slight ventral shift of the most dorsolateral fibers of the ventral spino-cerebellar, spino-tectal and lateral spino-thalamic systems, due to a decrease in the diameter of the spinal cord. This bundle of degenerated fibers can be traced through the brain stem to upper pons levels where the largest portion of the fibers (also those of greatest diameter) shift dorsad to enter the cerebellum as components of the ventral spino-cerebellar tract. There are still many smaller degeneration granules that continue in the brain stem to the dorsal thalamus along spino-thalamic fibers; a few degenerated fibers can be traced to the superior colliculus as spino-tectal fibers. Therefore, the degenerated fibers which were traced forward from the spinal cord include bundles of the ventral spino-cerebellar, the lateral spino-thalamic and the spino-tectal tracts, the spino-cerebellar fibers being the most prominent and most discrete portion of the group. The smaller components of the bundle are apparently scattered among the ventral spino-cerebellar fibers, as well as medial to them, and it is difficult to separate one component from the other at spinal cord levels in this material. Since the above described fibers have their origin caudal to the level of the spinal cord lesion (S3), they belong to the lower sacral and coccygeal portions of their respective fiber systems.

In the next monkey the ventrolateral column was sectioned bilaterally at the 7th lumbar segment (approximately three segments more cephalic than the lesion in the previously described cord). At L6 and L4 the scattered degenerated fibers are fairly evenly distributed through the relatively large ventral white column, with a few fibers extending into the lateral white column. At L2 there is a definite lateral shift of the degenerated fibers, as well as an absolute decrease in the size of the ventral white column, so that almost all of the degenerated fibers lie now at the periphery of the ventral portion of the lateral white column. These fibers continue to shift laterad and dorsad as they ascend through the thoracic cord, just as in the spinal cord of the previous monkey. Since the degenerated bundle is larger in this monkey than in the previously described spinal cord (with a lesion at S3) there is a greater dorsoventral extent of this degenerated bundle in the monkey with the higher lesion as the fibers concentrate and shift dorsad. At planes through the cervical enlargement (C7; fig. 2 b) the bundle is more dorsal than elsewhere in its course and farther from the midline, due partly to the huge increase in spinal cord size at this level. There is a slight ventral shift of these fibers as upper cervical cord levels are reached. The dorsalmost fibers of the degenerated bundle in the spinal cord of this monkey are in approximately the same position as all of the degenerated fibers resulting from the lesion at the third sacral segment and hence are from the caudalmost segments of the cord (below S3); the additional fibers present in the more ventral and medial portion of the degenerated fiber bundle in the cord with the lesion at L7 are from more cephalic segments which are nevertheless below the level of the lesion (i.e., from between L7 and S3). The degenerated group of fibers resulting from the lesion at L7 can be traced to the cerebellum, the optic tectum and the dorsal thalamus. The largest fibers belong to the ventral spino-cerebellar system. In the cord the fibers largest in diameter are located at the periphery of the bundle; the deeper group of degenerated fibers are of smaller diameter and presumably belong to the spino-tectal and lateral spino-thalamic systems.

The spinal cord lesion in the next monkey is in the third lumbar segment. Since there are 7 lumbar segments in the monkey, and these segments are relatively large in size, one would expect a great increase in the number of degenerated fibers in the ventrolateral ascending fiber system. There are indeed many more such degenerated fibers than in the cords of the other two monkeys. At the first lumbar segment many evenly scattered degeneration granules lie near the midline but extend dorsolaterad to a region approximately equidistant between the dorsal and the ventral roots. As this bundle of fibers ascends in the spinal cord there is a gradual shift and a concentration of degenerated fibers dorsolaterad. At lower thoracic levels practically all of the fibers are situated in the ventral part of the lateral white column. There is little change in the degenerated bundle in the upper thoracic segments other than a further dorsal concentration of degeneration granules. At cervical enlargement levels (C7; fig. 2 c) the degenerated component of the ventrolateral bundle has shifted farther dorsolaterad, leaving a large area of undegenerated fibers in the ventral white column, and the most ventral part of the lateral white column has only a few degenerated fibers. Above the cervical enlargement there is again a slight ventral shift of the degenerated fascicles.

Lesions were placed at L2 in two monkeys. Since these lesions are only one segment more cephalad than that in the spinal cord of the last described monkey, little difference can be expected other than a slight increase in number of degenerated fibers. In both monkeys with cord lesions at L2 there is a slight increase in the amount of degenerated fibers over the number seen in the monkey with a cord lesion at L3. The degenerated fibers are scattered, just above the lesion, in the ventral white column and the ventral part of the lateral white column. As they ascend, there is a gradual dorsolateral shift and a concentration of degenerated fibers, until the cervical enlargement is reached, then a much more pronounced dorsolateral shift of the degenerated bundle can be seen.

In a macaque spinal cord with a lesion at T12 there is complete, bilateral degeneration of all the ascending fibers in the ventral and the lateral white columns. At T12, just above the level of the lesion, the ventrolateral ascending fibers are scattered throughout the ventral white column and the ventral part of the lateral white column but they are concentrated predominantly in the ventral column near the midline. At the 10th thoracic level the most concentrated portion of the ventrolateral ascending bundle has shifted slightly laterad. At the 7th thoracic segment these fibers lie still farther laterad and dorsolaterad. They are now mainly in the lateral white column; on reaching the cervical enlargement (fig. 2 d) they lie well within the lateral white column, with only a few fascicles on the surface of the cord in the most ventral part of the lateral column.

Lesions were placed in the spinal cords of two monkeys at T7 and T8. Since these lesions were only one segment apart, they will not be discussed separately. Just above the level of the lesion (lesion at T8) there is a heavy degeneration in the ventral white column and the ventral part of the lateral white column on the right side. At T5, this degeneration is concentrated in the ventral portion of the lateral white column until, on reaching the first thoracic segments, practically all of the degenerated fibers are in the lateral white column where they form a relatively large bundle. On reaching the cervical enlargement (fig. 2 e), the fibers shift farther dorsolaterad. This material shows that there is a relatively small addition of new degenerated fibers from thoracic levels.

A lesion placed in the first thoracic segment caused interruption and degeneration of the ascending fibers in most of the left ventral white column and in all of the ventral half of the left lateral white column. At the 8th cervical segment the material shows a very large bundle of degenerated fibers at the periphery of the left ventral and ventral portion of the left lateral white column, extending from near the midline dorsolaterad to meet the ventralmost degenerated fibers of the dorsal spino-cerebellar system. The degenerated bundle has shifted laterad and has become more compact at C6 (fig. 2 f). There are still a large number of degenerated fibers in the left ventral white column. The 4th cervical segment shows a compact bundle of degenerated fibers occupying a large portion of the available area in the periphery of the ventral half of the left lateral white column.

In the remaining two monkeys there were lesions of the ventral spino-cerebellar tract at the 7th and 5th cervical segments. They show a slight but definite increase in the overall size of the ventrolateral ascending degenerated fibers. The increase is in the ventromedial part of the bundle, since the dorsal extent of the most dorsolateral fibers of the bundle is no greater than was seen in the material obtained from animals in which the lesions were more caudally placed.

THE TERMINATION OF THE FIBERS OF THE VENTRAL SPINO-CEREBELLAR TRACT

Since most of the cord lesions have involved fibers of both the dorsal and the ventral spino-cerebellar systems, at times it has been difficult, if not impossible, to determine exactly the specific distribution of the ventral spino-cerebellar fibers. However, in three monkeys (lesions at Ca 1, S3 and L7) in which the cord lesions are well below the origin of the dorsal spino-cerebellar tract, the spino-cerebellar termination can be assumed to be entirely from the ventral spino-cerebellar system. Because of the caudal location of the lesion in such cases, the degeneration is relatively scanty but definite.

In a monkey with a lesion in the caudal portion of the spinal cord (at Ca 1), there are degenerated fibers of the ventral spino-cerebellar tract ending predominantly in the ventral part of the pyramid, the uvula and the central lobule. There are a few scattered degenerated fibers to the culmen and the declive but none to the lingula. In the monkey with a lesion at the 7th lumbar segment the degeneration is chiefly in the rostral portion of the anterior lobe of the cerebellum. The degenerated fibers terminate mainly in both parts of the central lobule, with a few fibers ending in the rostral part of the culmen. There are also a fair number of degenerated fibers in the lingula. In addition, there are some degeneration granules in the ventral part of the pyramid.

One is able to follow many ventral spino-cerebellar fibers arising from higher segments of the spinal cord to the same cerebellar terminations described above. However, because of their intermingling with degenerated dorsal spino-cerebellar fibers, it is often difficult to determine what proportion of the degenerated fibers ending on a given lobule belong to the ventral spino-cerebellar system. Nevertheless, one is justified in concluding that the ventral spino-cerebellar tract terminates, within the vermis, in the lingula, the central lobule, the culmen, the declive, the pyramid and the uvula.

DISCUSSION AND SUMMARY

It has been long known that many of the fibers of the ventrolateral ascending fiber system of the spinal cord belong to the ventral spino-cerebellar tract, but it has been considered difficult to differentiate these fibers from other pathways in the region, i.e., from the lateral spino-thalamic tract and the spino-tectal system. The fibers in the ventral spino-cerebellar tract are considerably larger in diameter than are those of the lateral spino-thalamic and spino-tectal tracts (Thiele and Horsley, '01; Collier and Buzzard, '03; Häggqvist, '36; and others). In the present study this difference in size of fibers has provided a means of identifying the ventral spino-cerebellar system, a necessary procedure before its localization pattern can be determined.

Previously, there has been no pattern of localization determined for the ventral spino-cerebellar system although the material illustrated by several investigators (Walker, '40; Weaver and Walker, '41; and others) suggests such a pattern. Certainly many of the degenerated fibers described by Walker ('40) and Weaver and Walker ('41) belong to the ventral spino-cerebellar system.

The topographic pattern of localization in the ventral spino-cerebellar tract is very similar to that described for the lateral spino-thalamic tract (fig. 3). However, the fibers of the spino-cerebellar system are more superficial and slightly more ventromedial than are the components of the lateral spino-thalamic system arising from the same segments.

As seen in upper cervical cord, the fibers of the ventral spino-cerebellar tract which arise at caudal and sacral levels are located in the most dorsolateral part of the tract; fascicles from the lumbar cord lie next to those from sacral levels in the lateral white column; fibers arising from lower and upper thoracic segments are located in the intermediate part of the bundle; and, finally, in the most ventromedial portion of the tract are ventral spino-cerebellar fibers arising from the cervical cord.

It should be stressed, however, that after the various components of the ventral spino-cerebellar tract have arisen from their cells of origin in the dorsal funicular gray, and, in part at least, have crossed the midline, they swing first ventrad and then forward. As they go forward, they gradually shift dorsad until they have attained their characteristic position at cervical levels. This dorsolateral shift of ventral spino-cerebellar tract fibers can be seen clearly in figure 1. If there is such a dorsolateral shift of the ventral spino-cerebellar fibers, one might expect that lesions of the tract at various levels of the cord would also show such a pattern of localization. In figure 2, several cervical cord sections are presented from material obtained from monkeys with progresssively higher lesions. The ventral spino-cerebellar degeneration is greater in the spinal cords of the monkeys with upper and lower thoracic lesions than in those with lesions at lumbar and sacral levels. The dorsal extent of the degenerated fibers of the ventral spino-cerebellar system is as great whether the lesion is in the sacral region of the cord or at the first thoracic segment. The increase in degenerated fibers is in the more ventral portions of the tract, with the degenerated fascicles arising from upper thoracic segments being located in the more ventromedial part of the bundle. The undegenerated fibers seen in these photomicrographs adjacent to the most ventromedial degenerated fascicles of the system belong to the components of the ventral spino-cerebellar tract arising above the levels of the lesions.

The dorsal extent of the ventral spino-cerebellar tract has been rather accurately determined by various investigators. The reason for this is apparent when it is recalled that, regardless of the level, so long as the lesion involves all of the tract, the longest fibers will always be degenerated. Such fibers are located in the dorsalmost portion of the tract and so mark the dorsal limits of the ventral spino-cerebellar system.

There is disagreement regarding the ventromedial extent of the ventral spino-cerebellar tract. There can be no question that many of its fibers lie very near the midline at lumbar and thoracic levels (fig. 1). Since the fibers shift progressively dorsolaterad after they have entered the tract, at even a short distance above the level of a lesion it is difficult to determine accurately the ventromedial limits of the bundle, for the ventromedial portion of it will be occupied by undegenerated fibers arising above the level of the spinal cord lesion. At cervical levels, many fibers of the ventral spino-cerebellar tract are located also in the ventral white column, fairly near the ventral median fissure.

The shift of the ventral spino-cerebellar tract, like that of the dorsal spino-cerebellar tract (Yoss, '52) and of the lateral spino-thalamic tract (Walker, '40) is greatest through the cervical enlargement. As upper cervical cord levels are reached, the ventral spino-cerebellar fibers shift slightly ventrad.

None of the material studied shows any transference of fibers from the ventral to the dorsal spino-cerebellar system such as was described by Schäfer and Bruce ('07) and Bruce ('10). Bruce ('10) saw fibers shifting dorsad from what he considered to be ventral spino-cerebellar tract to the dorsal spino-cerebellar system. It is suggested by the present writer that this transference of Bruce's was, in reality, the dorsal shift of the dorsal spino-cerebellar tract as described by Yoss ('52). The more ventral extent of the ventral portion of the dorsal spino-cerebellar fibers has been pointed out by Gardner and Cuneo ('45) and others.

The projection of the ventral spino-cerebellar fibers upon the cerebellum, as here described, is not in complete agreement with many observers (Mott, 1892; Bruce, 1898; MacNalty and Horsley, '09; Horrax, '15; Beck, '27; Chang and Ruch, '49; and others) who, for the most part, traced ventral spino-cerebellar fibers to the anterior lobe of the cerebellum only. The results presented in this paper for the monkey are in essential agreement with the work of Anderson ('43) on rats in which the major portion of the fibers have been traced to the vermis of the anterior lobe and to the pyramid, the uvula and the declive; the lingula receives only occasional degenerated fibers of the ventral spino-cerebellar tract.

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PLATE 1

EXPLANATION OF FIGURE

1 Representative cord levels from a monkey with a spinal cord lesion at S3. Note the dorsolateral shift of the degenerated fibers of the ventral spino-cerebellar tract as they ascend toward the brain. Abbreviation: v.s.c.t., ventral spino-cerebellar tract. Marchi stain. × 7½.

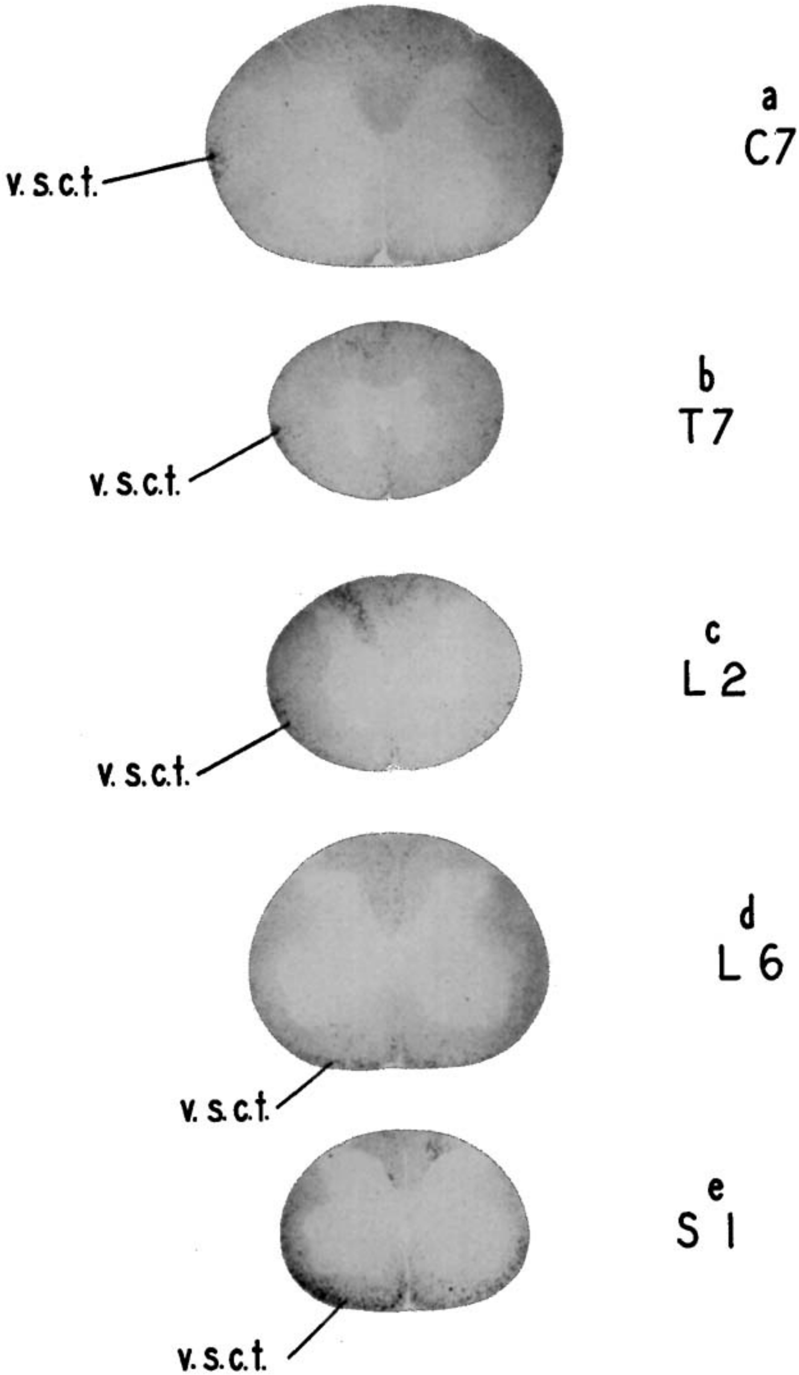
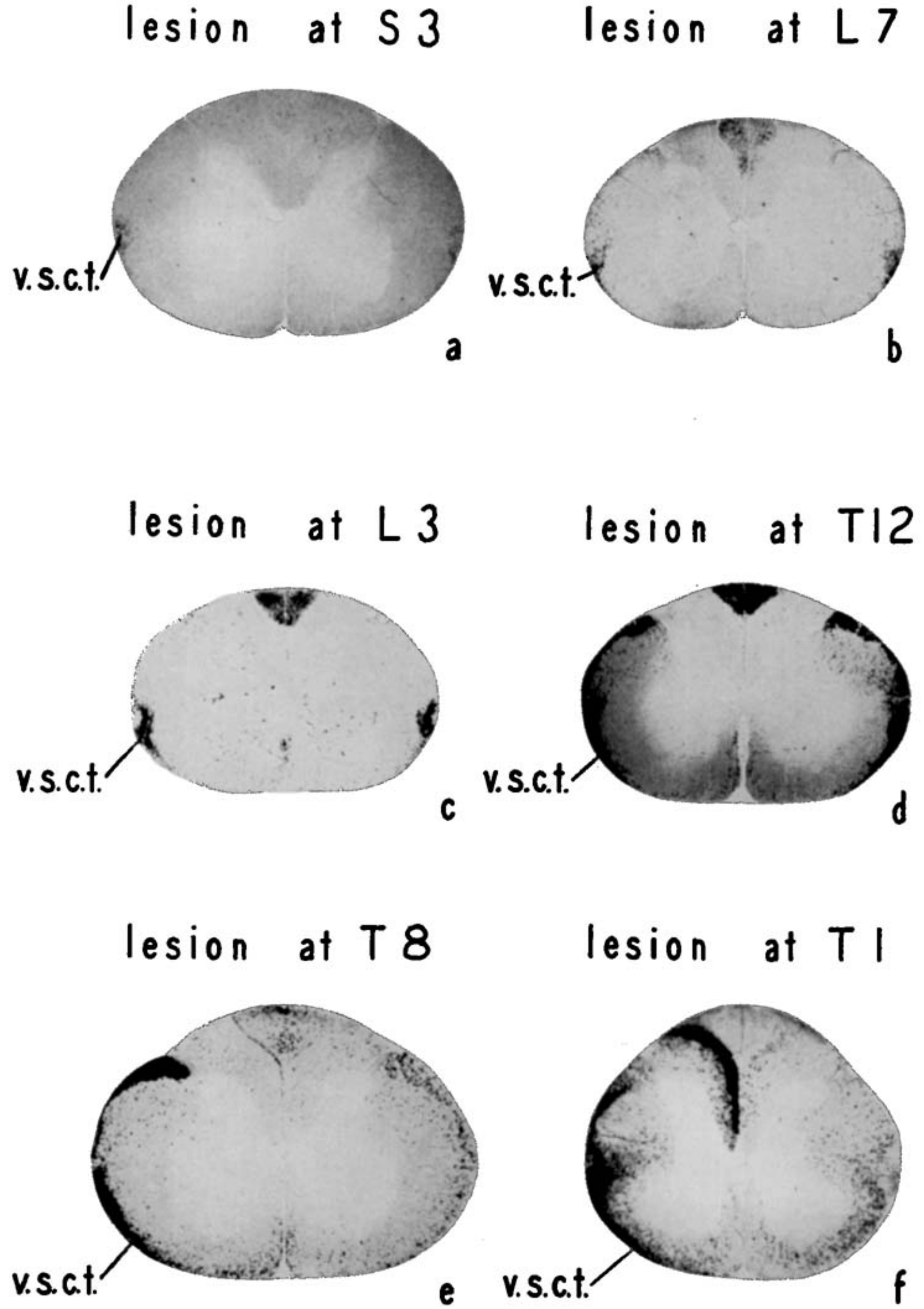
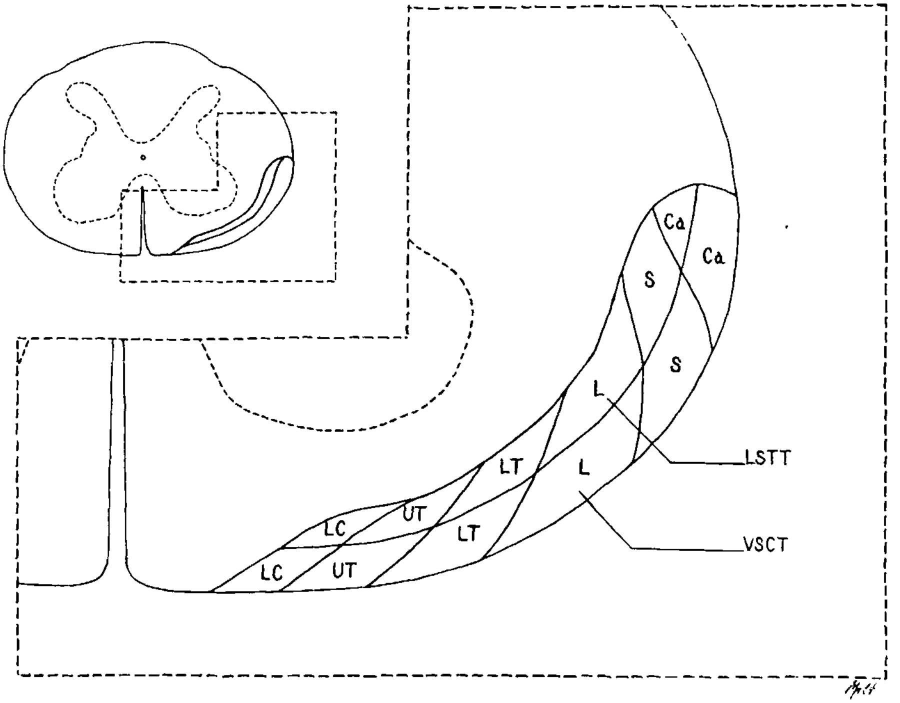

v. s. c. t.
a
C7
v. s. c. t.
b
T7
v. s. c. t.
c
L2
v. s. c. t.
d
L6
v. s. c. t.
e
S1

PLATE 2

EXPLANATION OF FIGURE

2 Cervical cord sections from 6 different monkeys with spinal cord lesions at the indicated levels. Note the increase in number of degenerated fibers in the ventrolateral group of ascending fascicles as a result of the more rostral lesions. Abbreviation: v.s.c.t., ventral spino-cerebellar tract. Marchi stain. × 7½.


lesion at S3
v.s.c.t.
a
lesion at L7
v.s.c.t.
b
lesion at L3
v.s.c.t.
c
lesion at T12
v.s.c.t.
d
lesion at T8
v.s.c.t.
e
lesion at T1
v.s.c.t.
f



3 A diagrammatic representation of the pattern of localization within the ventral spino-cerebellar and the lateral spino-thalamic tracts of the monkey at cervical levels. Note the dorsolateral to ventromedial pattern of localization within both systems. Abbreviations: Ca, caudal; L, lumbar; LC, lower cervical; LT, lower thoracic; LSTT, lateral spino-thalamic tract; S, sacral; UT, upper thoracic; VSCT, ventral spino-cerebellar tract.