TOPOGRAPHICAL DISTRIBUTION OF SPINOTHALAMIC FIBRES IN THE THALAMUS OF THE SPIDER MONKEY*

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INTRODUCTION

The ventral nucleus of the thalamus receives two systems of afferent ascending fibres of ultimate spinal origin: the medial lemniscus fibres arising from the nuclei gracilis et cuneatus, and the spinothalamic fibres originating from various levels of the spinal cord. In comparison with the studies on the arrangement of the former system the topographical analysis of the thalamopetal fibres from the spinal cord is incomplete.

Many dorsal root fibres, after ascending in the dorsal column, effect synapses in the bulbar nuclei with secondary neurons which pass to the thalamus. This indirect relation of dorsal root and thalamus was discovered in the same year (1885) by Edinger and by Flechsig. The direct connexion of the spinal cord and thalamus was unknown until 1889, when Edinger observed in fish, frogs and cat embryos that cells in the dorsal horn give rise to axons which pass through the ventral commissure, ascend in the opposite anterolateral funiculus and seemingly end in the thalamus. This was soon confirmed by Auerbach (1890) in degeneration preparations. Wallenberg (1899) and Kohnstamm (1900) demonstrated the existence of such fibres in rabbits, and Tooth (1892) and Mott (1895) in monkeys. Tooth made a lesion in the lateral region of the spinal cord at the level of the first cervical nerve in the bonnet monkey and traced the degeneration as high as the pons. After division of the anterolateral fasciculus on one side in monkeys, Mott could follow a few degenerated fibres apparently going to the thalamus; but he did not make a detailed analysis of their destination within the thalamus.

In Le Gros Clark's (1936) work on the topographical arrangement of the thalamic terminations of ascending tracts in macaques only two of eight monkeys were devoted to a study of the spinothalamic tract. These were subjected to spinal hemisection at C_4–C_5 in the one case and at Th_3–Th_4 in the other. Unfortunately, the termination in the thalamus of degenerated

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fibres from the cervical hemisection was indeterminable owing to the presence of pseudo-Marchi granules, so that differential topographical projection could not be established.

In 1938 Walker extended this study to a chimpanzee (1938*b*) and two macaque monkeys (1938*a*). All the lesions in his experiments were at a cervical level, and he did not study the regional thalamic termination of spinal fibres from different levels of the cord. Weaver & Walker (1941) in studying the topographical arrangement of the spinothalamic tract in the brain stem carried out anterolateral cordotomies and midline postero-anterior myelotomies at various levels. They were able to demonstrate only a relative lateral to medial projection of lumbar and cervical components of the spinothalamic tract.

In man, Patrick (1893) was probably the first to follow the ascending fibres in the fasciculus of Gowers through the brain stem, but he traced them only as far as the region of the inferior quadrigeminal body. However, in cats he (1896) failed to find any degeneration above the pons after transection or hemisection of the spinal cord.

In 1896 Hoche described in the brain of a patient with an interruption of the spinal cord at C_9–C_{10}, fibres in the anterolateral fasciculus coursing cephalad as far as the inferior colliculus, where they turned back through the brachium conjunctivum to the cerebellum. Hoche apparently had no conception of a spinothalamic component in the ascending degeneration. Von Sölder (1897) also failed to follow the fibres in Gowers's fasciculus farther than the ventromedial border of the medial geniculate body. The credit for the first discovery of the termination of spinothalamic fibres in man should go to Quensel (1898). In a case with a spinal lesion at C_9–C_{10}, he not only traced the degeneration to the nucleus externus thalami, but also observed that fibres cross through the posterior commissure to the other side of the thalamus. Three years later Henneberg (1901) also described in man the termination of Gowers's fasciculus in the most posterior and ventral portions of the lateral nucleus of the thalamus. In 1910, Goldstein traced the degenerated fibres from the lower spinal cord of a man with a lumbar tumour to the ventral thalamus.

The difficulty in producing experimental degeneration of spinothalamic fibres above the pons in lower mammals and the uncertainty of staining technique, especially in human material, have delayed the understanding of this great afferent system for many years. Even with human material and modern techniques, demonstration of the termination of the spinothalamic fibres is not always successful. Gardner & Cuneo (1945), working on optimal material (from a fatality 21 days after anterolateral cordotomy), were puzzled by the scarcity of degenerating fibres near the thalamus. They suggested that spinothalamic fibres lose their myelin sheaths in the thalamus or that relatively few direct fibres reach the thalamus.

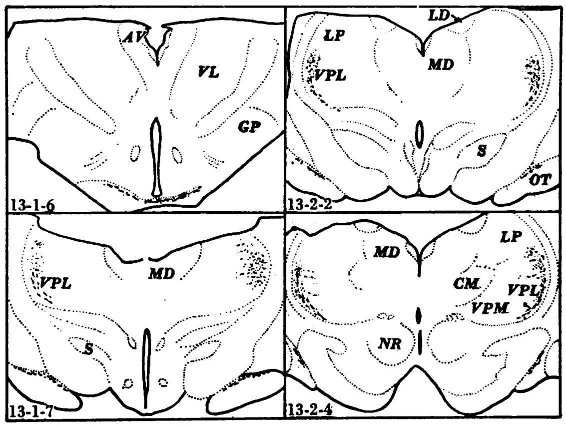
In an experiment on a cat, sacrificed 14 days after an anterolateral cordotomy in the second cervical segment, we have confirmed the observation of earlier workers that the degeneration cannot be traced above the pons.

However, in the experiments on spider monkeys we have demonstrated not only the existence of direct spinal fibres to the thalamus, but also a topographical arrangement of the fibres in the thalamic nucleus.

EXPERIMENTAL RESULTS

Experiment 1. *Spider monkey series no.* 13; *adult, male. Transection of the conus medullaris at* Ca_1 (1 *Sept.* 1944). *Sacrificed* 1 *Oct.* 1944. *Swank-Davenport preparations* (*Text-fig.* 1)

Lesion. The transection is histologically complete. Sections through the interrupted region of the cord show that the nervous tissue was completely destroyed and replaced by scar formation and disintegrated stroma-like materials including scattered black dust-like particles. There was no sign of infection or softening in any part of the cord.



Text-fig. 1. Sketches of serial sections showing the distribution of degenerated fibres in the thalamus after spinal transection at Ca_1 (SMS 13).

Histological examination of the thalamus. The degenerated fibres can be readily traced from the lesion through the spinal cord and into the brain stem. At the caudal border of the midbrain the degenerated fibres are grouped in an area just ventral to the round mass of the inferior colliculus where some fibres may be contributed to the parabigeminal body. Further cephalad they occupy the dorsolateral tegmental region. In the most cranial part of the midbrain a fraction of the degenerated fibres crosses in the dorsal division of the posterior commissure to the opposite side. Because of a gap in the serial sections, the exact course of these crossed fibres cannot be followed; but it is clear that none attains the pulvinar, though they approach that structure. The great majority of the degenerated fibres proceed in a loose cluster farther forward to the posterior end of the thalamus. Here they tend to be grouped along the lamina medullaris lateralis and then reach the dorsolateral part of the nucleus ventralis posterolateralis where they end. The terminations of the degenerated fibres, as manifested by fine, dark, dust-like particles, are limited to the dorsolateral border of the nucleus. In the posterior thalamus some coarse fibres in the form of short irregular rods are seen coming from the medial aspect and usually making a sharp angle with fibres running along the lateral medullary lamina (Text-fig. 1).

Experiment 2. Spider monkey series no. 17; one-year-old female. Spinal transection at Ca_1 (28 Nov. 1944). Sacrificed 11 Dec. 1944. Swank-Davenport preparations (Pl. 1, fig. 1; Pl. 2).

Lesion. Sections at the level of the lesions show that no nervous tissue was left intact and the general outline of the cross-section of the spinal cord is unrecognizable. Microscopically the lesion appears as an irregular patch of black particles. However, the nerve roots surrounding the spinal cord which originate from higher segments are yellow in colour with occasional black granules and are little damaged.

Histological examination of the thalamus. The medulla and the posterior part of the midbrain of this animal were cut in longitudinal sections to gain a better orientation of the cerebellum.

Frontal sections of the thalamus were also made. This proved to be one of the best preparations so far as the degeneration in the thalamus is concerned. In the lowest sections from this block of tissue, spinothalamic fibres are seen grouped chiefly in an area between the corpus geniculatum mediale and the nucleus medialis mesencephali. They are dorsal to the medial lemniscus fibres and dorsomedial to the lateral lemniscus fibres. The majority of the degenerated fibres, after entering the posterior thalamus are crowded into the lamina medullaris lateralis which is entirely lateral to the field H_1 of Forel. The most conspicuous feature of the sections taken just above the superior colliculus is the crossing of a considerable number of degenerated fibres through the dorsal division of the posterior commissure (Pl. 1, fig. 1). These decussating fibres after separating from the spinothalamic tract, turn medially in a gentle curve to the opposite side. After crossing, they are directed towards the pulvinar, but do not enter that structure. By following the course of these crossing fibres section by section, it is clear that they are destined for the nucleus ventralis posterolateralis of the thalamus.

Anterior to the medial geniculate body, the degenerated fibres tend to be dispersed and to radiate laterally, but most of them are soon incorporated into the lateral medullary lamina along the ventrolateral border of the ventral nucleus. Some other fibres proceed farther forwards to the medial part of the ventral nucleus, then turn lateralwards and finally end in a very well-localized area in the dorsolateral border of the ventral nucleus. The latter fibres, which are partially intermingled with fibres crossing through the posterior commissure, are the cause of the scattered horizontally placed, short shreds of degeneration products in the posterior part of the thalamus. In some sections they appear to be in transit from the medial structures of the thalamus. Both the fibres taking this course and the fibres passing along the ventrolateral part of the lateral medullary lamina terminate in a narrow strip at the dorsolateral border of the ventral nucleus (Pl. 2). The ventrolateral part of this nucleus seems to receive no terminating degenerated fibres, since decomposition products with the characteristic dust-like appearance of degenerated nerve endings are not present there in spite of numerous large degenerated fibres of passage.

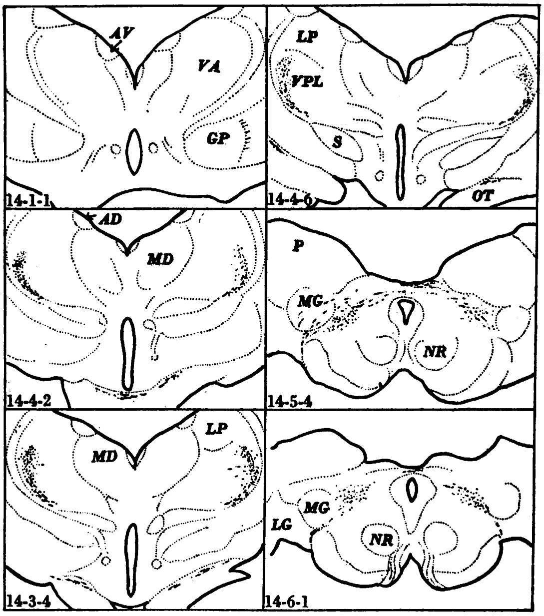
In more anterior sections, the horizontally running fibres are no longer seen, but the small area of termination and the course of fibres from the lateral medullary lamina remains distinct.

Experiment 3. *Spider monkey series no.* 14; *adult, female. Left hemisection at* Ca_1 (8 *Sept.* 1944). *Sacrificed* 26 *Sept.* 1944. *Swank-Davenport preparations* (Text-fig. 2; Pl. 1, fig. 2).

Lesion. The hemisection of the cord was complete except for a part of the sulcomarginal funiculus near the ventral median sulcus. On the right side the dorsomedial margin of the dorsal column was involved in the lesion.

Histological examination of the thalamus. The course of the degenerated fibres in the spinal cord and medulla have been described elsewhere (Chang & Ruch, 1947). At the level of the inferior colliculus the degenerating fibres stream dorsalwards along with the lateral lemniscus and a little medial to it. They then occupy a rather large area just ventrolateral to the oval nucleus of the inferior colliculus. In the anterior part of the midbrain they remain in the dorsal tegmental region. In the sections from the caudal end of the thalamus a considerable number of degenerated fibres pass through the dorsal half of the posterior commissure to the other side (Pl. 1, fig. 2). A large proportion of the degenerated fibres can be followed through the lateral medullary lamina to the nucleus ventralis posterolateralis of the thalamus. There are some short and horizontally directed fibres present in the posterior half of the ventral nucleus, which are apparently coming from the medial aspect of the thalamus. The terminal arborizations of the degenerated thalamopetal fibres, manifested by a characteristic ashy or dust-like appearance, are confined to a narrow and slightly curved strip bordering the dorsolateral sector of the nucleus ventralis posterolateralis. The boundaries of this area are rather sharp. In the ventrolateral border of this nucleus, especially at the level of posterior thalamus, a bunch of coarse degenerated fibres is present. Undoubtedly, these are fibres of passage since there is no sign of breaking up of the large osmium granules into fine splinters suggestive of degenerated nerve terminals.

On the other side of the thalamus degenerated fibres are distributed in the corresponding area of the nucleus ventralis posterolateralis of the thalamus, but two significant differences are worthy of mention. First, the number of the degenerated fibres is much greater in the right thalamus than might be expected in view of the great inequality in intensity of degeneration in the two sides of the spinal cord, medulla and midbrain. Secondly, the area of the right thalamus in which degenerated fibres terminate is not so restricted as on the left (operated) side. The distribution of the degenerated fibres in the thalamus is shown in the sketches in Text-fig. 2.



Text-fig. 2. Sketches of serial sections showing the distribution of degenerated fibres in the thalamus after spinal transection at Ca_1 (SMS 14).

Experiment 4. *Spider monkey series no.* 18; *one-year-old male. Unilateral section of the ventrolateral funiculus at* C_3 *on the right side* (5 *Jan.* 1945). *Sacrificed* 26 *Jan.* 1945. *Swank-Davenport preparation* (Text-fig. 3).

Lesion. The operation was designed to produce a unilateral lesion restricted to the fasciculus of Gowers. Although the primary lesion was confined to the anterolateral funiculus, the fibres in the fasciculus of Flechsig also underwent Wallerian degeneration. Fortunately, the involvement of Flechsig's fasciculus does not affect the picture of degeneration in the thalamus.

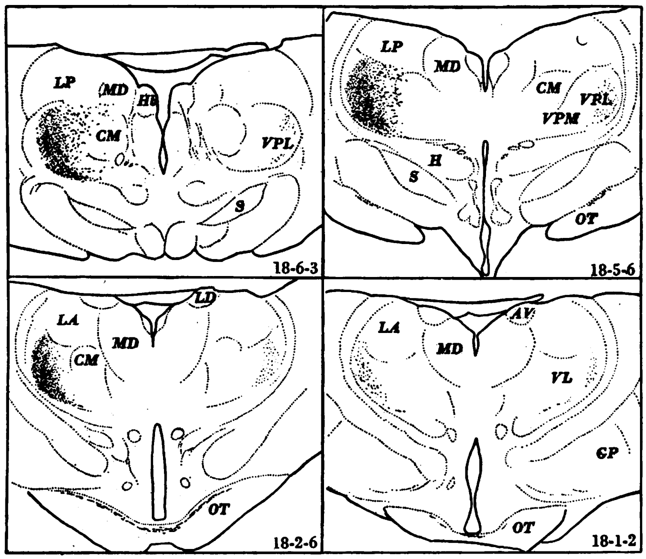
The area damaged by primary intention is shaped like a crescent with the concavity directed medially.

Histological examination of the thalamus. At the cephalic end of the midbrain the degenerated spinothalamic fibres are mingled with the undegenerated ones of the medial lemniscus system and occupy a large area between the medial geniculate body and the nucleus lateralis mesencephali. There is a gradual blending of the spinothalamic fibres with medial lemniscus fibres at this level and the topographical distinctness of the two systems becomes less and less clear, while the lateral lemniscus remains separated from them.

Degenerated fibres passing to the opposite side by way of the dorsal division of the posterior commissure are distinctly shown in many sections at this level;

the heavily myelinated ventral division of the commissure is completely free from degeneration. After crossing they continue laterally for a considerable distance toward the ventral border of the pulvinar, but none can be traced into that nucleus.

As the degeneration is traced farther forward to the posterior thalamus, a large number of widely dispersed degenerating fibres in the lateral region of the centrum medianum fan out laterally to the ventrolateral part of the ventral nucleus of the thalamus. Those elongated fragments of fibres are arranged in flat curves. The density of these fibres is greater in the posterior thalamus than in the anterior part. Another group of degenerated fibres is more densely



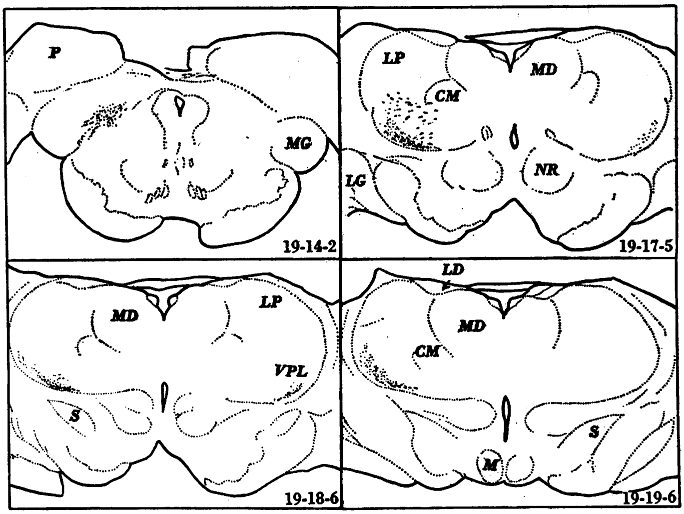
Text-fig. 3. Sketches of serial sections showing the distribution of degenerated fibres in the thalamus after a cordotomy on the right side at C_3 (SMS 18).

aggregated in the lateral medullary lamina and proceeds along the ventrolateral border of the ventral nucleus. The terminations of the degenerated fibres are distributed throughout the nucleus centralis posterolateralis of the thalamus. The most abundant disintegration products from the nerve terminals are found in the most lateral part of this nucleus. The apparent separateness of this lateral area of degeneration is enhanced by the presence of coarse fibres of passage. The size and arrangement of the elongated shreds of decomposition products in the centrum medianum and the nucleus arcuatus suggest that these nuclei may not constitute a terminus but are traversed by the spinothalamic fibres. The margin of the area with fine particles of degeneration at the dorsal aspect of the nucleus ventralis posterolateralis is well delimited from the nucleus lateralis (Text-fig. 3). Sections through the anterior part of the thalamus show that the degenerations do not extend beyond the oral end of the ventral nucleus.

The distribution of the degenerated fibres in the thalamus of the right side is similar in position, but much less dense than that in the left thalamus as described above.

Experiment 5. *Spider monkey series no.* 19; *adult, female. First operation: transection of the spinal cord at* Ca_1 (13 *July* 1945). *Second operation: left hemisection of the spinal cord between* L_1 *and* Th_{13} (10 *Jan.* 1946). *Sacrificed* 30 *Jan.* 1946. *Swank-Davenport preparation* (Text-fig. 4).

Lesion. The extent of the first lesion is not known since the caudal segments of the cord at Ca_1 was not sectioned for histological purposes. At autopsy that part of the cord was found shrunken and deformed. The permanent



Text-fig. 4. Sketches of serial sections showing the distribution of degenerated fibres after a left hemisection at I_1 6 months after total transection at Ca_1 (SMS 19).

paralysis of the tail guarantees the complete separation of the conus from the above structures. Sections taken just above the first lesion, i.e. at S_2, show that the ascending degenerations from the first operation have been largely cleared and the descending degenerations from the second lesion are limited to the left side.

The second lesion was confined to the left half of the spinal cord. The medial margin of the lesion is sharp and does not encroach on the other side. The hemisection is complete except for a very narrow strip along the median line which is a little distorted.

Histological examination of the thalamus. While ascending to the anterior region of the midbrain, the degenerating fibres on the left side are, as in all the other specimens, mainly grouped in the region between the dorsal tegmental region and the medial geniculate body, and are partly mingled with normal fibres of other origin. The location of the degenerated fibres is more dorsomedial with reference to the medial lemniscus. Slightly higher up, the degenerated fibres are again present in the dorsal portion, and dorsal portion only, of the posterior commissure. After crossing, series of dark beads can be followed well laterally. In more anterior sections, the degenerated fibres enter the nucleus ventralis posterolateralis by two different routes, first, a medial-lateral approach from the region about nucleus arcuatus and the lateral half of the centrum medianum, and, second, an inferior approach by way of the ventrolateral border of the ventral nucleus. Although the coarse fibres are distributed to an extensive field, the area of termination seems to be limited to a small region in the ventrolateral sector of the nucleus ventralis posterolateralis. At the mid-thalamic level where the horizontally placed large fibres of passage are greatly reduced in number, the degenerations are clearly restricted to the lateral border of that nucleus (Text-fig. 4). The characteristic narrow band of degeneration with fine particles at the dorsolateral corner of the ventral nucleus, constantly present in all the other preparations, was apparently cleared of degeneration products. Thus Text-fig. 4 gives a negative picture of the thalamic terminus of fibres from the caudal region. In many sections the degenerated fibres are seen radiating successively in an arciform fashion from the lateral medullary lamina to the ventral nucleus, where they end.

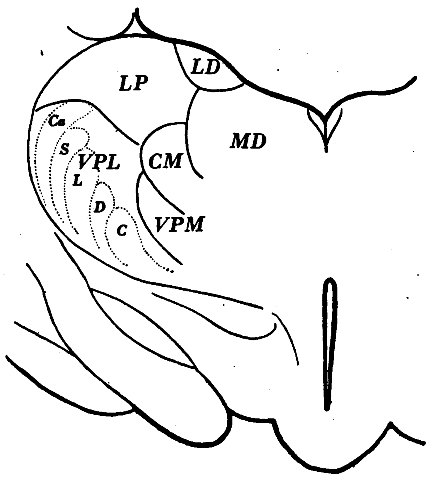
DISCUSSION

Topographical distribution of spinothalamic fibres in the thalamus

The topographical projection of spinothalamic fibres in the thalamus as revealed in the present investigation resembles closely that of the medial lemniscus system. As demonstrated by Le Gros Clark (1936) & Walker (1938*a*), the fibres arising from the nucleus gracilis, which receives impulses from the lower extremities, are projected rather to the nucleus ventralis posterolateralis and those from the nucleus cuneatus, relaying the nerve impulses from the arms, to the nucleus ventralis posteromedialis.

The degeneration in the thalamus of spider monkeys with a lesion at the caudal region of the cord is strictly confined to the most dorsolateral band of the nucleus ventralis posterolateralis and the medial portion of this nucleus was involved only when the spinothalamic tract was sectioned at a cervical level. The area of degeneration in the thalamus following a lumbar lesion does not extend medially as far as that produced by a cervical lesion. More crucial is the fact that the most dorsolateral region of the nucleus ventralis posterolateralis was free of osmium granules after a lumbar lesion performed six months after a total transection of the caudal segment of the cord. It is evident that the degeneration products of the spinothalamic fibres from the caudal cord had been cleared when the second operation was made, and no fresh degeneration in that area was produced. Therefore both positive and negative evidence demonstrates that the most dorsolateral corner of the nucleus ventralis posterolateralis of the thalamus receives direct fibres from the caudal cord, and constitutes the tail area of that nucleus.

A comparison of the location and extent of the degeneration fields in the ventral nucleus of the thalamus following spinal lesions at three different levels suggests a precise segmental representation in which afferent fibres from the lowest part of the cord terminate in the most lateral zone of the nucleus ventralis of thalamus, and those from more cranial segments project successively to the more medial zones. These concentric zones of termination are so arranged that the lateral is more dorsally placed and the medial more ventrally. The sketch in Text-fig. 5 shows the plan of this topographical arrangement. In some normal myelin sheath preparations the loose bundles of very fine myelinated fibres from the ventral medullary lamina are seen arching dorsally in gentle curves into the ventral nucleus of the thalamus so that the nucleus is divided into several concentric laminae like those shown in Text-fig. 5. The outer two strands of arching fibres are usually more prominent than the inner, which are composed of fine myelinated fibres and are faintly stained in our specimens. This feature of the myelo-architectonics of the thalamus has been noticed by Poliak (1932). He described concentrically arranged, semicircular laminae of thalamopetal fibres in the lateral (ventral) nucleus of the thalamus and pointed out the significance of this regular organization.



Text-fig. 5. Diagram showing the topographica arrangement in the thalamus of spinothalamic fibres from different levels of the spinal cord.

The plan of the topographical representation of various segments of the body in the thalamus as suggested by degeneration studies of spinothalamic fibres is consistent with that based on retrograde degeneration experiments and on physiological experiments.

Extensive studies of the thalamocortical projections of the thalamus have been made by Le Gros Clark (1936) and by Walker (1938*a*) who located the cells of the thalamus that undergo retrograde degeneration following ablation of different areas of the cerebral cortex. The superior segment of the post-central gyrus receives projection fibres from the most lateral region of the nucleus ventralis posterolateralis, and the mid-postcentral area from the medial portion of that nucleus. From physiological and clinical evidence it is known that the superior portion of the postcentral gyrus is concerned with the somatic sensibility of the lower limb and the subjacent region of the postcentral gyrus is concerned with the arm. More medially still is the nucleus ventralis postero-medialis, which receives fibres from the trigeminal system and projects to the inferior or face region of the sensory area; it is concerned with the sensibility of the face including taste (Blum, Walker & Ruch, 1943; Patton, Ruch & Walker, 1944).

The functional localization of the thalamus as investigated by the method of local strychninization by Dusser de Barenne & Sager (1937) is in agreement with the results of anatomical studies. Injection of a small amount of strychnine into the lateral region of the lateral and ventral nuclei of the thalamus produced sensory disturbances in the hind legs, whereas strychninization of the medial region produced disturbances in the arms.

The organization of the somatic afferent fibres at several levels of the nervous system seems to be determined by topographical principles. In 1900 Wallenberg first described an orderly termination of the secondary sensory neurons in the thalamus of rabbits. He proved that the so-called law of eccentric position of the long tracts postulated by Kohnstamm (1900) for Gowers' fasciculus is applicable to the thalamus as well as to the spinal cord and brain stem. The law states that the fibres originating most caudally occupy the most peripheral position, while the fibres arising from more cephalic segments of the spinal cord take an inner course in the ascending tract. The thalamus of the spider monkey, because of the extraordinary development of the tail region of the spinal cord, constitutes a special test of this theory. And the dorsolateral termination of fibres derived from the tail is exactly that predicted by the Kohnstamm-Wallenberg hypothesis. There seems no doubt that the primate thalamus, or at least the thalamus of the spider monkey, has been differentiated to such a degree that different segments of the body are represented in an orderly manner in rather restricted laminae of the ventral nucleus of the thalamus.

There is of course a considerable overlapping in the thalamus of the contributions from successive dermatomes. In view of the small cross-sectional area of the thalamus some overlapping of the dermatomic projection of the spinothalamic fibres in the thalamus is to be expected. The maximal projection area for each individual segment of the body may not necessarily be a thin sharply delimited strip. However, the thalamic fields for tail, legs, arms and face are definitely more sharply separated from one another in the sense that fibres from the same region of the spinal cord, i.e. sacro-caudal, lumbar or cervical, tend to be more closely grouped together and divided off by strands of fibres, whereas more overlapping exists within each sub-region. The thalamic overlapping of dermatomic contributions appears to be the anatomical counterpart of the overlapping of cortical fields for different segments of the cord as schematized by Woolsey, Marshall & Bard (1942). The trigeminal, cervical, thoraco-lumbar and sacro-caudal divisions are each represented in a specific region of the postcentral gyrus with the projection of each individual segment belonging to the same spinal division exhibiting a higher degree of overlapping.

Decussation of spinothalamic fibres in the posterior commissure

In all preparations from spider monkeys with spinal lesions degenerated fibres are constantly present in the dorsal part of the posterior commissure and pass laterally after decussation to the opposite thalamus. The crossing of the spinothalamic fibres through the posterior commissure has received little attention. In the literature only one mention of spinothalamic fibres crossing through the posterior commissure has been encountered (Quensel, 1898). Recently, Keene (1938) found in the monkey that degenerated fibres can be traced through the posterior commissure to the ipsilateral thalamus after the commissure was sectioned on one side near the midline. However, she was unaware of the spinal origin of these fibres.

The posterior commissure is actually a decussation rather than a true commissure. It is a collection of crossing fibres of various origin and termination. Besides the familiar components connecting the nucleus of Darkschewitch with the fasciculus longitudinalis medialis there are, according to Keene's analysis, at least five other components in the posterior commissure, namely fibres running to or in: (1) the tegmental region and the capsule of the red nucleus; (2) the habenular ganglia and the fasciculus retroflexus Meynerti; (3) the pineal body; (4) the corpus striatum or even the cortex; and (5) the thalamus.

Histologically, the posterior commissure is divided into two parts, a dorsal and a ventral. The ventral part is composed of coarse myelinated fibres. Fibres in the dorsal part are fine and run laterally for a considerable distance. The degenerations resulting from spinal lesions were always limited to this fine-fibred dorsal part of the commissure. According to Muskens (1914) the horizontal laterally coursing fibres may go to the globus pallidus, but in our sections degenerated fibres cannot be followed that far.

The problem of ipsilateral sensory representation

The discovery of crossed spinothalamic fibres in the posterior commissure serves to reconcile certain discordant functional and anatomical observations. It is commonly taught that each thalamus is linked only with the contralateral side of the body by the spinothalamic tract and the medial lemniscus system, and that the spinothalamic fibres cross immediately after their origin in the spinal cord. The bilateral connexion of the spinothalamic tract with the thalamus by an additional, supraspinal decussation has been overlooked since Quensel's brief mention of it (1898). For example, Walker (1938*a*) observed but was unable to account for the degeneration in both thalami following a hemisection of the cord and concluded with reservations that both thalami receive fibres from one spinothalamic tract.

A bilateral representation of cutaneous sensibility in the thalamus and cortex has been experimentally established by Dusser de Barenne & Sager

(1937) and confirmed for the face by Woolsey, Marshall & Bard (1942) with electrical techniques. Strychninization of one cortex or of one thalamus produces sensory disturbances in the skin of both sides of the body with the strongest symptoms manifested on the contralateral side. Dusser de Barenne pointed out that such bilaterality is not due to interhemispheric connexions between the sensory cortex of the two sides, since bilateral symptoms persisted after extirpation of one hemisphere. Moreover, anatomical search for a crossed connexion between thalamus and cortex has been unsuccessful, therefore the crossing of the sensory impulses must occur below the thalamic level.

Clinical investigation by Déjerine & Roussy (1906) also suggests a bilateral representation of cutaneous sensibility in the thalamus. Destructive lesions of the ventrolateral nucleus of the thalamus result in severe hypo-aesthesia and hypo-algesia and disturbances in deep sensibility. However, cutaneous sensibility to some degree recovers while deep sensibility is permanently lost. The recovery of cutaneous sensory function must depend upon the persistence of intact fibre connexions of the remaining thalamus with the two sides of the body. The present finding that the spinothalamic tract of one side reaches both thalami by way of fibres crossing in the posterior commissure provides an anatomical basis for bilateral cutaneous sensory representation of thalamus and cortex.* The permanent loss of deep sensibility on one side of the body after the unilateral destruction of the thalamus is accounted for by the single and complete decussation in the medulla of the fibres of the medial lemniscus system which is concerned with the conduction of proprioceptive sensibility.

SUMMARY

1. A topographical distribution in the thalamus of the spinothalamic fibres from three levels of the spinal cord has been demonstrated on the basis of Marchi preparations from five spider monkeys.

2. The spinothalamic fibres terminate exclusively in the nucleus ventralis posterolateralis in a laminated fashion so that fibres from the caudal segments of the cord are distributed to the extreme dorsolateral strip and those from the sacro-lumbar and the thoraco-cervical regions are distributed to successively more ventromedial laminae of this nucleus.

3. A part of the spinothalamic fibres cross through the dorsal portion of the posterior commissure and terminate in the nucleus ventralis posterolateralis of the opposite thalamus. These fibres are believed to form an anatomical basis for ipsilateral sensory representation in the thalamus and cortex.

* Foerster (1927) and others have suggested on the basis of cordotomy cases that some fibres of the spinothalamic system ascend the spinal cord on the side of entry, and such fibres could not be distinguished in our experiments from those of ventrolateral origin. However, with more radical cordotomies and more complete loss of pain sensibility, the hypothesis of an ipsilateral spinal pain pathway has lost favour. Thus it would seem that some fibres of the spinothalamic tract undergo double decussation.

ABBREVIATIONS

AD, nucleus anterodorsalis; *AV*, nucleus anteroventralis; *CM*, centrum medianum; *GP*, globus pallidus; *H*, H field of Forel; *Hb*, habenula; *LA*, nucleus lateralis anterior; *LD*, nucleus lateralis dorsalis; *LG*, corpus geniculatum laterale; *LP*, nucleus lateralis posterior; *M*, corpus mamillare; *MD*, nucleus medialis dorsalis; *MG*, corpus geniculatum mediale; *NR*, nucleus ruber; *OT*, tractus opticus; *P*, pulvinar; *S*, nucleus subthalamicus; *VA*, nucleus ventralis anterior; *VL*, nucleus ventralis lateralis; *VPL*, nucleus ventralis posterolateralis; *VPM*, nucleus ventralis posteromedialis.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Unretouched photomicrograph showing the decussation of spinothalamic fibres in the dorsal part of posterior commissure (SMS 17, spinal transection at Ca_1). 20 ×.

Fig. 2. Unretouched photomicrograph showing the degenerated fibres in the posterior commissure (SMS 14, spinal hemisection at Ca_1). 20 ×.

PLATE 2

Unretouched photomicrograph showing termination of degenerated fibres in the dorsolateral region of the nucleus ventralis posterolateralis of the thalamus (SMS 17, spinal transection at Ca_1). 70 ×.

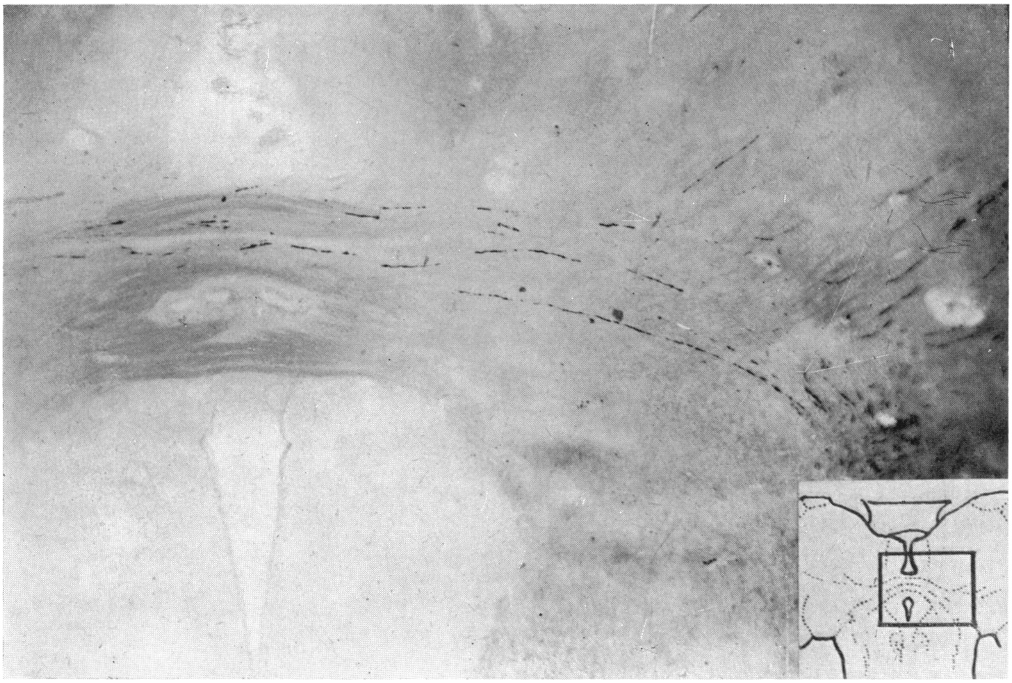
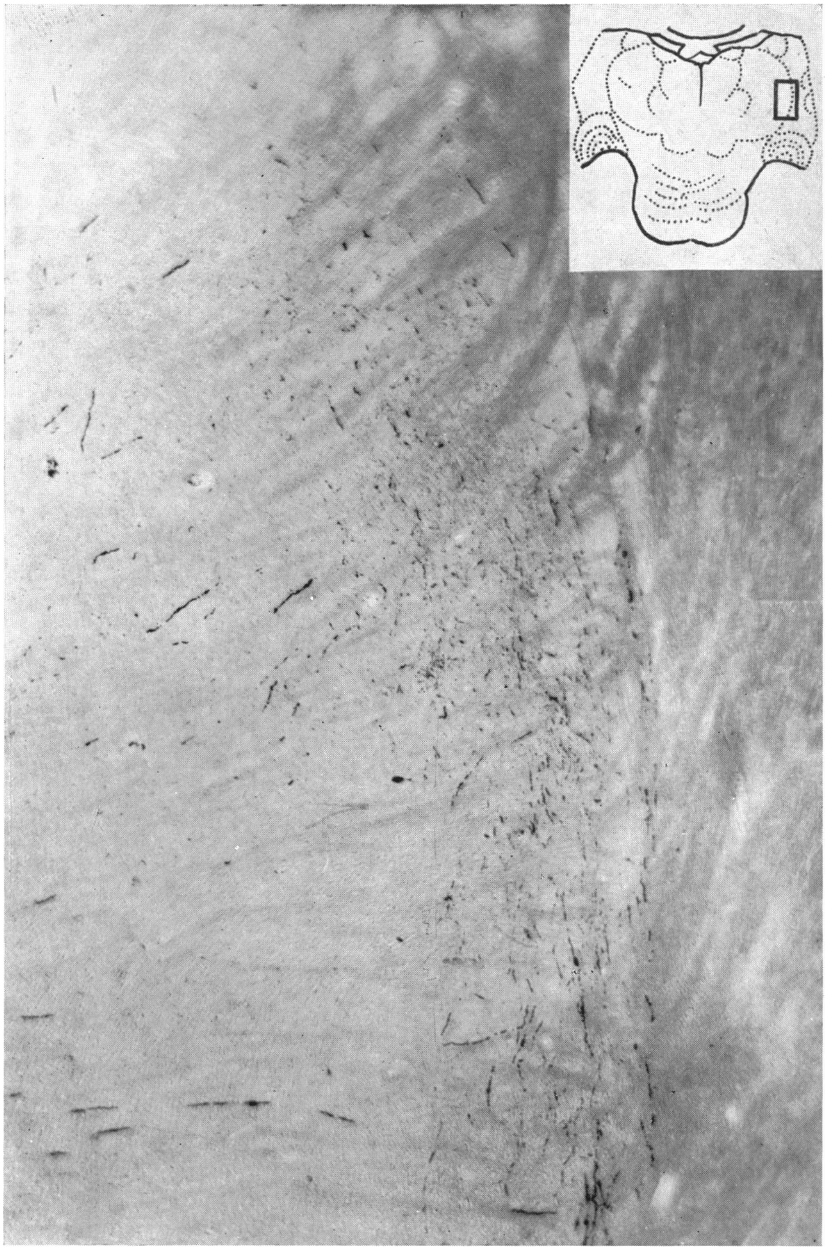


Fig. 1.

Fig. 2.

CHANG AND RUCH—SPINOTHALAMIC FIBRES IN THALAMUS OF SPIDER MONKEY



CHANG AND RUCH—SPINOTHALAMIC FIBRES IN THALAMUS OF SPIDER MONKEY