An Experimental-Anatomical Study on the Spinothalamic Tract in the Cat

By

Kahee Niimi, Shiroyuki Fujita, Kumashige Abe and Syosuke Kawamura

The Third Department of Anatomy, Okayama University
Medical School, Okayama, Japan

Much has been written concerning the spinothalamic tract in the rabbit, monkey and man. However, many early and more recent investigators using the cat have not been able to trace this tract to the thalamus by the Marchi method (Patrick, '93, '96; Chang and Ruch, '47; Morin et al., '52). In recent years silver techniques have been widely utilized in demonstrating precise fiber connections of the brain and spinal cord. Getz ('52) demonstrated terminal degeneration in the thalamus by the Glees method following cordotomy in the cat. Thereafter, Morin and Thomas ('55), Nauta and Kuypers ('58), Anderson and Berry ('59) and Terada ('60) studied the spinothalamic tract of the cat by the Nauta method and traced axon degeneration to the thalamus. Recent studies by use of the evoked potential method also demonstrated the spinothalamic tract in the cat as well as in the monkey (Mountcastle and Henneman, '49; Berry et al., '50).

In the monkey Clark ('36) found degeneration in the nuclei of the internal lamina, in addition to the ventral thalamic nucleus following hemisection of the spinal cord. Recently, Bowsher ('57, '61) and Mehler et al. ('60) demonstrated degeneration in the intralaminar nuclei (including centre médian nucleus) by the Nauta method following anterolateral cordotomy in the monkey and man. Also in the cat Getz, Nauta and Kuypers, Anderson and Berry, and Terada described the spinal afferents to the intralaminar and related nuclei.

The present study attempts to trace the precise course and termination of the spinothalamic tract and to clarify the relation of

This article is dedicated to Prof. emeritus Dr. Ko Hirasa wa to commemorate his retirement from Kyoto University.
this tract to the neighboring long ascending tracts, such as the spino-olivary, spinoreticular and spinocerebellar tracts.

Material and Methods

Upper cervical cordotomy was performed on 8 adult cats and three of these, which had adequate lesions for study of the spino-thalamic tract, were used in the present investigation. In cats 1 and 2 the anterolateral funiculus was sectioned at the level between the first and second cervical segments. In cat 3 the lateral funiculus including the lateral cervical nucleus was damaged at the upper level of the first cervical segment. After a survival period of 7 days the animals were sacrificed and perfused intracarotidly with normal saline followed by a solution of 10% neutral formalin. The brains and cervical cords were removed, fixed in 10% neutral formalin for five days and then cut about 10 mm. thick transversely. After fixation in 10% neutral formalin for one month, these cut blocks were sectioned serially at 30μ on the freezing microtome and impregnated by the Nauta-Gygax ('54) silver technique.

Text-fig. 1. Cross-sections through the upper cervical cord to show lesions (hatched area).

Results

Cat 1

In this case the left anterolateral funiculus was extensively cut at the junction of the first and second cervical segments. The lesion involved the ventralmost part of the anterior horn (Text-fig. 1). The dorsal roots of C₁ and C₂ of the operated side were partially damaged.

At levels of the pyramidal decussation the degenerated fibers found in and around the medial accessory olive are regarded as the
spino-olivary and spinothalamic fibers. Fibers in the lateral reticular nucleus and reticular formation correspond to the spinoreticular tract, and those lying lateral and dorsolateral to the lateral reticular nucleus correspond to the spinocerebellar tract. At this level degenerated fibers are concentrated in the most lateral part of the posterior funiculus. They may be caused by damage to the dorsal roots. Some of them are seen to enter the ventral part of the dorsal column nuclei, particularly the cuneate nucleus. It should be mentioned that a few fibers of the spinoreticular tract reach the hypoglossal nucleus.

In more rostral sections degenerated fibers are found in the dorsal accessory and medial accessory olives (the spino-olivary tract), but not in the main olive. A considerable number of degenerated fibers are also present dorsolateral, lateral and ventral to the dorsal accessory olive and dorsolateral to the ventrolateral part of the medial accessory olive (the spinothalamic tract). At these levels degenerated fibers are distributed diffusely in the reticular formation dorsal and dorsolateral to the inferior olivary complex (the spinoreticular tract). They are dispersed dorsomedially; some of them enter the hypoglossal nucleus, the nucleus of the solitary tract and the inferior vestibular nucleus, but do not reach the dorsal nucleus of the vagus. Near the periphery of the lateral funiculus degenerated fibers are concentrated and continue dorsolaterally into the restiform body (the spinocerebellar tract), but some fibers enter the ventral extremity of the spinal trigeminal nucleus.

As the inferior olivary complex disappears, the degenerated fibers of the spinothalamic tract are dispersed somewhat laterally, with a few fibers entering the lateral paragigantocellular nucleus. Some of them spread also dorsally and are joined by the degenerated spinoreticular fibers. The facial nucleus contains scattered degenerated axons which may be derived from the spinoreticular and spinocerebellar tracts.

Rostrally the degenerated spinothalamic fibers decrease somewhat in number and are confined to a region ventromedial to the superior olivary nucleus to be separated from the spinoreticular and spinocerebellar fibers. They send no fibers to the superior olivary nucleus, but a few fibers are distributed to the medial trapezoid nucleus. The spinoreticular fibers are distributed dorsolaterally, with some fibers entering the lateral vestibular nucleus. The spinocerebellar fibers are found ventrolateral and lateral to the facial nucleus and extend dorsolaterally.

In sections through the lower pons the degenerated spinothalamic
fibers migrate lateralward to course rostrally through the medial lemniscus, particularly its lateral portion. The spinoreticular fibers ascend diffusely through the lateral reticular formation. As the upper pons is approached, the spinothalamic fibers are restricted to the lateral portion of the medial lemniscus. Only a few fibers, however, spread dorsolaterally to the lateral lemniscus, dorsomedially to the reticular formation and ventrally to the lateral pontine nucleus.

At inferior collicular levels the degenerated spinothalamic fibers are scattered within the dorsolateral portion of the medial lemniscus. Some fibers are seen to enter the inferior colliculus by way of the lateral lemniscus. Within the inferior colliculus a small number of beaded axons are scattered in its ventralmost part, the majority of them being of small caliber. A few fibers pass through the reticular formation to the lateral and ventrolateral part of the central gray substance, in which scattered fine beads and a few fine granules are found. The spinoreticular degenerated fibers are markedly reduced in amount and are scattered in the lateral part of the reticular formation. Some of them run dorsomedially into the central gray.

As the caudalmost level of the superior colliculus is reached, the spinothalamic tract is confined to the most dorsal portion of the medial lemniscus, sending fibers to the central gray substance and the superior colliculus. The spinoreticular fibers are very scarce at this level. Most of the degenerated fibers found in the reticular formation are regarded as the fibers of passage from the spinothalamic tract to the central gray.

At middle levels of the superior colliculus the degenerated spinothalamic fibers are directed dorsomedially to the superior colliculus and medially to the central gray through the reticular formation where some fibers appear to terminate. It is of interest to note that very few fibers are seen to cross through the commissure of the superior colliculus. Within the superior colliculus degenerated fibers are present in the stratum opticum and stratum griseum medium, where fine fragmentary chains of beads are scattered irregularly. In the stratum album medium some transversely running beaded axons are found, but they are considered to be fibers of passage.

At rostral levels of the superior colliculus the degenerated spinothalamic fibers are largely concentrated in the medial lemniscus ventromedial to the medial geniculate body. From here degenerated fibers spray out dorsolaterally into the magnocellular part of the medial geniculate body, and medially into the lateral portion of the central gray substance through the reticular formation with a few
Text-fig. 2. Projection drawings of representative transverse sections through the medulla oblongata, pons and mesencephalon of cat 1. Nauta-Gygax method.
fibers entering the pretectal nucleus and the nuclei of the posterior commissure. The magnocellular part of the medial geniculate body, particularly its medial portion, undergoes degeneration which is represented by many irregularly scattered degenerated beads, some fine degenerated granules among cells and a few pericellular axon fragments. In the pretectal nucleus a few degenerated beads are scattered and are restricted mainly to its ventral part. Only very few beads are found in the lateral part of the substantia nigra, but nothing definite can be stated concerning their termination.

In sections through the posterior commissure very few fibers are seen entering the posterior commissure and run across the midline into the contralateral side, but their farther course cannot be traced definitely. At the rostralmost level of the posterior commissure the majority of the degenerated spinothalamic fibers are distributed to the posteromedial and posterolateral ventral nuclei, and the parafascicular nucleus, but very few fibers enter the suprageniculate nucleus. The posteromedial ventral nucleus contains degenerated beads running laterally and dorsolaterally. Within the posterolateral ventral nucleus a small number of fragmentary chains of beads are found in its ventromedial part. Throughout the parafascicular nucleus degenerated beads with a few granules are scattered. It should be mentioned that a few degenerated axons enter the subthalamic nucleus, particularly its dorsolateral part.

At levels of the habenular commissure the degenerated fibers of the spinothalamic tract begin to divide into medial and lateral groups. The medial group of fibers is distributed to the ventral nuclei, where degenerated fibers are found in the medial part of the posterolateral ventral nucleus and the adjacent portion of the posteromedial ventral nucleus. Within the latter nucleus most fibers are regarded as fibers of passage, but some appear to end therein. Beneath the ventral nuclei a small number of degenerated axons are seen to run into the zona incerta, with a few fibers entering the subthalamic nucleus. On the other hand, the lateral group of fibers is directed dorsally through the mediallymost part of the posteromedial ventral nucleus to be distributed to the parafascicular and centre médian nuclei, in which irregularly arranged beaded axons and scattered granules are found.

In sections through the anterior part of the lateral geniculate body the above-mentioned two groups of fibers begin to separate clearly from each other. Within the ventral nuclei, fragmentary chains of beads and fine granules are scattered in the posterolateral
Text-fig. 3. Projection drawings of representative transverse sections through the diencephalon of cat 1. Nauta-Gygax method.
ventral nucleus and the most lateral part of the posteromedial ventral nucleus. In the former nucleus degenerated fibers tend to be interwoven in a reticular fashion. At these levels some degenerated fibers are seen running dorsolaterally through the thalamic fasciculus and the zona incerta to enter the ventromedial part of the thalamic reticular nucleus, though a few fibers appear to terminate in the zona incerta. Within the reticular nucleus very few pericellular axon fragments are found, in addition to the fragmentary beads of axons. The medial group of degenerated fibers is distributed to the centre médian nucleus and partly to the lateral central nucleus. It is of interest to note that a few degenerated beads and granules are scattered in the most ventrolateral part of the dorsomedial nucleus.

At levels just in front of the lateral geniculate body the lateral group of degenerated fibers is distributed mainly in the posterolateral ventral nucleus. A small number of degenerated axons are also found in the thalamic fasciculus and the zona incerta. The medial group of degenerated fibers is distributed in the lateral central nucleus and, to lesser amount, in the paracentral nucleus.

More rostrally, the degenerated spinothalamic fibers are found mainly in the ventral nuclei and partly in the intralaminar nuclei. The posterolateral ventral nucleus, except for its dorsalmost portion, contains a considerable number of irregularly scattered fine granules and some pericellular axon fragments, in addition to beaded axons. Also in the posteromedial ventral nucleus fine degenerated granules are predominating. At these levels a few degenerated fibers are seen to enter the ventromedial part of the reticular nucleus, where very few pericellular axon fragments are discernible. No degenerated fibers are found in the zona incerta and the thalamic fasciculus.

After the disappearance of the posteromedial ventral nucleus the degenerated spinothalamic fibers are found largely in the posterolateral ventral nucleus. Passing rostrally they decrease in amount and, as this nucleus disappears, they continue for some extent to the ventrolateral part of the lateral ventral nucleus, where a few fragmentary beads of axons and only very few granules are scattered. Within the lateral central nucleus a few beaded axons are found, while the paracentral nucleus contains no degenerated fibers.

In this case the spinothalamic tract on the side opposite to the lesion is almost free from degeneration. However, some crossed fibers through the posterior commissure and the commissure of the superior colliculus appear to be distributed to the midbrain and the dorsal thalamus. At upper mesencephalic levels very few degenerated fibers
are seen in the central gray, the superior colliculus and the magnocellular part of the medial geniculate body. Within the thalamus a few degenerated fibers are present in the posterolateral ventral nucleus and the adjacent part of the posteromedial ventral nucleus as well as in the centre médian, parafascicular, lateral central and paracentral nuclei.

**Cat 2**

The anterolateral funiculus on the left side was cut at the level between the first and second cervical segments as in cat 1. However, the lesion was smaller in extent, and the gray substance was hardly damaged (Text-fig. 1).

In this cat the degeneration of the spinothalamic and spino-olivary tracts is much milder than that in cat 1. The spinoreticular tract is not so severely degenerated, while the spinocerebellar tract shows marked degeneration.

The degeneration picture of the spinoreticular tract is essentially the same as in cat 1. At the lowest medullary levels degenerated spinothalamic and spino-olivary fibers are seen in the lateralmost part of the anterior funiculus. As the inferior olivary complex appears, they are found in and around the ventrolateral part of the dorsal accessory olive. After the disappearance of the inferior olivary nuclei the degenerated spinothalamic fibers are scattered in the limited region dorsolateral to the pyramid of the medulla oblongata. In the pons they are found in the dorsolateral part of the medial lemniscus, but only very few fibers are scattered in the dorsal part of the lateral pontine nucleus. At inferior collicular levels the degenerated spinothalamic fibers are distributed to the central gray substance and the most ventral part of the inferior colliculus. At levels of the superior colliculus they decrease further in number and only a few fibers are seen entering the magnocellular part of the medial geniculate body, the superior colliculus and the central gray through the reticular formation. Within the dorsal thalamus some degenerated fibers are found in the posterolateral ventral nucleus and the adjacent part of the posteromedial ventral nucleus. In addition, a few fibers are seen in the centre médian nucleus, and very few in the parafascicular and dorsomedial nuclei.

**Cat 3**

The lesion was produced in the right lateral funiculus at the upper level of the first cervical segment, involving the lateral cervical nucleus, the lateral edge of the dorsal horn and the most dorsolateral portion of the ventral horn (Text-fig. 1).
A considerable number of degenerated fibers from the lesion, regarded as coming largely, if not exclusively, from the lateral cervical nucleus, cross the midline through the anterior white commissure to course ventrally along the contralateral border of the anterior median fissure. At more rostral levels the degenerated fibers are seen to cross the midline among the fiber bundles of the most caudal part of the pyramidal decussation and run ventrally along the lateral edge of the uncrossed pyramidal tract of the opposite side. As passing rostrally the crossed degenerated fibers migrate ventrally.

Text-fig. 4. Projection drawings of representative transverse section through the first cervical cord and lowermost medulla oblongata of cat 3. Nauta-Gygax method.
and somewhat laterally to reach the ventral periphery of the anterior funiculus. They then assume a position dorsolateral and lateral to the pyramid of the medulla oblongata. As the medial accessory olive appears, most of the degenerated fibers are found around this nucleus, though some fibers pass through it. More rostrally the degenerated fibers are concentrated between the medial accessory, dorsal accessory and main olives and just lateral to these nuclei. It should be mentioned that the spinothalamic tract does not appear to send fibers to the inferior olivary complex. Very small groups of degenerated axons and some degenerated beads found within this complex are regarded as fibers of passage. At rostral levels of the inferior olivary complex, the majority of the degenerated fibers are assembled lateral to it.

As the nucleus of the facial nerve appears, the degenerated spinothalamic fibers are concentrated in the area of a transverse oval between the facial nucleus and the pyramid. Although a few fibers enter the lateral paragigantocellular nucleus, no fibers can be traced into the facial nucleus. At superior olivary levels the spinothalamic fibers are seen in the lateral part of the trapezoid body as an oblique oval mass of degenerated fibers, whose ventrolateral extremity reaches near the brain surface. In the section through the root of abducens nerve they are found around the ventral part of this root. At these levels no fibers are distributed to the superior olivary nucleus and the medial trapezoid nucleus.

In the lower pons the degenerated spinothalamic fibers are found just ventromedial to the medial trapezoid nucleus, where only a few degenerated beads are found. As passing rostrally they are accumulated in the lateral part of the medial lemniscus which forms a transversely elongated mass of fibers. Most of them are restricted to the medial lemniscus, but very few fibers exceed the boundaries of the medial lemniscus to spread around it.

At lower inferior collicular levels some of the degenerated spinothalamic fibers extend dorsolaterally to reach the ventral part of inferior colliculus by way of the lateral lemniscus, and only very few fibers are directed to the reticular formation and the central gray substance. As the middle level of the inferior colliculus is reached, the degenerated fibers entering the inferior colliculus increase in amount. A few fibers swing dorsomedially to enter the central gray through the reticular formation where scarcely any preterminals are found.

In sections through the superior colliculus most of the degenerated spinothalamic fibers are accumulated in the dorsal part of the medial
Text-fig. 5. Projection drawings of representative transverse sections through the medulla oblongata and pons of cat 3. Nauta-Gygax method.
lemniscus. Some fibers spread dorsally to the superior colliculus (stratum opticum and stratum griseum medium), and dorsomedially to the central gray substance by way of the dorsolateral part of the reticular formation where very few fibers appear to terminate. In addition, extremely few fibers are seen crossing the midline through the commissure of the superior colliculus. More rostrally some fibers begin to spread laterally to enter the magnocellular part of the medial geniculate body. It is of interest to note that these fibers are relatively more numerous than those found in the superior colliculus and the central gray.

At levels of the posterior commissure the degenerated spinothalamic fibers are concentrated in the region just ventromedial to the medial geniculate body. They are distributed to the magnocellular part of the medial geniculate body, the pretectal region, the reticular formation and the central gray substance. The degenerated fibers found in the reticular formation are regarded largely as fibers of passage, though some fibers appear to terminate there. Within the pretectal region degenerated fibers are seen to spread extensively into the pretectal nucleus and the nuclei of the posterior commissure. It should be mentioned that very few fibers enter the posterior commissure to cross to the contralateral side, but their farther course cannot be followed definitely.

As the habenular commissure is reached, many degenerated spinothalamic fibers course rostrilaterally to enter the posterolateral and posteromedial ventral nuclei, the suprageniculate nucleus and the magnocellular part of the medial geniculate body. Some fibers spread into the thalamic fasciculus, the zona incerta and the subthalamic nucleus. Other fibers, as passing rostrally, take a dorsal course to be distributed to the parafascicular and centre médian nuclei.

At more rostral levels the degenerated fibers divide clearly into two groups: fibers to the ventral nuclei and those to the intralaminar and related nuclei. Within the ventral nuclei degenerated fibers are found in the posterolateral ventral nucleus and the adjacent part of the posteromedial ventral nucleus, both of which contains many preterminal axons and some fibers of passage. A few degenerated fibers are also present in the thalamic reticular nucleus and the zona incerta. On the other hand, some of the degenerated fibers in the parafascicular and centre médian nuclei pass farther rostrally to enter the lateral central nucleus. In the paracentral nucleus only a few degenerated fibers are scattered. Very few degenerated beaded axons are found in the medial central nucleus, but it is uncertain whether
Text-fig. 6. Projection drawings of representative transverse sections through the mesencephalon and diencephalon of cat 3. Nauta-Gygax method.
they actually terminate there. It is of interest to note that a few
degenerated fibers enter the lateralmost part of the dorsomedial
nucleus adjacent to the lateral central nucleus.

As passing rostrally the degenerated fibers in both ventral and
intralaminar nuclei gradually decrease in amount. After the disap-
ppearance of the posteromedial ventral nucleus, a limited number of
degenerated fibers are found in the posterolateral ventral nucleus,
particularly its lateral part, the rostral pole of which, however,
contains scarcely any degenerated fibers. At these levels only a few
degenerated fibers are scattered in the lateral central nucleus, but
hardly any degeneration is found in the paracentral nucleus. In this
case no degenerated fibers are seen in the lateral ventral nucleus
unlike cat 1.

The spinothalamic tract on the operated side is slightly degene-
rated, while the spinoreticular tract is severely affected. This may
be due to the fact that the lesion is placed mainly in the lateral
funiculus, involving a small portion of the anterior funiculus. In
the upper mesencephalon very few degenerated fibers are found in
the superior colliculus and the central gray. Within the dorsal
thalamus some degenerated fibers are found in the ventral nuclei,
and the intralaminar and related nuclei as in cat 1. However, the
latter nuclei possess fewer degenerated fibers than do the former
nuclei. The fibers found in the mesencephalon and thalamus on the
operated side are considered to be derived at least in part from
recrossed fibers through the posterior commissure and the commis-
sure of the superior colliculus.

Discussion

The spinothalamic tract has been studied by numerous early
workers, using various mammals, particularly the rabbit, monkey
and man (Tooth, '92; Mott, '92, '95; Quensel, '98; Wallenberg, '99, '00; Kohnstamm, '00; Thiele and Horsley, '01;
Henneberg, '01; Collier and Buzzard, '03). In carnivores
Probst ('00) traced degeneration to the anterior ventral nucleus
of the thalamus following cervical cordotomy by the Marchi method.
However, later workers have failed to demonstrate the spinothalamic
tract in carnivores, particularly in the cat (Chang and Ruch, '47;
Morin et al., '52; Beusekom, '55). Recent studies using the
silver methods could trace this tract to the thalamus also in the cat
(Getz, '52; Nauta and Kuypers, '58; Anderson and Berry,
Getz demonstrated the direct spinothalamic tract in the cat by means of the Glees method, which was not able to give a description of the course of this tract. Later studies using the Nauta method succeeded in tracing the course and termination of the cat spinothalamic tract. In addition, these studies clarified the projection of the spinothalamic tract not only to the ventral thalamic nuclei, but also to the diffuse thalamic projection system. Recent studies using the evoked potential method also revealed the existence of the spinothalamic tract in the cat (Mountcastle and Henneman, '49; Berry et al., '50).

There has been much discussion concerning the origin of the spinothalamic tract in the cat. It was formerly said that this tract arises in the dorsal horn, which receives dorsal root fibers at various cord levels as in primates. Recently, however, it has been known that the spinothalamic tract is difficult to demonstrate, if the spinal cord is cut at levels caudal to the upper cervical segment. Morin and Thomas ('55) revealed that no spinothalamic fibers are found in the cat following lesions caudal to C2, that lesions of the dorsal cord quadrants at C1-C2 destroying the lateral cervical nucleus result in degeneration of dorsolateral part of the opposite medial lemniscus ending in the lateral part of the ventrolateral thalamic nucleus, and that lesions of the medial lemniscus are followed by chromatolysis of the opposite lateral cervical nucleus. They concluded that the lateral cervical nucleus is regarded as the origin of the spinothalamic tract in the cat. Seki ('62) and Terada ('60) agreed with Morin and Thomas. Cat 3 of our cases with the lesion involving the lateral cervical nucleus also confirms the results of Morin and Thomas, but it cannot be decided whether the spinothalamic fibers arise exclusively in the lateral cervical nucleus. Anderson and Berry ('59) demonstrated the degeneration in the thalamus following upper thoracic cordotomy. This indicates that there might be some spinothalamic fibers originating from the thoracic or lower cord levels as seen in primates. However, nothing can be said concerning the spinothalamic fibers arising in spinal regions other than the lateral cervical nucleus from our cases.

The spinothalamic tract is related closely to the spino-olivary and spinoreticular tracts particularly at spinal and inferior medullary levels. Therefore, our cases of anterolateral cervical cordotomy (cats 1 and 2) cannot reveal the isolate course of the spinothalamic tract at lower levels. However, our case of destruction of the lateral cervical nucleus (cat 3) can demonstrate the relatively isolated course of this
An Experimental-Anatomical Study on the Spinothalamic Tract in the Cat

There is a diversity of opinion as to whether collaterals from the spinothalamic tract are distributed to the inferior olivary complex. Our results from cat 3 indicate that this tract send no fibers to the inferior olivary complex.

Wallenberg ('00) divided the ascending fibers from the spinal cord into a dorsal and a ventral group. The former may correspond to the spinothalamic tract, and the latter to the spinoreticular tract. Nauta and Kuypers ('58) distinguished between the dorsal and ventral groups, and designated them as the classical spinothalamic tract and the diffuse tegmental pathway respectively. Anderson and Berry ('59) did not differentiate between these groups. They named these long ascending fibers the lateral tracts and described their course and branching within the brain stem in detail. According to them, the lateral tracts send fibers to the reticular formation, as they ascend through the medulla oblongata and pons. After sending spinotectal fibers to the superior colliculus, the main mass of the lateral tracts ends in the posterolateral ventral nucleus, while the medial spinothalamic tract from the lateral tracts are distributed to the intralaminar nuclei.

There has been much discussion concerning the collaterals of the spinothalamic tract to the reticular formation of the brain stem. Our results reveal that the spinothalamic tract sends scarcely any fibers to the reticular formation of the medulla oblongata and pons, excepting a few fibers spreading laterally to the lateral paragiantocellular nucleus and medial trapezoid nucleus. In the pons only very few spinothalamic fibers are seen to spread ventrally to the lateral pontine nucleus. Anderson and Berry ('59) also observed preterminal degeneration in the lateral part of the rostral pontine nuclei. The facial nucleus has been said to receive fibers from both spinothalamic and spinocerebellar tracts (Nauta and Kuypers, '58). Our results indicate that the former tract does not send fibers to the facial nucleus.

At midbrain levels the degenerated spinoreticular fibers decrease markedly in number, while the diverging fibers from the spinothalamic tract increase. It is evident by a comparison of cat 1 with cat 3 that the fibers directed to the superior and inferior colliculi come solely from the spinothalamic tract. Nauta and Kuypers ('58), however, stated that the tectum receives some fibers also from the diffuse tegmental pathway. In the present study the central gray and reticular formation are seen to receive fibers from both spinothalamic and spinoreticular tracts at inferior collicular levels. As passing rostrally, they receive more fibers from the spinothalamic
tract, and at rostral levels of the superior colliculus they receive no fibers from the spinoreticular tract. This differs from the results of Nauta and Kuypers ('58), who regarded the degenerated fibers in the central gray and the mesencephalic reticular formation as coming from the spinoreticular tract.

According to our results, some spinothalamic fibers spread laterally into the magnocellular part of the medial geniculate body. This was already observed by Lewandowsky ('04). Nauta and Kuypers ('58) stated that the first signs of termination of the classical spinothalamic pathway appear in the region immediately adjoining the medial aspect of the medial geniculate body, apparently including a small medial part of the latter's magnocellular nucleus. Bowsher ('61) found preterminal degeneration in the magnocellular and supra-

Table 1. Summary of terminal axon degeneration of the spinothalamic tract.

<table>
<thead>
<tr>
<th>Mesencephalon</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Substantia grisea centralis</td>
<td>+</td>
</tr>
<tr>
<td>Formatio reticularis mesencephali</td>
<td>±</td>
</tr>
<tr>
<td>Colliculus superior</td>
<td>#</td>
</tr>
<tr>
<td>Colliculus inferior</td>
<td>+</td>
</tr>
<tr>
<td>Substantia nigra</td>
<td>±?</td>
</tr>
<tr>
<td>Nucleus ruber</td>
<td>−</td>
</tr>
<tr>
<td>Diencephalon</td>
<td></td>
</tr>
<tr>
<td>Nucleus medialis dorsalis</td>
<td>±</td>
</tr>
<tr>
<td>Centre médian nucleus</td>
<td>#</td>
</tr>
<tr>
<td>Nucleus parafascicularis</td>
<td>#</td>
</tr>
<tr>
<td>Nucleus centralis lateralis pars anterior</td>
<td>+</td>
</tr>
<tr>
<td>Nucleus centralis lateralis pars posterior</td>
<td>±</td>
</tr>
<tr>
<td>Nucleus paracentralis</td>
<td>±</td>
</tr>
<tr>
<td>Nucleus centralis medialis</td>
<td>±?</td>
</tr>
<tr>
<td>Nucleus ventralis medialis</td>
<td>−(+)</td>
</tr>
<tr>
<td>Nucleus ventralis lateralis</td>
<td>±</td>
</tr>
<tr>
<td>Nucleus ventralis posteromedialis</td>
<td>+(+)</td>
</tr>
<tr>
<td>Nucleus ventralis posterolateralis</td>
<td>#</td>
</tr>
<tr>
<td>Nucleus suprageniculatus</td>
<td>±</td>
</tr>
<tr>
<td>Corpus geniculatum mediale pars magnocellularis</td>
<td>+</td>
</tr>
<tr>
<td>Nucleus pretectalis</td>
<td>±</td>
</tr>
<tr>
<td>Nuclei commissurae posteriors</td>
<td>±</td>
</tr>
<tr>
<td>Nucleus reticularis thalami</td>
<td>±</td>
</tr>
<tr>
<td>Zona incertae</td>
<td>±(+)</td>
</tr>
<tr>
<td>Nucleus subthalamicus</td>
<td>±</td>
</tr>
</tbody>
</table>

The following signs indicate the presence or absence of terminal axons: −, absent; ±?, doubtful; ±, very small amount; +, small amount; #, moderate amount; ##, large amount. The plus sign in parenthesis (+) represents the presence of degenerating fibers of passage, and +(+) means the presence of both terminal axons and fibers of passage.
geniculate subnuclei of the medial geniculate complex in the monkey. It has long been known that the spinothalamic tract ends in the ventral thalamic nuclei. Recent studies further revealed that it terminates in the posterolateral ventral nucleus (Getz, '52; Anderson and Berry, '59). In addition to this nucleus, the lateral part of the posteromedial ventral nucleus was described as the terminal region of the spinothalamic tract (Nauta and Kuypers, '58). The present study indicates that the spinothalamic fibers continue farther rostrally to the ventrolateral part of the lateral ventral nucleus. There have been no authors who described the degeneration in this nucleus following cordotomy. However, Chang and Ruch ('47) depicted the degeneration in the ventrolateral part of the lateral ventral nucleus in text-fig. 3. The somatotopic organization of the spinal fibers within the ventral thalamic nuclei was originally suggested by Wallenberg ('00), and more recently by Clark ('36) and Walker ('37, '38). The findings of these authors were confirmed and expanded by Chang and Ruch ('47), who stated that in the spider monkey the spinothalamic fibers terminate exclusively in the posterolateral ventral nucleus in a laminated fashion, so that fibers 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 lamina of this nucleus. Mehler et al. ('60) also obtained similar results in the rhesus monkey and described the parcellated distribution of spinothalamic terminals in the posterolateral ventral nucleus. However, such a pattern of termination cannot be demonstrated in the cat. Anderson and Berry ('59) observed in the cat that spinothalamic fibers interrupted at upper thoracic levels projected only to the most caudal and lateral aspect of the posterolateral ventral nucleus, whereas interruption at upper cervical levels produces degeneration rostrally through the entire nucleus. However, nothing can be said concerning this problem from our cases.

The termination in the intralaminar nuclei of the spinothalamic tract has been described by many authors. Cajal ('11) observed the fibers from the medial lemniscus and the secondary tract of the trigeminal nerve projecting to the nuclei in the caudal internal medullary lamina. Río ('31) described such a group of fibers as a medial division of the medial lemniscus. Getz ('52), using the Glees method, found degeneration in the lateral central and paracentral nuclei following cordotomy. According to Nauta and Kuypers ('58), the diffuse spinal pathway bifurcates abruptly into an
intrathalamic and a subthalamic fiber system, as the termination of
the classical spinothalamic tract in the ventral thalamic nucleus
appears. The intrathalamic fiber group turns steeply dorsalward
and enters the parafascicular nucleus-centromedian complex. A n d e r-
s o n and B e r r y ( ' 5 9 ) also found degeneration in various intra-
 laminar nuclei.

Within the parafascicular nucleus the degeneration of spinal fibers
was observed by N a u t a and K u y p e r s ( ' 5 8 ) , and A n d e r s o n
and B e r r y ( ' 5 9 ) in accordance with our results. However, G e t z
( ' 5 2 ) failed to demonstrate degeneration in the parafascicular
nucleus. In the monkey M e h l e r et al. ( ' 6 0 ) and B o w s h e r ( ' 6 1 )
traced spinothalamic fibers to this nucleus. The projection of the
spinothalamic tract to the centre médian nucleus was described in
the cat by N a u t a and K u y p e r s , A n d e r s o n and B e r r y , and
T e r a d a ( ' 6 0 ) . However, M e h l e r et al. and B o w s h e r , using
the monkey, failed to demonstrate degeneration in the centre médian
nucleus. According to A n d e r s o n and B e r r y ' s description, the
degeneration in the lateral part of the internal medullary lamina
(presumably the centre médian nucleus) is denser than that in more
medial parafascicular nucleus. The present findings also reveal such
a tendency.

G e t z ( ' 5 2 ) , and N a u t a and K u y p e r s ( ' 5 8 ) produced degene-
ration in the lateral central and paracentral nuclei following cordotomy
in the cat. A n d e r s o n and B e r r y ( ' 5 9 ) observed degeneration in
the lateral central nucleus only in cases of cervical cordotomy. In
the monkey M e h l e r et al. ( ' 6 0 ) and B o w s h e r ( ' 6 1 ) could trace
spinal fibers to these intralaminar nuclei. Our results also confirm
those of the above authors. It has been denied by most authors
that the medial central nucleus receives spinothalamic fibers. Ac-
cording to our results, only very few beads are found in this
nucleus, but it is difficult to decide whether they actually terminate
there.

There is a diversity of opinion as to whether the degenerated
fibers seen in the intralaminar and related nuclei are derived from the
(classical) spinothalamic tract or from the spinoreticular tract (diffuse
spinal pathway). N a u t a and K u y p e r s ( ' 5 8 ) stated that the classical
spinothalamic tract terminates in the ventral thalamic nucleus, while
the diffuse spinal pathway continues into the parafascicular nucleus-
centromedian complex, and that the diencephalic distribution areas
of these two pathways appear to overlap to a certain extent. On the
contrary, A n d e r s o n and B e r r y ( ' 5 9 ) stated that after diverging
from the ventrolateral tract (spinothalamic tract) the medial spinothalamic fibers course through the central tegmental fasciculus into the intralaminar nuclei. Our results appear to give strong support to Anderson and Berry's view. However, the possibility cannot be excluded that a few spinoreticular fibers may enter the intralaminar and related nuclei.

Only a few authors observed degeneration in the lateral part of the dorsomedial nucleus of the thalamus (Anderson and Berry, Mehler et al.). The present study confirms their findings. Getz ('52) found terminal degeneration in the posterior part of the lateral nucleus. However, our experiments give negative results. In all of our cases slight degeneration is found in the suprageniculate nucleus. Bowsher ('61) observed some preterminal degeneration in the suprageniculate subnucleus of the medial geniculate complex following anterolateral cordotomy in the monkey.

Getz ('52) observed degeneration in the thalamic reticular nucleus of the cat following cordotomy by the Glees method. Bowsher ('57, '61) found a few scattered degenerated fibers within the reticular nucleus in the monkey and man. The present study reveals that very few fibers from the cervical cord appear to terminate in the ventromedial part of the reticular nucleus. Anderson and Berry, and Mehler et al. failed to find any degeneration in this nucleus.

Nauta and Kuypers ('58) described the subthalamic component as a continuation of the diffuse spinal pathway. Anderson and Berry ('59) found degeneration in the lateral hypothalamus and the subthalamus. In our cases some spinothalamic fibers are seen to enter the subthalamic nucleus and the zona incerta. Extremely few beads are found in the substantia nigra, but nothing definite can be stated concerning their termination in this center.

Although the majority of spinothalamic fibers are crossed at spinal levels, it appears likely that a certain proportion are uncrossed in the cat as in primates. However, our results cannot demonstrate these fibers definitely, because the lesion is not limited to the lateral cervical nucleus in cat 3. Chang and Ruch ('47) reported the recrossing of the spinothalamic fibers through the dorsal part of the posterior commissure in the spider monkey. According to findings of Mehler et al. ('60), decussating fibers of spinal origin are observed at medullary levels, particularly at the level of the pars oralis of the gigantocellular nucleus. Other decussating fibers are also found in the tectal and posterior commissures. Bowsher ('61) also con-
firmed the crossing of the spinothalamic fibers through the posterior commissure and at lower levels. In carnivores, Probst ('00) reported the crossing of the spinothalamic tract through the posterior commissure. Anderson and Berry ('59) also noted the crossing in the posterior commissure in the cat. In the present experiments a few fibers are seen to cross the midline through the posterior commissure and commissure of the superior colliculus.

In humans the lateral and ventral spinothalamic tracts have been described. It cannot be stated definitely which tract corresponds to the spinothalamic tract in the cat. However, it appears likely that the lateral spinothalamic tract corresponds to the spinothalamic tract in the cat, and the ventral spinothalamic tract is comparable to the cat spinoreticular tract. On the contrary, Kuru ('49) stated that the spinothalamic tract found in animals may correspond to the ventromedial (ventral) spinothalamic tract of man. Considerable doubt exists in the literature as to the course and termination of the human spinothalamic tract, particularly at levels rostral to the midbrain, so that it is difficult to compare the spinothalamic tract of the cat with that of man with sufficient accuracy.

In the cat the spinothalamic fibers are considered to originate largely, if not exclusively, in the lateral cervical nucleus, unlike the primates. Therefore, a number of ascending fibers from various levels of the spinal cord may relay in the lateral cervical nucleus to the spinothalamic tract. Anderson and Berry ('59) demonstrated degenerated spinothalamic fibers following upper thoracic cordotomy in the cat. If so, the spinothalamic tract would also contain some direct fibers from lower spinal levels as in primates.

**Summary**

The spinothalamic tract in the cat is considered to arise largely, if not exclusively, in the lateral cervical nucleus. After crossing the anterior white commissure it ascends in the anterolateral funiculus of the upper cervical cord to lie dorsolateral to the pyramid of the medulla oblongata. As the inferior olivary complex appears, it gradually shifts laterally. It should be mentioned that the spinothalamic tract does not appear to send fibers to the inferior olivary complex.

At pontine levels the spinothalamic tract ascends in the lateral part of the medial lemniscus. It sends scarcely any fibers to the reticular formation and certain nuclei of the medulla oblongata and
pons, but only a few of its fibers enter the lateral paragigantocellular nucleus, the medial trapezoid nucleus and the pontine nuclei, particularly the dorsal part of the lateral pontine nucleus.

In the midbrain a marked branching of the spinothalamic tract is observed. This tract sends fibers to the magnocellular part of the medial geniculate body, the superior and inferior colliculi, the pretectal nucleus and the nuclei of the posterior commissure. A small number of its fibers spread dorsomedially to enter the central gray substance through the reticular formation in which only a few fibers appear to terminate at superior collicular levels. It is of interest to note that very few fibers cross through the posterior commissure and commissure of the superior colliculus.

The main terminal area of the spinothalamic fibers in the dorsal thalamus is the ventral nuclei. The majority of these fibers end in the posterolateral ventral nucleus, the adjacent portion of the posteromedial ventral nucleus and the ventrolateral part of the lateral ventral nucleus. A considerable number of spinothalamic fibers are distributed to the intralaminar and related thalamic nuclei, that is, the centre médian nucleus, the parafascicular nucleus, the lateral central nucleus, the paracentral nucleus, the dorsomedial nucleus and the suprageniculate nucleus. In addition to the dorsal thalamic distribution, some fibers enter the zona incerta, the subthalamic nucleus, and only very few fibers appear to terminate in the ventromedial part of the thalamic reticular nucleus.

The spinoreticular tract ascends through the reticular formation of the medulla oblongata and pons, sending fibers to the reticular formation, including the lateral reticular nucleus, and some nuclei of the cranial nerves. At upper pontine levels its fibers decrease markedly in number, and are scarce in inferior collicular levels. However, the possibility cannot be excluded that a few spinoreticular fibers enter the intralaminar and related nuclei.

This work was aided by grants from the Ministry of Education for Scientific Research, for which the authors wish here to express their deepest thanks.

References


---


Marburg, O.: Zur Frage des “Anterolateral-Tractes” von Gowers (Tractus spino-
An Experimental-Anatomical Study on the Spinothalamic Tract in the Cat 279


Mott, F. W.: Experimental injury upon the afferent tracts of the central nervous system of the monkey. Brain, 18, 1–20, 1895.


280 N. Niimi, S. Fujita, K. Abe and S. Kawamura


Abbreviations

A, Nucleus ambiguus
Bc, Brachium conjunctivum
Bp, Brachium pontis
C, Nucleus cuneatus
Ca, Commissura anterior alba
Cci, Commissura colliculi inferioris
Ccs, Commissura colliculi superioris
Ce, Nucleus cuneatus externus
Cem, Centre médian nucleus
Cgl, Corpus geniculatum laterale
Cgm, Corpus geniculatum mediale
Cl, Colliculus inferior
Cl, Nucleus centralis lateralis
Cm, Nucleus centralis medialis
Cp, Commissura posterior
Cr, Corpus restiforme
Cs, Colliculus superior
Dp, Decussatio pyramidum
Dv, Nucleus dorsalis n. vagi
F, Nucleus n. facialis
Fim, Fasciculus longitudinalis medialis
Flp, Fasciculi longitudinales pontis
Fr, Formatio reticularis
Hg, Nucleus n. hypoglossi
Ic, Nucleus intercalatus
Ll, Lemniscus lateralis
Lm, Lemniscus medialis
Lp, Nucleus lateralis posterior
Md, Nucleus medialis dorsalis
Ncp, Nuclei commissurae posterioris
Npl, Nucleus pontis lateralis
Nsp, Nucleus tractus spinalis n. trigemini

Oc, Nucleus n. oculomotorii
Od, Nucleus olivaris accessorius dorsalis
Om, Nucleus olivaris accessorius medialis
Op, Nucleus olivaris principalis
Os, Nucleus olivaris superior
Pc, Nucleus paracentralis
Pdc, Pedunculus cerebri
Pf, Nucleus parafascicularis
Pgl, Nucleus paragigantocellularis lateralis
Ph, Nucleus prepositus hypoglossi
Pr, Nucleus pretectalis
Py, Pyramis medullae oblongatae
R, Nucleus ruber
Rl, Nucleus reticularis lateralis
Rt, Nucleus reticularis thalami
Sg, Nucleus suprageniculatus
Sgc, Substantia grisea centralis
Sm, Nucleus submedius
Sn, Substantia nigra
So, Nucleus tractus solitarii
Sth, Nucleus subthalamicus
Tm, Nucleus trapezoidalis medialis
Tsp, Tractus spinalis n. trigemini
Ve, Nucleus vestibularis inferior
Ve, Nucleus vestibularis lateralis
Vem, Nucleus vestibularis medialis
Vi, Nucleus ventralis lateralis
Vm, Nucleus ventralis medialis
Vpl, Nucleus ventralis posterolateralis
Vpm, Nucleus ventralis posteromedialis
Zi, Zona incerta
Explanation of Plate

All figures are photomicrographs from transverse sections through the brain stem of the cat. Nauta-Gygax method. ×400.

1. Inferior colliculus of the operated side. Cat 1.
2. Pretectal nucleus of the side opposite to the lesion. Cat 3.
3. Magnocellular part of the medial geniculate body of the operated side. Cat 1.
7. Dorsomedial nucleus of the side opposite to the lesion. Cat 3.
9. Thalamic reticular nucleus of the side opposite to the lesion. Cat 3.