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SPINAL PROJECTIONS OF THE DORSAL ROOT FIBERS IN THE CAT

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INDEXING WORDS

dorsal root; projection; spinal cord; rostrocaudal extent

SYNOPSIS

This report focuses on the less well-known rostrocaudal extents of terminal field of the dorsal root. For this purpose, the degenerating fibers originating from the dorsal rhizotomy were traced by using Nauta-Gygax and other silver impregnation methods. The rostrocaudal extent of the terminal field in the posteromarginal nucleus is 1 segment in each direction, that in the proper sensory nucleus is 2-3 segments in each direction, and that in the intermediomedial nucleus and in the medial motor cell group is 3-4 segments in each direction. Descending branches of the lower cervical roots project to the rostral part of the thoracic nucleus through the dorsolateral fiber plexus. The rostrocaudal extent of terminal field of each root in the centrobasal nucleus and its lateral motor cell group is different depending upon the entering level into the intumescences; namely, the extent of the dorsal root which enters the caudal part of the intumescences extends more caudally than rostrally and that of the dorsal root which enters the caudal part extends more rostrally than caudally.

INTRODUCTION

This report attempts to summarize some of our findings on the projection of the dorsal root throughout the spinal cord in the cat.[9, 30, 34)]

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Although many authors reported in detail on the projection site of the dorsal root by means of the Golgi method,[26, 29] the degeneration method,[11, 12, 18, 27, 28] the HRP method[1, 2, 13] and the autoradiographic method,[15, 23] there are only a few reports which describe the rostrocaudal extent of the terminal field. We tried to investigate the spinal projection of the dorsal root with special attention to the rostrocaudal extent of the terminal site. The receptive organization of the spinal cord for primary afferents was also examined.

MATERIALS AND METHODS

In the present study, 30 healthy adult cats anesthetized by intraperitoneal injection of sodium pentobarbital (40–50 mg/Kg) were used. Every dorsal root of cervical, thoracic, and lumbosacral levels were rhizotomized by the aid of surgical microscope. Namely, the dorsal root was exposed by laminectomy and each of the rootlets were severed with microsurgical scissors at the proximal side of the spinal ganglion. After the 5th to 12th surgical day the animal was deeply anesthetized and sacrificed by means of intravascular perfusion of physiological saline followed by 10% formalin. The brain and entire spinal cord were removed. After the fixation in 10% formalin for periods ranging from 1–4 months, they were embedded in 25% gelatine and serially sectioned at 40 μm thickness in transverse plane on a freezing microtome. Every fifth section of the spinal cord was stained by Nauta-Gygax,[17] Ebbesson-Heimer,[5] and other silver impregnation methods.[4, 6, 32] The degenerated dorsal root fibers were depicted by using microprojector (Table 1).

RESULTS

(A) PROJECTION PATHWAYS IN THE SPINAL CORD.

1. The transverse course at the level of entrance.

Most of the dorsal root fibers enter the dorsal column, but a few of them directly enter Lissauer's tract and terminate in lamina I. The dorsal root fibers which enter the dorsal column pass ventrally through laminae I and II as thick fiber bundles and enter the posterior horn. Many of them course ventrally toward the intermediate zone, but a part of them curve dorsolaterally to terminate in laminae III and IV. The dorsal root fibers which enter the intermediate zone form a dense fiber

Table 1. Experimental materials investigated in this study.

Root Cut	Survival days	Fixation period	Impregnation method
C-1	7	2-M	N-G
C-2	6	3-M	N-G, E-H
C-2	7	3-M	N-G
C-3	7	4-M	N-G
C-4	7	2-M	N-G
C-5	7	3-M	N-G
C-6	7	2-M	N-G, E-H
C-7	7	2-M	N-G
C-8	7	3-M	N-G
T-1	7	2-M	N-G
T-1	7	2-M	N-G
T-2	7	1-M	N-G
T-3	7	2-M	N-G
T-4	7	2-M	N-G
T-5	7	3-M	N-G
T-5	7	2-M	N-G
T-6	7	2-M	N-G
T-7	7	2-M	N-G, E-H
T-8	7	2-M	N-G
T-9	7	2-M	N-G
T-10	7	2-M	N-G
T-10	7	2-M	N-G
T-11	7	2-M	N-G
T-12	7	2-M	N-G
T-13	7	2-M	N-G,
T-13	7	2-M	N-G, F-H(I)
L-1	8	2-M	N-G,
L-2	7	1-M	N-G, W
L-3	11	2-M	N-G, F-H(II)
L-4	4	2-M	N-G, F-H(II), E
L-5	7	3-M	N-G, E-H
L-6	7	1-M	N-G
L-7	7	2-M	N-G, E-H
S-1	7	3-M	N-G
S-2	8	3-M	N-G, E-H
S-3	7	3-M	N-G, E-H

Abbreviations

E : Eager, E-H : Ebbesson-Heimer, F-H(I) : Fink-Heimer I, F-H(II) : Fink-Heimer II, N-G : Nauta-Gygax, W : Wiitanen.

plexus in the central part of lamina VI, but it also extends to the centroventral part of lamina V and the centrodorsal part of lamina VII. This plexus is called the dorsolateral (DL) plexus and corresponds to Imai and Kusama's[12] dorsolateral preterminal fiber plexus. This fiber plexus sends terminals to several parts of the spinal gray : the thoracic nucleus, the centrobasal nucleus, and the lateral part of the anterior horn. The plexus also sends fibers to the ventrolateral region of the central canal to form a plexus which is called the ventromedial (VM) fiber plexus and corresponds to Imai and Kusama's[12] ventromedial preterminal fiber plexus. The VM fiber plexus sends the terminal to the intermediomedial nucleus, the central cervical nucleus and the medial part of the anterior horn (Figs. 1 and 2).

2. The ascending and descending courses in the spinal cord.

Fibers in the already-mentioned tracts and plexuses, the dorsal column, Lissauer's tract, and the DL and VM plexuses, bifurcate into ascending and descending branches. The ascending and descending branches pass through 1 or 2 segments in Lissauer's tract. Dorsal root fibers of C1 do not form the DL plexus. Fibers of the DL plexus of the upper cervical roots are scanty in contrast to those of the VM plexus and in many instances the fibers of both plexuses fuse to make single plexus. However, as for the other dorsal roots, each DL plexus exceeds the VM plexus of the same root in its rostrocaudal extent. The rostrocaudal extent of each DL and VM plexuses in the lower cervical and upper thoracic level is larger than that in the other levels. The rostral end of the VM plexus reaches the level of the medulla oblongata. The rostrocaudal extents of these plexuses of the dorsal roots examined in this study are shown in Fig. 3. Ascending branches of every dorsal root in the dorsal column reach the medulla. On the other hand the descending branches in the dorsal column pass only several segments downward.

(B) PROJECTION SITES IN THE SPINAL GRAY AND THEIR ROSTROCAUDAL EXTENTS.

1. Lamina I (posteromarginal nucleus).

Dorsal root fibers of every level except those of C1 enter the nucleus passing through the dorsal column and Lissauer's tract. They generally terminate in the medial or central part of the nucleus, but those of C2 terminate in the whole area of the nucleus when observed in the transverse section. Generally the terminal field of every dorsal root fiber extends one more segment in both rostral and caudal directions from the segment of entrance (Fig. 4).

2. Lamina II (substantia gelatinosa).

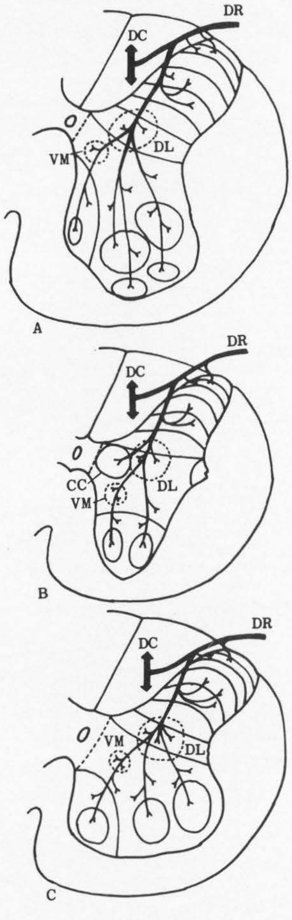

Fig. 1
Schematic representation showing the course and the terminal sites of the dorsal root fibers in the spinal gray.

A : the lower cervical segment.
B : the thoracic and upper lumbar segment.
C : the lower lumbar segment.

Abbreviations
CC : Clarke's column, DC : dorsal column, DL : dorsolateral fiber plexus, DR : dorsal root, VM : ventromedial fiber plexus.

Fig. 2
Photomicrograph representing the dorsolateral and ventromedial fiber plexuses in L7 segment after L7 dorsal root section. (Ebbesson-Heimer technique)

Abbreviations
CC : central canal, DL : dorsolateral fiber plexus, PSN : proper sensory nucleus, VM : ventromedial fiber plexus.

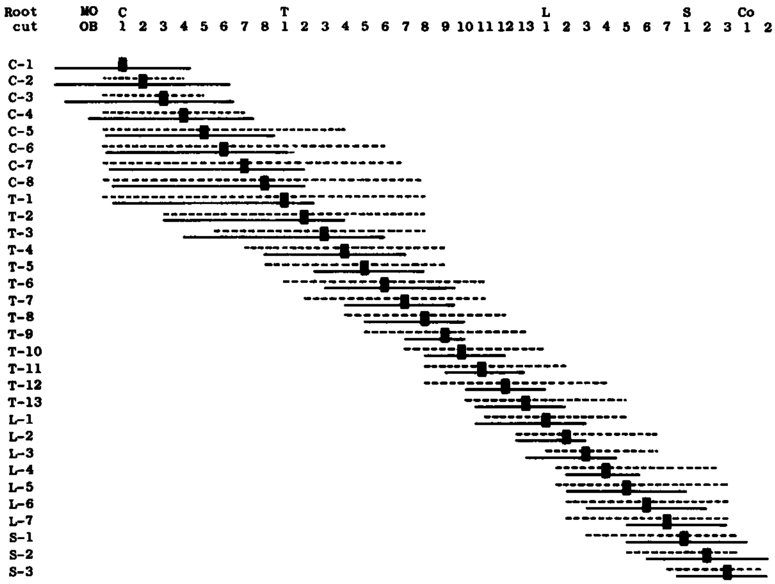

Fig. 3 The rostrocaudal extent of the dorsolateral and ventromedial plexuses.

Levels of the spinal cord and the medulla oblongata are shown on abscissa, and the sectioned dorsal roots are noted on ordinate. Black box, dashed line and broken line indicate entrance segment of the root, dorsolateral plexus and ventromedial plexus, respectively.

Abbreviations
MO : medulla oblongata, OB : obex.

Dorsal root fibers of every level which run ventrally toward the base of the posterior horn and the intermediate zone pass through the medial part of lamina II. But very few dorsal root fibers terminate in this lamina.

3. Laminae III and IV (proper sensory nucleus).

Dorsal root fibers of C3 to S3 terminate in the whole area of the proper sensory nucleus after passing through laminae I and II at the level of rhizotomy. Dorsal root fibers of C1 directly enter the proper sensory nucleus from the dorsal column and terminate in the ventromedial part of this nucleus in the same level. Ascending branches of the dorsal root fibers of C1 to C4 reach the caudal part of the spinal trigeminal nucleus.

In addition to this ipsilateral termination of the proper sensory

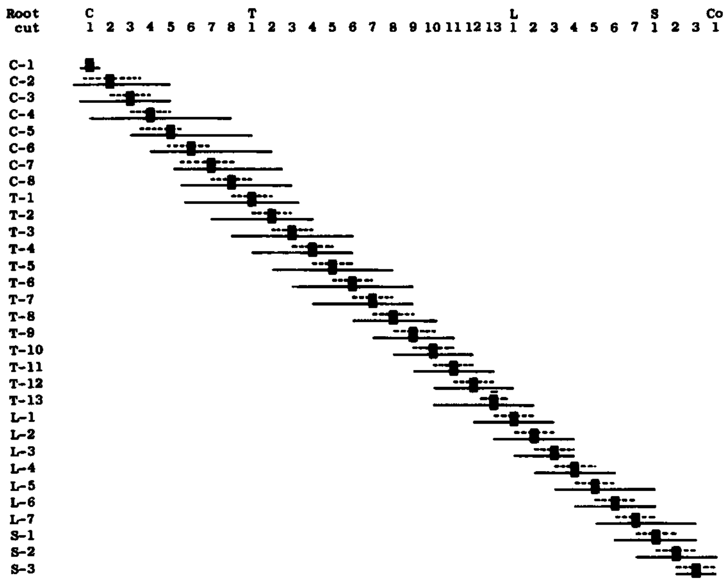

Fig. 4 The rostrocaudal extent of the terminal fields in the posterior horn.

Dashed and broken lines indicate the rostrocaudal extent in the posteromarginal nucleus and proper sensory nucleus, respectively.

nucleus, dorsal root fibers of S3 cross the dorsal gray commissure and terminate contralaterally in the medial part of lamina IV as well as in the neighbouring dorsomedial part of lamina V at the same level. In a similar fashion dorsal root fibers of S2 terminate contralaterally in S2, S3 and Col segments. The distribution area of each dorsal root gradually decreases in a rostrocaudal direction with the increase of distance from its entrance. But a consistent pattern of the decrease of the distribution area does not seem to exist. Generally the terminal field of each dorsal root extends 2–3 segments more in both rostral and caudal directions from the entrance (Fig. 4).

4. Laminae V, VI, and VII.

A. Centrobasal nucleus.

At the level of the C4–T1 and L4–S2 segments the fibers from the DL plexus terminate in the centrobasal nucleus which is located in the central part of laminae V and VI. The rostrocaudal extent of the terminal field of each dorsal root in the centrobasal nucleus is shown in Fig. 5. As shown in the figure, the terminal fields of the dorsal roots which enter

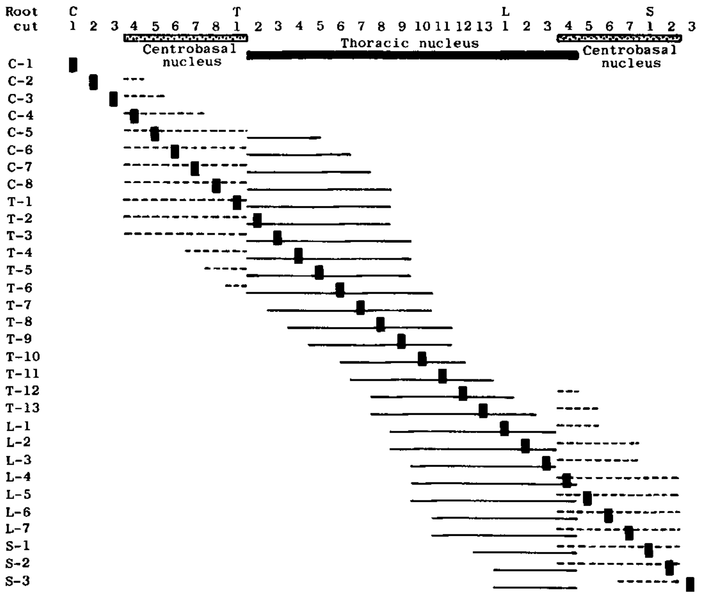

Fig. 5 The rostrocaudal extent of the terminal fields in the centrobasal nucleus and the thoracic nucleus.

Dashed and broken lines indicate the rostrocaudal extent in the thoracic nucleus and the centrobasal nucleus, respectively.

the rostral part of the cervical and lumbar intumescences extend more caudally than rostrally, and those of the dorsal roots which enter the caudal part of the intumescences extend more rostrally than caudally.

B. Thoracic nucleus.

The thoracic nucleus which is located in the medial part of lamina VII from the T2 to L4 segment receives the descending branches of the dorsal root fibers of C5-L4, both ascending and descending branches of the dorsal root fibers of T2-L4 and the ascending branches of the dorsal root fibers of L5-S3 through the DL plexus. The distribution area of the dorsal root fibers arising from the lower thoracic level in this nucleus are greater than that arising from the other levels. The rostrocaudal extent of the terminal field of each dorsal root is shown in Fig. 4. Dorsal root fibers of lower cervical, upper thoracic and upper lumbar segments terminate in the dorsal or lateral part of this nucleus, and dorsal root fibers of lower thoracic, lower lumbar and sacral segments terminate in the whole area of this nucleus when observed in the transverse section (Fig. 6A).

C. Central cervical nucleus and intermediomedial nucleus.

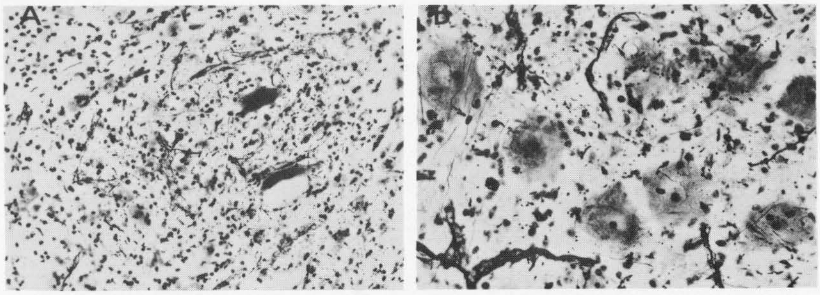

Fig. 6 Photomicrograph representing the degenerating fibers in the thoracic nucleus (A) and the lateral motor cell group (B) after L6 root section. (Nauta-Gygax technique)

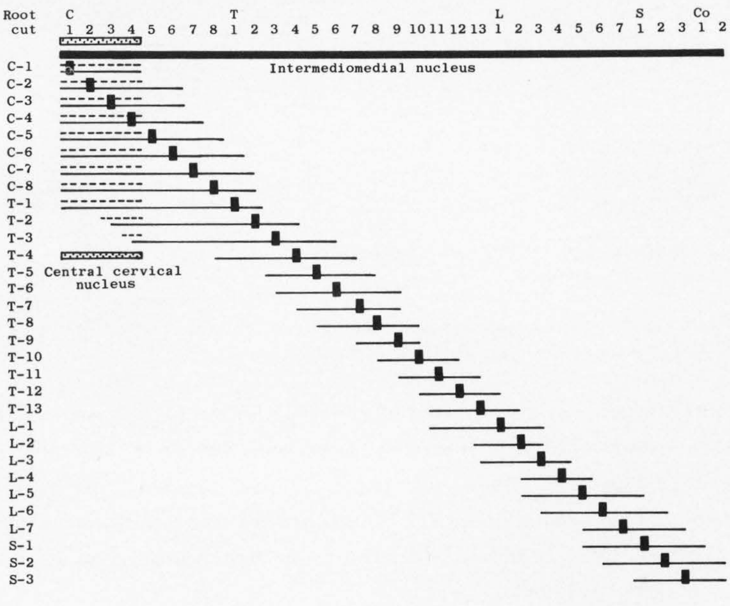

Fig. 7 The rostrocaudal extent of the terminal fields in the intermediomedial nucleus and the central cervical nucleus.

Dashed and broken lines indicate the rostrocaudal extent in the intermediomedial nucleus and the central cervical nucleus, respectively.

The central cervical nucleus exists in C1–C4 segments as a fairly large cell group and the intermediomedial nucleus exists in all segments as a small cell group. Both nuclei lie in the ventromedial part of the intermediate zone and receive the fibers from the VM plexus. In the upper cervical segments where both nuclei exist, it is usually difficult to differentiate the distribution area of the dorsal root fibers in each nucleus. Generally the terminal field of lower thoracic and lumbosacral

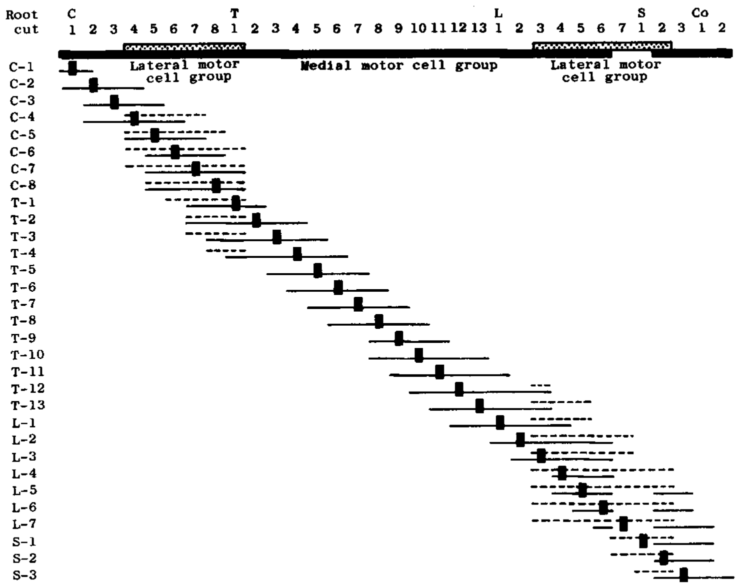

Fig. 8 The rostrocaudal extent of the terminal fields in the motor cell group.

Dashed and broken lines indicate the rostrocaudal extent in each motor cell group.

dorsal roots in the intermediomedial nucleus extends 3-4 segments more in both rostral and caudal directions from the entrance segment (Fig. 7). Dorsal root fibers of C1-T3 terminate in the central cervical nucleus. Among them dorsal roots of C1-T1 terminate in the whole area of the nucleus, but those of T2 and T3 terminate in the caudal part of the nucleus (Fig. 7).

5. Lamina IX (motor cells in the anterior horn).

As it is difficult to assess small quantitative differences of the terminal fibers in various motor cell subgroups, we summarize these subgroups into medial and lateral motor cell groups according to Rexed.[24, 25]

In the upper cervical (C1-C4) segments lamina IX consists of the medial motor cell groups including the spinal accessory nucleus. In the cervical (C4-T1) and lumbar (L3-S1) intumescences it consists of medial and lateral motor cell groups, and in the thoracic and upper lumbar (T2-L2) segments it consists of medial motor cell groups only. The dorsal root fibers not only reach the medial and lateral motor cell groups passing through the VM and DL plexus at the segment of its entrance, but they also reach these cell groups at the segments above and below the entrance segment (Fig. 6B). The dorsal root fibers arising from C1-C4 project to the spinal accessory nucleus. The rostrocaudal extent of the terminal field of each dorsal root is shown in Fig. 8. As shown in the figure, the terminal field in the medial motor cell groups extends 2-3 segments more in both rostral and caudal directions from the segment of entrance. Concerning the lateral motor cell groups, the terminal fields of the dorsal root fibers which enter the spinal cord at the rostral part of the intumescences extend more caudally than rostrally, and the terminal fields of the dorsal root fibers which enter the spinal cord at the caudal part of the intumescences extend more rostrally than caudally. Generally the rostrocaudal extent of the terminal field of the cervical and thoracic dorsal roots is shorter than that of the lumbosacral dorsal roots.

DISCUSSION

The distribution of dorsal root fibers in lamina I has been examined by several investigators by means of various methods.[11, 15, 23, 27, 28, 29] But as far as its rostrocaudal extent is concerned, there are only few reports. Imai[11] reported that dorsal root fibers project to the various parts in lamina I and that these fibers ascend 1-3 segments and also descend 1-3 segments from the level of the rhizotomy. Szentágothai[29] reported that its rostrocaudal extent is only 1 segment in each direction by Golgi method. In our research every dorsal root fiber except those of C1 and C2 project mainly to the medial or central part of lamina I and its rostrocaudal extent is 1 segment in each direction from the entrance segment of the root. Although Rethelyi et al.[23] described the contralateral projection of the dorsal root fibers to lamina I by autoradiographic method, we could not find the contralateral projection.

Whether dorsal root fibers terminate in lamina II or not is inconsistent. Use of Nauta-Gygax method[17] by Imai,[11] Petras,[18] Sterling and Kuypers[28] and of electron microscope by Ralston[20, 21] showed few terminals in lamina II. In contrast, Sprague and Ha[27] and Szentágothai[29] using Nauta-Gygax method,[17] and Heimer and Wall[10] and Rethelyi and Szentágothai[22] using both Fink-Heimer method[6] and electron microscope found terminals of the dorsal root in lamina II.

But in the present study few dorsal root fibers appear to terminate in lamina II even by Fink-Heimer method[6] or by other silver impregnation methods which are considered able to impregnate terminal degenerations. Recently by using the autoradiographic method, LaMotte[15] and Rethelyi et al.[23] reported that the substantia gelatinosa is labeled heavily following the injection of triciated amino acid in the spinal ganglia. These results which are not consistent with ours may be partly due to the difference of survival time in cases of the degeneration study.[23]

Topographic organization of the projecting fibers to laminae III and IV as well as their character of sensation was studied electrophysiologically.[8, 14] By anatomical investigation of the proper sensory nucleus,[12, 28] it was reported that the dorsal roots of rostral segments distribute to the lateral part of this nucleus and the dorsal roots of more caudal segments distribute to the medial part of the nucleus in the cervical cord. Moreover, the results of the investigation of the electrophysiologically identified primary afferent fiber being filled with HRP in the lumbosacral cord support these results.[1] Though in our study the manner of distribution of some dorsal roots fibers coincide with the above-mentioned pattern, we did not find a consistent manner of distribution in the proper sensory nucleus throughout the cord. There is a slight difference in the rostrocaudal extent of the terminal field in the proper sensory nucleus among investigators : 1-2 segments rostrally and 1-3 segments caudally,[11] 1-2 segments in each direction,[27] 2 segments in each direction.[29] But in our study the rostrocaudal extent of terminal field of each dorsal root was usually 2-3 segments in each direction. The contralateral projection of the sacral dorsal roots to the dorsal horn is demonstrated in our study. These results coincide with the reports of previous authors.[26, 27] It was recently reported that in cats, at high cervical and caudal levels of the spinal cord, crossed afferent fibers were seen after dorsal rhizotomy,[3] but in our observation, no upper cervical dorsal root projects to the contralateral side.

Imai and Kusama[12] by using degeneration method reported that the distribution of the dorsal root in the intermediate zone can be divided into two preterminal fiber plexuses- dorsolateral and ventromedial. They described their rostrocaudal extents in the spinal gray especially in the cervical segments. We revealed the precise extent of these fiber plexuses of each dorsal root except the coccygeal ones. Present findings are not consistent with those of Imai and Kusama[12] which indicate that fibers of upper cervical and some thoracic roots form only a ventromedial preterminal fiber plexus. Though in our study it was usually difficult to differentiate the DL plexus of the upper cervical roots from the VM plexus of the upper cervical roots, and the DL plexus of the thoracic and upper lumbar roots was less developed, we could still observe that the DL plexus of the above-mentioned roots is in similar location to that of other roots. Recently morphological studies of afferent fibers identified by electrophysiological technique indicated that afferent fibers of group Ia give off collaterals to laminae VI and VII in the lumbosacral cord.[2, 13] These collateral ramifications in the diagram appear to correspond to the fibers of our DL plexus. Therefore, it may be presumable that upper cervical and thoracic roots considered to include group Ia muscle afferents form the DL plexus.

The centrobasal nucleus which seems to correspond to the middle part of lamina V, central part of lamina VI and dorsal part of lamina VII,[27] the lateral portion of intermediate gray,[29] the centrobasilar region of the dorsal horn and the neighbouring zona intermedia,[18, 19] and the central part of laminae V and VI [28] receives dorsal root fibers. But these authors described little on its rostrocaudal extent. In this study we not only revealed that the centrobasal nucleus receives the dorsal root fibers, but also elucidated that the rostrocaudal extents of each of the dorsal root fibers in the nucleus are related to their entering position into the intumescences.

The central cervical nucleus is known to receive afferents mainly from the dorsal roots of C1–C4 [12, 18] and partially from lower cervical dorsal roots.[12] However, in our study not only cervical but also upper thoracic (T1–T3) dorsal root fibers project to this nucleus through the VM plexus. According to a Golgi study the afferents from the dorsal funiculus form a dense plexus in the central cervical nucleus.[33] This plexus seems to coincide partially with our VM plexus.

There are many reports that indicate the termination of dorsal root fibers in the intermediomedial nucleus.[18, 19, 27] Sterling and Kuypers [28] reported that irregular "burst" of terminal degeneration was seen in a group of cells occupying the medial parts of the junction between laminae VII and VIII. This area of termination appears to correspond to the intermediomedial nucleus. These authors described a little on the rostrocaudal extent of termination in the intermediomedial nucleus. In our study the extent of termination of the dorsal root in the lower thoracic and lumbosacral levels was 3-4 segments in both rostral and caudal directions.

Liu,[16] Grant and Rexed [7] and Imai[11] have published detailed accounts of degeneration in Clarke's column following dorsal rhizotomy in the cat. In our study the thoracic nucleus in the upper thoracic segments gets the descending branches of the lower cervical (C5-C8) dorsal root fibers through the DL plexus. Present findings corroborate those of Liu [16] and Imai [11] which indicated afferent projections to Clarke's column from all cervical dorsal roots except the upper ones, and differ from those of Grant and Rexed [7] which indicated that the cervical and T1 dorsal roots project no fibers to Clarke's column.

Motor neurons of the anterior horn in lamina IX are devided into the lateral and medial cell groups and in the intumescences the lateral group develops more than the medial one. Previous observations [27, 28] indicated that the number of degeneration fibers in motor cell groups diminish sharply immediatelly rostral and caudal to the cut root. But in our study the distribution of dorsal root fibers to motor cell groups is considerably large in rostrocaudal extent in comparison with the previous reports. Dorsal roots of C1-C4 project to the spinal accessory nucleus in the upper cervical cord. These findings are similar to those of Liu [16] which indicated that dorsal roots of C1-C3 project to this nucleus. The difference of rostrocaudal extent of the terminal field is thought to be relevant to the functional difference of fore- and hindlimbes.

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