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Central distribution of efferent and afferent components of the pudendal nerve in rat

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Summary. Central distribution of efferent and afferent components of the pudendal nerve was examined in the rat by the horseradish peroxidase (HRP) method after HRP application to the central cut end of the pudendal nerve. The pudendal motoneurons were located in the dorsolateral, dorsomedial and lateral groups at L5 and L6. Each of the dorsolateral and dorsomedial groups constituted a slender longitudinal cell column. Pudendal motoneurons in the lateral group were scattered at L5, rostrodorsally to the dorsolateral group. The neurons in the dorsolateral and lateral groups were labelled with HRP applied to the nerve branch innervating the ischiocavernosus and sphincter urethrae muscles. The neurons in the dorsomedial group were labelled with HRP applied to the branch supplying the sphincter ani externus and bulbospongiosus muscles. Some dendrites of pudendal motoneurons in the dorsomedial group extended to the contralateral dorsomedial group. These crossing dendrites were observed not only in male rats but also in female. The average number of the pudendal motoneurons in the dorsolateral and dorsomedial groups were larger in male rats than in female. A few neurons of the intermediolateral nucleus at upper L6 were also labelled with HRP applied to the dorsalis penis (clitoridis) nerve. Axon terminals of the pudendal nerve were distributed, bilaterally with an ipsilateral predominance, to the gracile nucleus, as well as to the dorsal horn and dorsal commissural gray from L4 to S2. A few labelled axons were seen in the intermediolateral nucleus at L6 and S1. Axon terminals from the dorsalis penis nerve were distributed more medially in the dorsal horn than those from the perinealis nerve.

Key words: Pudendal nerve – Onuf's nucleus – Spinal cord – Rat – HRP

Introduction

The pudendal nerve contains afferent nerve fibers from the genital, perigenital and perineal regions, and efferent nerve fibers innervating the striated pelvic muscles, in particular the external anal and urethral sphincters. It constitutes an important component in the neural system which subserves excretory and sexual functions (Kuru 1965; Weiss 1972; DeGroat and Booth 1980). Central distribution of efferent and afferent components of the pudendal nerve has been studied in the cat (Ueyama et al. 1984), monkey (Roppolo et al. 1985; Ueyama et al. 1985a) and rat (McKenna and Nadelhaft 1986) (for further review, see Schrøder 1985). In the cat and monkey, pudendal motoneurons are located in a nucleus corresponding to the Onuf's nucleus in man (Onuf 1899, 1900; Mannen et al. 1977, 1982; Schrøder 1981, 1985). In the rat, however, pudendal motoneurons are situated in two separate areas in the ventral horn (Schrøder 1980; McKenna and Nadelhaft 1986), showing sexual dimorphism (Breedlove and Arnold 1980, 1981, 1983; Breedlove et al. 1983; Jordan et al. 1982).

In the present study, as a continuation of our previous studies on the organization of pudendal motoneurons and primary afferent fibers (Sato et al. 1978; Konishi et al. 1978, 1985; Ueyama et al. 1984, 1985a, b), central distribution of efferent and afferent components of the pudendal nerve was examined in both male and female rats by the horseradish peroxidase (HRP) method after applying the enzyme to the central cut end of the trunk or a branch of the pudendal nerve. The present study has confirmed and extended the results of the previous studies (Schrøder 1980; McKenna and Nadelhaft 1986); some new findings were obtained, in particular, concerning autonomic and afferent components of the pudendal nerve in the rat. A part of the results reported here has been published in brief form elsewhere (Ueyama et al. 1958b).

Materials and methods

The experiments were carried out in 38 Wister rats of both sexes, weighing 250 to 350 g. Each rat was anesthetized with intraperitoneal injection of sodium pentobarbital (5 mg/100 g body weight); supplement doses were given, when necessary, during long surgical procedures. The pudendal nerve was exposed unilaterally in the ischiorectal fossa. The trunk or a branch of the pudendal nerve was cut, and the central cut end was inserted into a piece of polyethylene tube which was filled with 30% HRP (Toyobo Grade-1-C) dissolved in 0.9% saline. The open end of the tube was sealed with silicon grease or closed by heating. The central cut end of the nerve was allowed to be in contact with HRP for 2 to 6 hours. During this period, the preparation was monitored under an operation microscope, and body fluids which tended to accumulate in the area of the dissection were removed periodically. Subsequently the tube

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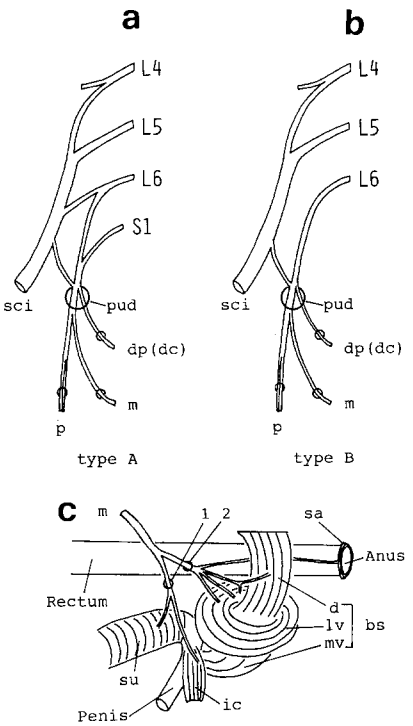

Fig. 1 a–c. Diagrams showing two types of the pudendal nerve (**a**, **b**) and peripheral branches of the muscle nerve supplying the striated pelvic muscles (**c**). The pudendal nerve (*pud*) is composed of the muscle (*m*), dorsalis penis (clitoridis) (*dp* or *dc*) and perinealis nerve (*p*). The muscle nerve is composed of the branch 1 supplying the ischiocavernosus (*ic*) and sphincter urethrae muscles (*su*), and the branch 2 innervating the dorsal (*d*), lateral ventral (*lv*) and medial ventral (*mv*) parts of the bulbospongiosus (*bs*) and sphincter ani externus (*sa*) muscles. Circles indicate the regions where HRP application was made. *sci*, sciatic nerve

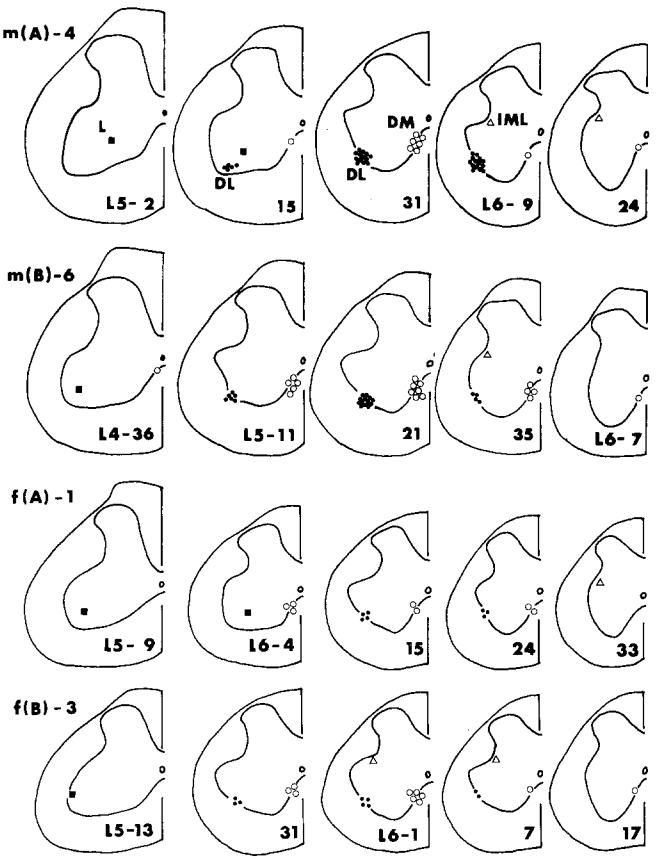

Fig. 2. Projection drawings made from five series of cross sections of the L5, L6 and S1 cord segments showing the location of neuronal cell bodies labelled after HRP application to the trunk of the pudendal nerve. Pudendal motoneurons of the dorsolateral group (*filled circles*), dorsomedial group (*open circles*) and lateral group (*filled squares*), and preganglionic parasympathetic neurons in the intermediolateral nucleus (*open triangles*) are plotted in one to one fashion in two male (*m*) and two female (*f*) rats with the pudendal nerve of the type A (*A*) or B (*B*). The number of each section indicates the position of the section in the series of complete serial sections of 60-μm thickness in each cord segment. Bar = 500 μm

and its contents were carefully removed, the central cut end of the nerve was washed lightly with 0.9% saline and wrapped in silicon grease, and the wound was closed.

After a postoperative survival period of 36 to 48 h, the rats were deeply reanesthetized with an intraperitoneal injection of sodium pentobarbital (10 mg/100 g body weight) and perfused transcardially with 500 to 1000 ml of 3.5% paraformaldehyde in 0.1 M phosphate buffer (pH 7.3), followed by 500 ml of the same buffer containing 10% sucrose. The lower brainstems, spinal cords and dorsal root ganglia of the lumbar and sacral cord segments were removed immediately, saturated with a solution of 25% sucrose in the same buffer at 4° C, and then cut on a freezing microtome in a serial section of 60 μm thickness, transversely, horizontally or sagittally. The sections were processed for HRP reaction by the tetramethylbenzidine method (Mesulam 1978) or diaminobenzidine method (Streit and Reubi 1977), then mounted on to gelatinized slides and counterstained with 0.5% neutral red or 10% cresyl violet. The groups of motoneurons were named according to Schrøder (1980).

The number of HRP-labelled neuronal cell bodies was counted using bright field illumination and a magnification of 200 × in the serial sections treated with tetramethylbenzidine in each of 6 male and 6 female rats. The possibility of double counting of the same cell was corrected for by the method of Abercrombie (1946). The soma areas of HRP-labelled neurons were measured with an *X-Y* digitizer by using outlines drawn with the microscope drawing tube at a magnification of 500 × in a series of transverse sections and a series of horizontal sections treated with diaminobenzidine.

In 6 male and 6 female rats, the organization of the pudendal nerve on the side of the HRP application was examined macroscopically. The pelvic muscles were named according to McKenna and Nadelhaft (1986).

Results

Nerve roots constituting the pudendal nerve

The organization of the pudendal nerve was examined macroscopically in 6 male and 6 female rats (Fig. 1). The pudendal nerve was classified into 2 types on the basis of the nerve roots constituting the nerve. Type A (Fig. 1a) was composed of 3 roots; one was derived from the sciatic nerve, and the other two arose from the union of the ventral branch of the S1 nerve and a component of the ventral branch of the L6 nerve. The type A pudendal nerve was observed in 2 male and 2 female rats. Type B (Fig. 1b) was composed of 2 roots; one was a branch of the sciatic nerve

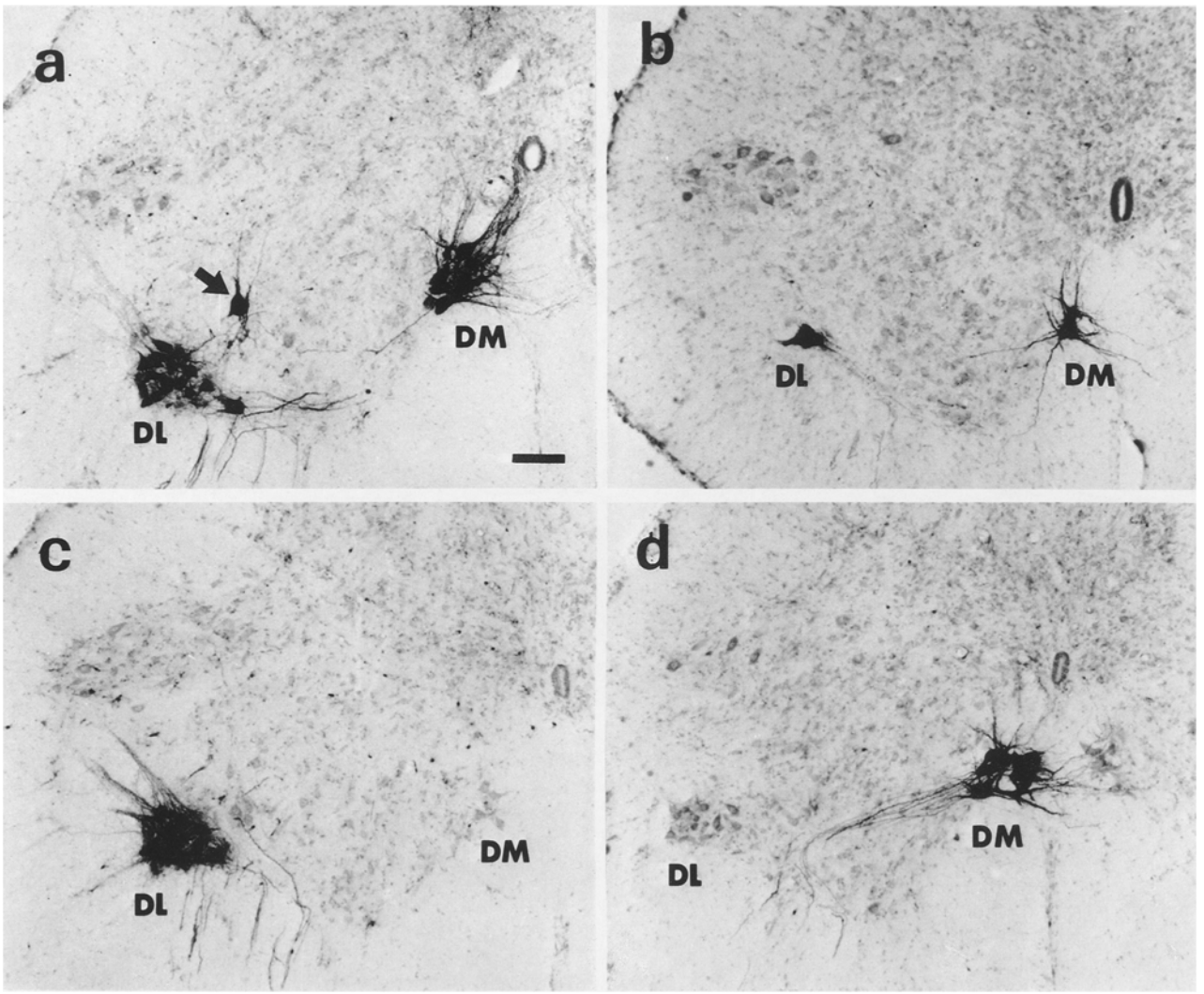

Fig. 3a–d. Photomicrographs of cross sections through the L6 cord segment showing pudendal motoneurons of the dorsolateral (*DL*) and dorsomedial (*DM*) groups, labelled after HRP application to the trunk of the pudendal nerve in a male (**a**) and a female (**b**) rat, and after HRP application to the muscle branch innervating the sphincter urethrae and ischiocavernosus muscles (**c**) in a male rat, and to the muscle branch supplying the sphincter ani externus and bulbospongiosus muscles (**d**) in a male rat. *Arrow* in (*a*) points to a labelled motoneuron in the laterl group. Bar = 100 μm

and the other was the ventral branch of the L6 nerve. Thus the type B pudendal nerve was lacking in components from the ventral branch of the S1 nerve. The type B pudendal nerve was observed in 4 male and 4 female rats.

Peripheral branches of the pudendal nerve

Three main branches were identified in the pudendal nerve; the dorsalis penis (clitoridis) nerve, perinealis nerve, and muscle branch (Fig. 1). The muscle branch was further divided into 2 large branches; one supplying the sphincter urethrae muscle and the ischiocavernosus muscle, and the other innervating the sphincter ani externus muscle and the dorsal, lateral ventral and medial ventral parts of the bulbospongiosus (bulbocavernosus) muscle (Fig. 1c).

Retrogradely labelled neurons

When HRP was applied to the trunk of the pudendal nerve (pud in Fig. 1), cell bodies of central neurons labelled with HRP were distributed ipsilaterally to the ventral horn of the L5 and L6 cord segments (Figs. 2, 3). A small number of neuronal cell bodies were also labelled in the intermediolateral nucleus at the upper levels of the L6 cord segment (Fig. 2). Labelled pudendal motoneurons were located in the dorsolateral, dorsomedial and lateral groups of Schrøder (1980) at the L5 and L6 cord segments. Labelled pudendal motoneurons in the dorsolateral group were located in the lateral corner of the ventral horn (Figs. 2, 3), constituting a slender cell column along the longitudinal axis of the spinal cord (Fig. 4a). At the middle levels of the cell column, the dorsolateral group was seen to protrude laterally into the lateral funiculus (Fig. 3a, c); at the caudal levels of the cell column, it was observed to shift dorsally along the lateral border of the ventral horn toward the intermediolateral nucleus (Fig. 2). The long axes of cell bodies of labelled neurons in the dorsolateral group were mainly oriented longitudinally along the long axis of the cell column, and longitudinally oriented dendrite bundles were prominent in the longitudinal sections (Fig. 4a).

Labelled pudendal motoneurons in the dorsomedial group were located in the ventral horn region near the apex of the ventral funiculus close to the midline (Figs. 2, 3).

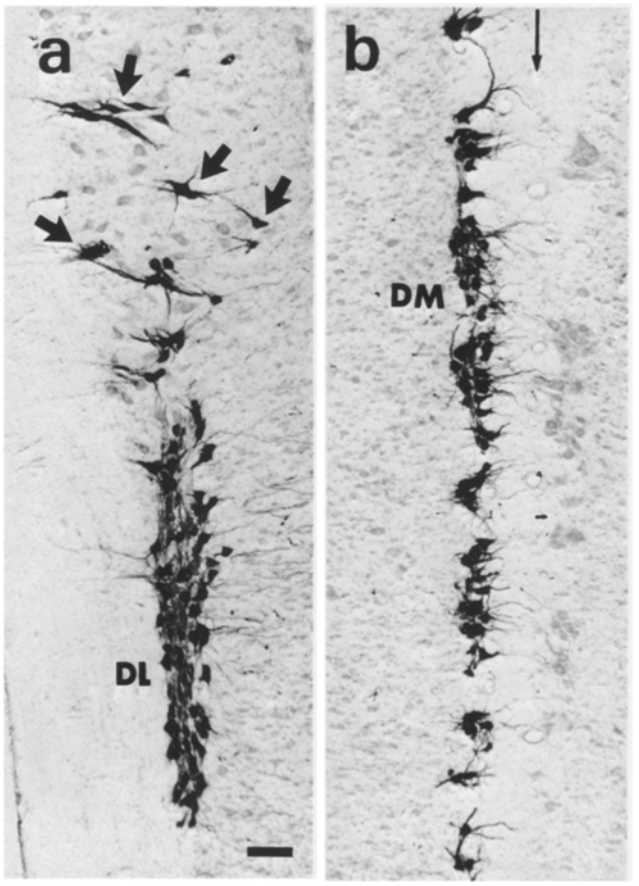

Fig. 4a, b. Photomicrographs of horizontal sections through the L6 cord segment showing pudendal motoneurons of the dorsolateral (*DL*), lateral (*L*) and dorsomedial (*DM*) groups, labelled after HRP application to the trunk of the pudendal nerve in a male rat. *Arrows* in (**a**) indicate labelled motoneurons in the lateral group. *Arrow* in (**b**) points to the midline. Bar = 100 μm

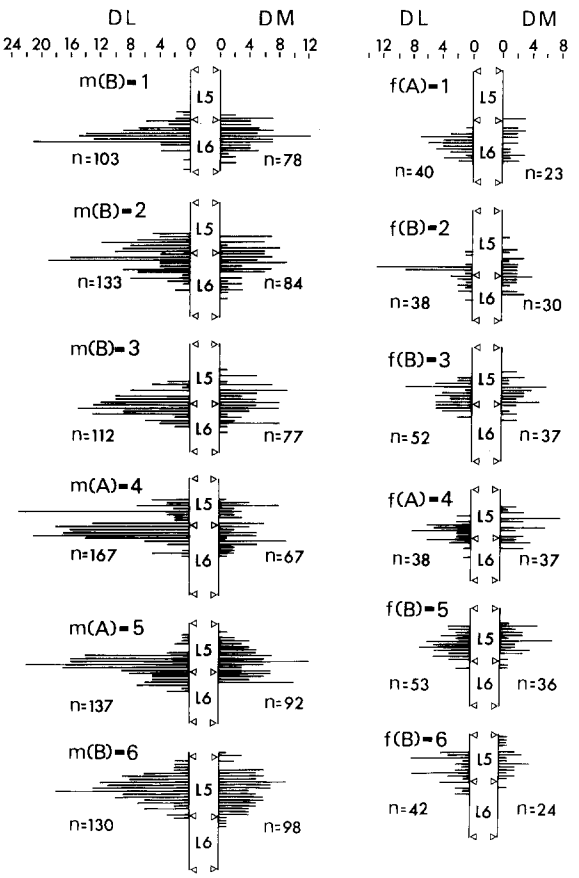

Fig. 5. Distribution of HRP-labelled pudendal motoneurons in six male (*m*) and six female (*f*) rats with the pudendal nerve of type A (**A**) or B (**B**). The number of pudendal motoneurons of the dorsolateral (*DL*) and dorsomedial (*DM*) groups labelled after HRP application to the trunk of the pudendal nerve was counted in every second section in each of the complete series of sections of 60-μm thickness. The filled columns represent the number of HRP-labelled neuronal cell bodies of pudendal motoneurons counted. Open triangles indicate the borders of the L5 and L6 cord segments. *n*, the total of HRP-labelled cell bodies counted in each rat

Although the dorsomedial group formed a cell column with longitudinally oriented dendrite bundles along the longitudinal axis of the spinal cord, the long axes of cell bodies of pudendal motoneurons in the dorsomedial group tended to be oriented transversely (Fig. 4b). The cell bodies of pudendal motoneurons in the dorsomedial group tended to be arranged in clusters along the longitudinal axis of the spinal cord (Fig. 4b). The dendrites of pudendal motoneurons in the dorsomedial group mainly extended rostrally, caudally, ventrolaterally, dorsally and medially (Figs. 3a, b, d; 4b). Some of the dorsally extending dendrites were traced into lamina X and the dorsal gray commissure (Figs. 3a, 7a), and some of the medially extending dendrites were observed to cross the midline to enter the dorsomedial group contralaterally (Fig. 3d). These crossing dendrites of pudendal motoneurons in the dorsomedial group were seen in both male and female rats. In the female rat, however, crossing dendrites were not so prominent and so frequent as in the male rat. Labelled pudendal motoneurons in the lateral group were small in number and were scattered in the ventral horn rostrodorsally and dorsomedially to the dorsolateral group (Figs. 2, 3a, 4a).

Although the rostrocaudal extent of the distribution of pudendal motoneurons was variable among the 12 rats examined, no sex difference was recognized in the position and distribution pattern of pudendal motoneurons (Figs. 2, 5). On the other hand, the average number of pudendal motoneurons in the dorsolateral and dorsomedial groups were significantly larger in male rats than in female ($P < 0.001$ in the Student's *t*-test) (Table 1). HRP-labelled neurons in the lateral group, however, showed no sex difference in the average number. The range of soma areas of pudendal motoneurons was broad, and that in male rats highly overlapped with that in female rats (Tables 2, 3); pudendal motoneurons in the dorsolateral and dorsomedial groups, however, tended to be larger in male rats than in female (Tables 2, 3. Also compare Fig. 3a with 3b).

After HRP application to the trunk of the pudendal nerve, a few neuronal cell bodies were consistently labelled within the intermediolateral nucleus at the upper levels of the L6 cord segment (in some rats, also at the lower levels of the L5 cord segment) (Figs. 2, 7a). These labelled neurons in the intermediolateral nucleus were apparently smaller than the labelled pudendal motoneurons in the dorsolateral, dorsomedial and lateral groups (Tables 2, 3). The HRP-labelled neurons in the intermediolateral nucleus showed no sex difference in the average number ($P > 0.05$ in the Student's *t*-test) (Table 1).

Table 1. Number of labelled neurons

	Male ($n=6$)		Female ($n=6$)	
	Range	Mean ±s.d.	Range	Mean ±s.d.
Motoneurons:				
dorsolateral group	230–145	178.8±28.2	71–52	62.7±6.7
dorsomedial group	121–94	106.5±10.0	53–28	43.6±8.9
lateral group	36–18	22.8±6.6	25–7	17.1±7.3
Intermediolateral nucleus neurons	9–2	5.6±2.2	10–4	6.8±2.2

When HRP was applied to the trunk of the muscle branch of the pudendal nerve (in 5 rats) (m in Fig. 1), labelled neuronal cell bodies were distributed to the dorsolateral, dorsomedial and lateral groups of motoneurons, but not to the intermediolateral nucleus. When HRP was applied to the muscle branch 1 (in 6 rats) (1 in Fig. 1c), labelled neuronal cell bodies were distributed to the dorsolateral (Fig. 3c) and lateral groups, but not in the dorsomedial group and intermediolateral nucleus. When HRP was applied to the muscle branch 2 (in 7 rats) (2 in Fig. 1c), labelled neuronal cell bodies were distributed to the dorsomedial group, but not in the dorsolateral and lateral groups and intermediolateral nucleus (Fig. 3d). When HRP was applied to the dorsalis penis (clitoridis) nerve (in 5 rats) (dp or dc in Fig. 1a, b), no labelled neurons were seen in the ventral horn, but a few neuronal cell bodies were labelled in the intermediolateral nucleus at the upper levels of the L6. When HRP was applied to the perineal nerve (in 5 rats) (p in Fig. 1a, b), no labelled neuronal cell bodies were found in the spinal cord.

HRP-labelled afferent components of the pudendal nerve

After HRP application to the trunk of the pudendal nerve in 12 rats, pudendal nerve afferent neurons were labelled in the L5 and L6 dorsal root ganglia in 5 rats, in the L6 and S1 dorsal root ganglia in 5 rats, and in L5, L6 and S1 dorsal root ganglia in 2 rats (Fig. 6). At the levels of entry of transganglionically labelled dorsal root fibers into the spinal cord, labelled fibers were observed over the full breadth of the Lissauer's tract (Fig. 7a). These fibers appeared to run both rostrally and caudally in the Lissauer's tract, sending collaterals into lamina I. At the entry regions, many labelled fibers were also observed to run ventromedially along the medial border of the dorsal horn (Fig. 7a). Some of them crossed the midline through the dorsal gray

Table 2. Soma sizes of labelled neurons in transverse sections

	Male		Female	
	Range (μm^2)	Mean±s.d. (μm^2)	Range (μm^2)	Mean±s.d. (μm^2)
Motoneurons:				
dorsolateral group	814–195	435.6±144.6 ($n=130$)	480–153	286.1±90.1 ($n=30$)
dorsomedial group	1064–445	784.2±219.8 ($n=69$)	1012–319	528.4±136.5 ($n=27$)
lateral group	1060–409	701.7±196.8 ($n=20$)	986–376	650.6±165.3 ($n=18$)
Intermediolateral nucleus neurons	279–117	199.7±48.3 ($n=24$)	246–101	164.2±42.7 ($n=20$)

Data were obtained from a male and a female rats.
n, number of cells measured

Table 3. Soma sized of labelled neurons in horizontal sections

	Male		Female	
	Range (μm^2)	Mean±s.d. (μm^2)	Range (μm^2)	Mean±s.d. (μm^2)
Motoneurons:				
dorsolateral group	1191–270	652.0±197.3 ($n=89$)	678–212	401.9±94.1 ($n=31$)
dorsomedial group	1435–478	834.2±197.0 ($n=63$)	560–298	420.7±89.2 ($n=22$)
lateral group	1183–354	618.2±192.6 ($n=39$)	807–217	560.9±168.2 ($n=29$)
Intermediolateral nucleus neurons	318–146	233.5±55.8 ($n=10$)	226–121	170.6±35.1 ($n=6$)

Data were obtained from a male and a female rats.
n, number of cells measured

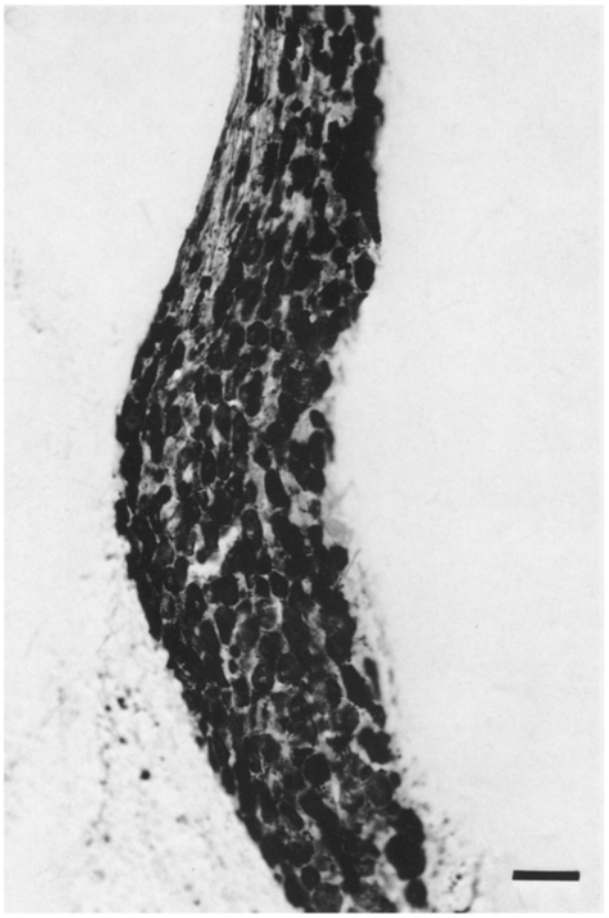

Fig. 6. Cell bodies in the L6 dorsal root ganglion, labelled after HRP application to the trunk of the pudendal nerve of a male rat. Bar = 100 μm

commissure (Fig. 7). Many axons appeared to end ipsilaterally in lamina I, the medial two-thirds or a half of laminae II–VI, the dorsal gray commissure and lamina X, and contralaterally in the dorsal gray commissure, lamina X and the medial one-third or a half of the dorsal horn. A few axons were also labelled in the region ventral to the central canal (Fig. 7b); these fibers appeared to run longitudinally along the central canal. Occasionally, retrogradely labelled dendrites of pudendal motoneurons in the dorsomedial group were seen to enter the region of the dorsal gray commissure where many labelled presumed axon terminals were distributed (Fig. 7a). A few labelled axons were also observed passing ventrally along the lateral edge of the dorsal horn into the region of the intermediolateral nucleus at the levels of the L6 and S1 cord segments (in some rats, also at the lower levels of the L5 cord segment). In the ipsilateral intermediolateral nucleus, it was often difficult to distinguish labelled possible axon terminals from retrogradely labelled dendrites of intermediolateral nucleus neurons (Fig. 7a). On the other hand, in the contralateral intermediolateral nucleus where no neuronal cell bodies were labelled, labelled possible axon terminals could be identified without difficulties (Fig. 7b).

The number of labelled axons decreased rapidly at the levels cranial or caudal to those of entry of labelled dorsal root fibers, and no labelled axonal components were found in the spinal gray cranial to the L4 cord segment and caudal to the S2 cord segment. A small number of labelled axons, however, were seen to ascend the spinal cord ipsilaterally through the dorsomedial part of the gracile funiculus. These labelled axons appeared to end ipsilaterally in the medial part of the gracile nucleus (Figs. 8, 9a). At the middle levels of the gracile nucleus, a few labelled axons were observed to cross the midline through the dorsal gray commissure to end contralaterally in the ventromedial part of the gracile nucleus (Figs. 8, 9b).

Afferent components in the pudendal nerve were labelled transganglionically after HRP application to the dorsalis penis (clitoridis) or perinealis nerve (Figs. 10–12), but not after HRP application to the muscle branch of the pudendal nerve. When HRP was applied to the dorsalis penis (clitoridis) nerve, labelled presumed axon terminals were distributed, at the levels of entry of labelled dorsal root fibers, ipsilaterally to lamina I and the medial part of laminae II–VI of the dorsal horn, the dorsal gray commissure and lamina X (Figs. 10a, 11). A few labelled fibers were traced along the lateral border of the dorsal horn to the intermediolateral nucleus. The number of labelled axons decreased rapidly at the levels cranial or caudal to those of entry of labelled dorsal root fibers, and no labelled presumed axon terminals were found in the spinal gray cranial to L4 cord segment and caudal to S2 cord segment (Fig. 11). In the medial part of the gracile nucleus, however, labelled axon terminals were seen bilaterally with an ipsilateral predominance.

When HRP was applied to the perinealis nerve, labelled presumed axon terminals were distributed, at the levels of entry of labelled dorsal roots, mainly ipsilaterally to the middle part of laminae I–VI of the dorsal horn and dorsal gray commissure, and contralaterally to the most medial part of the dorsal horn and dorsal gray commissure (Figs. 10b, 12). Some labelled fibers were also seen ipsilaterally in the lateral part of laminae V and VI of the dorsal horn. The number of labelled axons decreased rapidly at the levels cranial or caudal to those of entry of labelled dorsal root fibers, and no labelled presumed axon terminals were found in the spinal gray cranial to the L4 cord segment and caudal to the S2 cord segment (Fig. 12). In the medial part of the gracile nucleus, however, labelled axon terminals were seen bilaterally with an ipsilateral predominance. Labelled axon terminals in the gracile nucleus were more numerous after HRP application to the perinealis nerve than after HRP application to the dorsalis penis (clitoridis) nerve; no difference, however, was recognized in the area of distribution of labelled axon terminals in the gracile nucleus.

Discussion

The pudendal motoneurons innervating the sphincter urethrae, ischiocavernosus, sphincter ani externus and bulbospongiosus (bulbocavernosus) muscles constitute a slender longitudinal cell column in the ventral horn in the cat (Konishi et al. 1978, 1985; Sato et al. 1978; Yamamoto et al. 1978; Kuzuhara et al. 1980; DeGroat et al. 1981), monkey (Nakagawa 1980; Roppolo et al. 1985; Ueyama et al. 1985a), dog (Petras and Cummings 1978; Kuzuhara et al. 1980; DeAraujo et al. 1982) and rabbit (Nagashima et al. 1979). This cluster of pudendal motoneurons is generally considered homologous to the Onuf's nucleus in man (Onuf

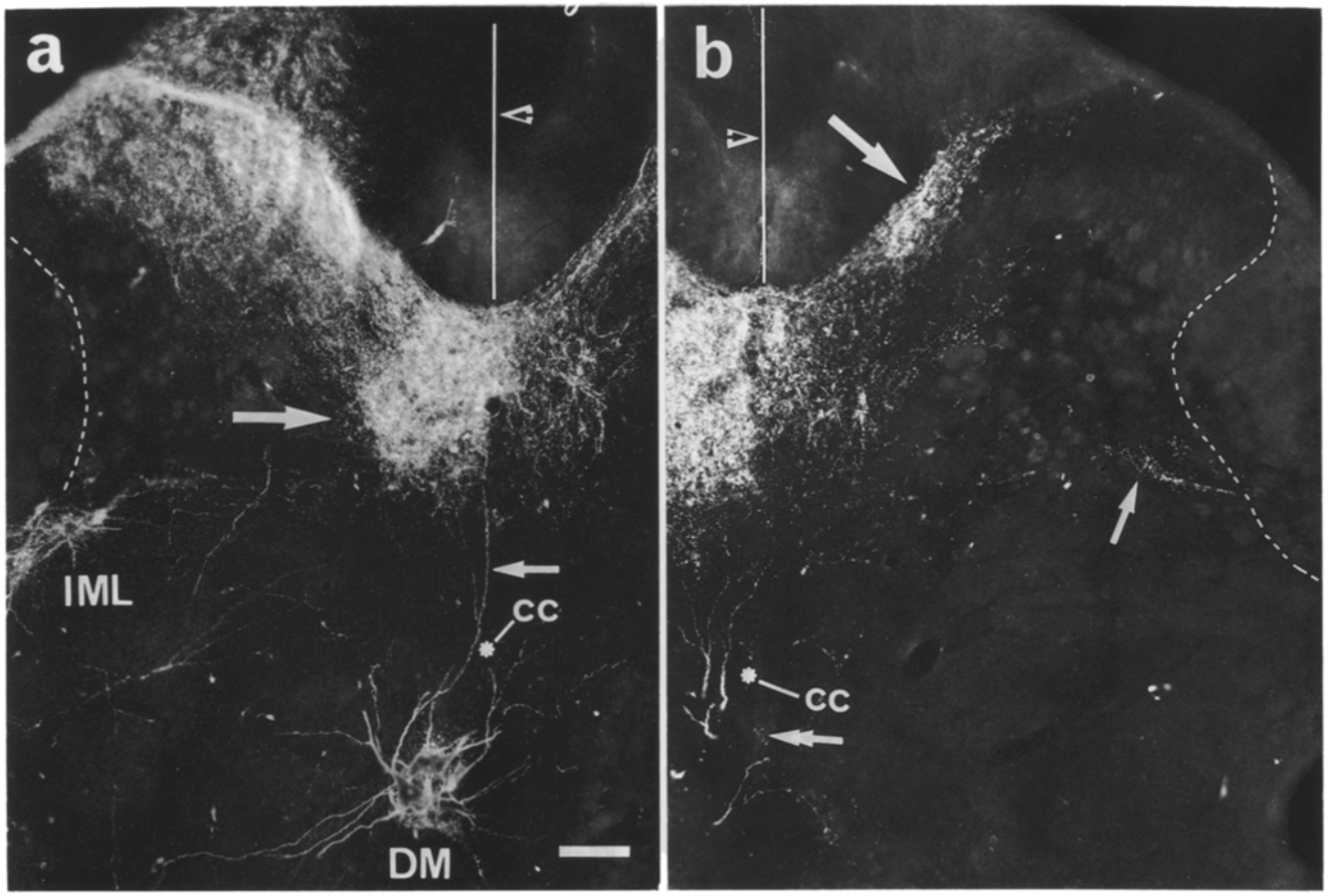

Fig. 7a, b. Dark-field photomicrographs of cross sections through the L6 cord segment of a male rat showing central distribution of primary afferent axons labelled after HRP application to the trunk of the pudendal nerve, on the sides ipsilateral (**a**) and contralateral (**b**) to the HRP application. *Larger arrows* in **a** and **b** indicate terminal fields of primary afferent neurons of the pudendal nerve in the dorsal gray commissure and medial part of the dorsal horn, respectively. A retrogradely labelled dendrite (*smaller arrow* in **a**) of a pudendal motoneuron is seen to extend to the dorsal gray commissure. In the ipsilateral intermediolateral nucleus (*IML*), retrogradely-labelled neuronal cell bodies are seen, but it is difficult to distinguish anterogradely-labelled presumed axon terminals from retrogradely-labelled dendrites. On the other hand, labelled possible axon terminals are seen in the contralateral IML (**a** *smaller arrow* in **b**), where no perikarya are labelled. *Double arrow* in **b** points to a small longitudinal fiber labelled in the region ventral to the central canal (*cc*). *Arrowheads* indicate the midline. Bar = 100 μm

1899, 1900; Mannen 1977, 1982; Schrøder 1981, 1985). In the rat, however, motoneurons supplying the sphincter urethrae and ischicavernosus muscles are located in the dorsolateral group, while those innervating the shincter ani externus and bulbospongiosus muscles are situated in the dorsomedial group. The Onuf's nucleus in the rat is, therefore, considered to comprise two widely separated sub-groups (Breedlove and Arnold 1980; Schrøder 1980; Katagiri et al. 1986; McKenna and Nadelhaft 1986). This was confirmed in the present study.

According to McKenna and Nadelhaft (1986), after application of HRP or fluorescent dyes to the L6-S1 trunk of the rat just before it enters the sacral plexus, motoneurons in the retrodorsolateral, dorsolateral, ventral and dorsomedial groups were labelled in the L5 and L6 cord segments. Katagiri et al. (1986) also observed labelled motoneurons in the ventral group, as well as in the dorsolateral and dorsomedial groups after injection of True Blue into the pudendal nerve of the rat. McKenna and Nadelhaft (1986), however, observed labelled motoneurons only in the dorsolateral and dorsomedial groups after applying HRP to the central cut end of the motor branch of the pudendal nerve in the rat. In the present study, pudendal motoneurons were found mainly in the dorsolateral and dorsomedial groups, and additionally in the lateral group, but no labelled motoneurons were observed in the ventral group after HRP application to the pudendal nerve. These discrepancies among the results of the present and previous studies appear to be ascribable, at least partly, to the difference of the level of the tracer application to the pudendal nerve.

The sexual dimorphism of the rat pudendal motoneurons in the dorsolateral group (Jordan et al. 1982) and the dorsomedial group (the spinal nucleus of the bulbocavernosus of Breedlove and Arnold 1980) has been well documented (Breedlove and Arnold 1980, 1981, 1983; Breedlove et al. 1982, 1983; Fishman and Breedlove 1985; McKenna and Nadelhaft 1986; Senegelaub and Arnold 1986). In agreement with these previous studies, the present study indicated that there were significantly more neurons in both dorsolateral and dorsomedial groups in the male rat than in the female, and that pudendal motoneurons in both dorsolateral and dorsomedial groups tended to be larger in male rats than in female. No sex difference, however, was recognized in pudendal motoneurons in the lateral group. Sex difference of pudendal motoneurons has also been reported in the Japanese monkey (Ueyama et al. 1985a); in

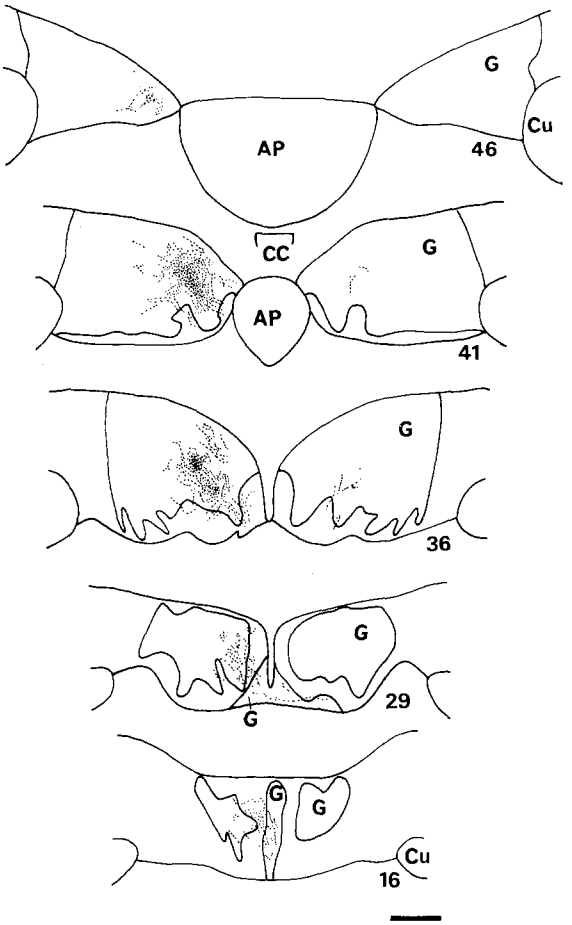

Fig. 8. Distribution of primary afferent axons in the dorsal column nuclei labelled after HRP application to the trunk of the pudendal nerve on the left side of a male rat. The numbers indicate the position of sections in a complete series of cross sections of 60-μm thickness. *AP*, area postrema; *CC*, central canal; *Cu*, cuneate nucleus; *G*, gracile nucleus. Bar = 200 μm

the adult Japanese monkey the average number of pudendal motoneurons was larger in the male than in the female, whereas no sex difference was found in the average some diameter of pudendal motoneurons. In the adult cat, no sex difference was recognized in pudendal motoneurons (Ueyama et al. 1984). Although the dorsal root ganglia were not examined systematically in the present study, McKenna and Nadelhaft (1986) reported a strong sexual dimorphism in the afferent neurons of the pudendal nerve in the rat. According to McKenna and Nadelhaft (1986) pudendal nerve afferent neurons were located in the L6 and S1 dorsal root ganglia, and they were larger and more numerous in the male rat than in the female.

In agreement with the previous studies (Breedlove and Arnold 1980; Schrøder 1980; Katagiri et al. 1986; McKenna and Nadelhaft 1986), the present study showed that the dorsomedial group of pudendal motoneurons in the male rat contained motoneurons supplying the sphincter ani externus and bulbospongiosus muscles. In the female rat, however, the bulbospongiosus muscle is lacking or extremely fine in gross dissections (cf. Hayes 1965; Breedlove and Arnold 1981; McKenna and Nadelhaft 1986). Therefore, most, if not all, pudendal motoneurons of the dorsomedial group in female rats are considered to innervate the sphincter ani externus muscle.

As reported previously (McKenna and Nadelhaft 1986), dendrites of pudendal motoneurons in the dorsomedial group were routinely observed to cross the midline to extend contralaterally into the dorsomedial group. A similar organization of motoneuron dendrites has been reported in hypoglossal motoneurons (Wan et al. 1982). Rose and Collins (1985) presumed that crossing dendrites of motoneurons in the dorsomedial group might be a substrate for synchronized activation of penile motoneurons. In the present study, however, crossing dendrites of motoneurons in the dorsomedial group were even seen in the female rat, though not so frequently and so conspicuously as in male rat. The crossing dendrites of motoneurons in the dorsome-

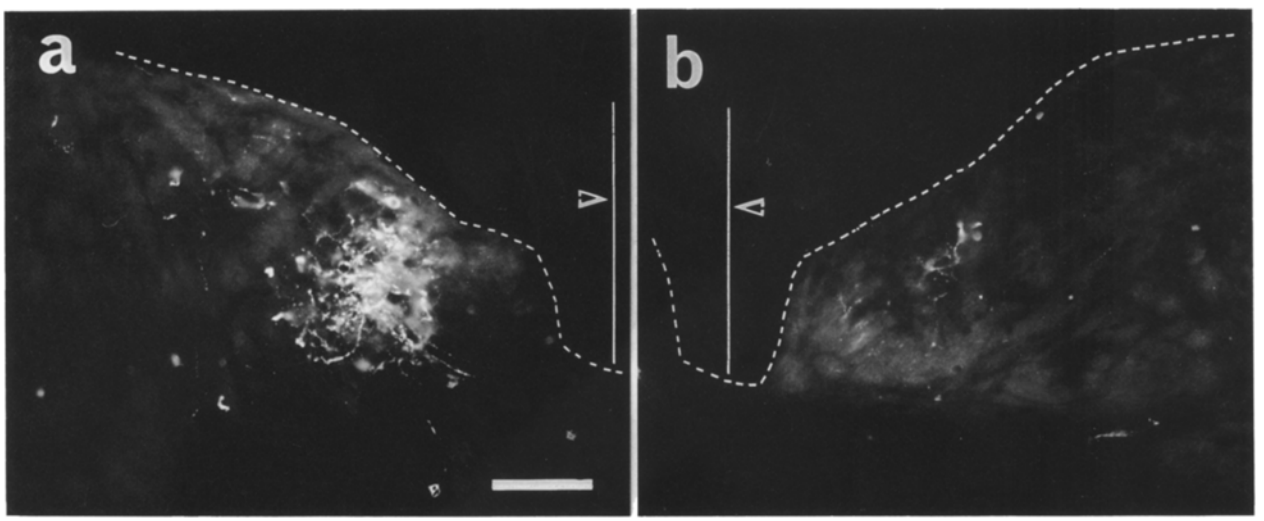

Fig. 9a, b. Dark-field photomicrograph of cross sections through the reticular part of the gracile nucleus showing presumed axon terminals labelled after HRP application to the trunk of the pudendal nerve of a male rat; on the sides ipsilateral (**a**) and contralateral (**b**) to the HRP application. *Arrowheads* point to the midline. Bar = 100 μm

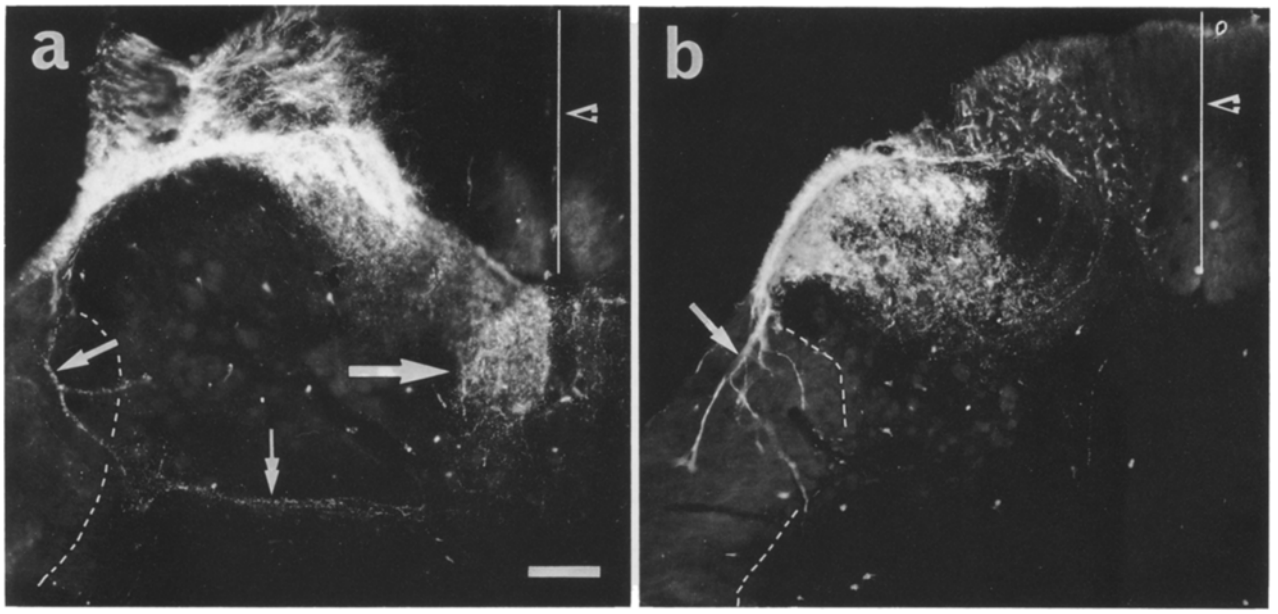

Fig. 10a, b. Dark-field photomicrographs of cross sections through the L6 cord segment of the male rats showing central distribution of primary afferent axons labelled after HRP application to the dorsalis penis nerve (**a**) or perinealis nerve (**b**) on the left side. Note that labelled axons in **a** are distributed more medially to the dorsal horn than those in **b**. *Larger arrow* points to the terminal fields of labelled axons in the dorsal gray commissure in **a**. *Double arrow* points to labelled axons which run horizontally toward the intermediolateral nucleus. Labelled axons in the lateral collateral pathway are indicated by *smaller arrows* in **a** and **b**. *Arrowheads* indicate the midline. Bar = 100 μm

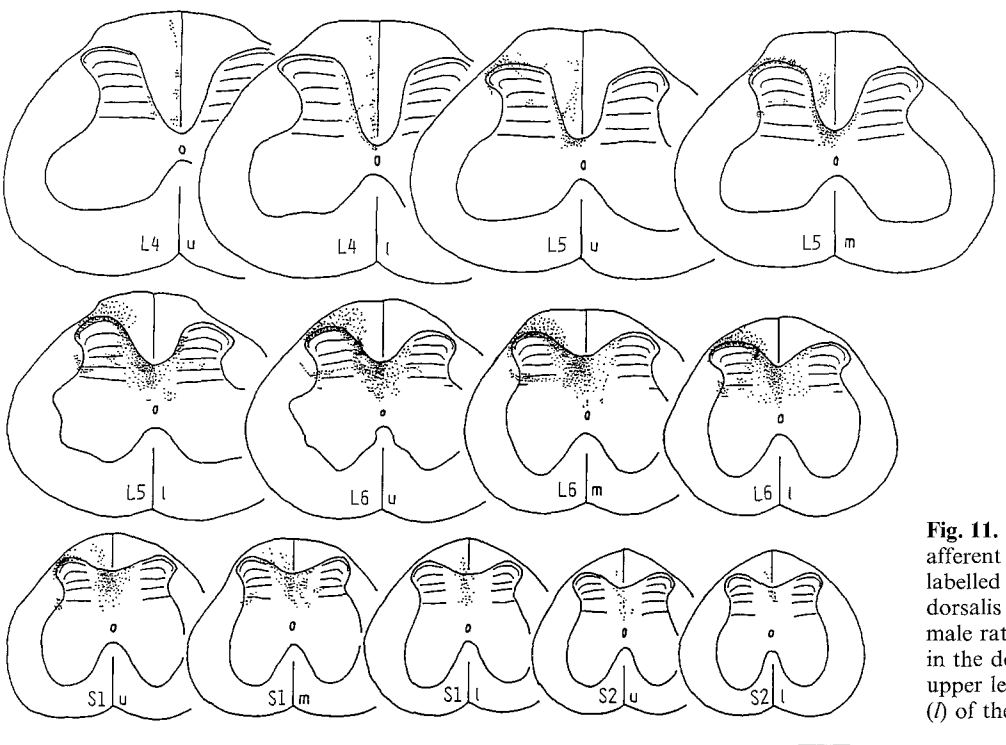

Fig. 11. Central distribution of primary afferent axons of the pudendal nerve (*dots*) labelled after HRP application to the dorsalis penis nerve on the left side of a male rat. Presumed labelled axon terminals in the dorsal horn are distributed from the upper level (*u*) of the L4 to the lower level (*l*) of the S2. m, middle level. Bar = 500 μm

dial group in the female rat appear to subserve coordinated activity of two halves of the sphincter ani muscles.

In the present study, a small number of neurons in the intermediolateral nucleus at the levels of the L6 cord segment were constantly labelled with HRP applied to the dorsalis penis (clitoridis) nerve. This result is in contrast to that of Núnez et al. (1986) who found no retrograde label in the spinal cord after HRP application to the dorsalis penis (clitoridis) nerve of the rat, but compatible to that of Katagiri et al. (1986) who observed labelled neurons in the intermediolateral nucleus at the levels of the caudal L6 and rostral S1 cord segments after pudendal nerve injection with True Blue. This finding by Katagiri et al. (1986) and the present one support the previous reports on the

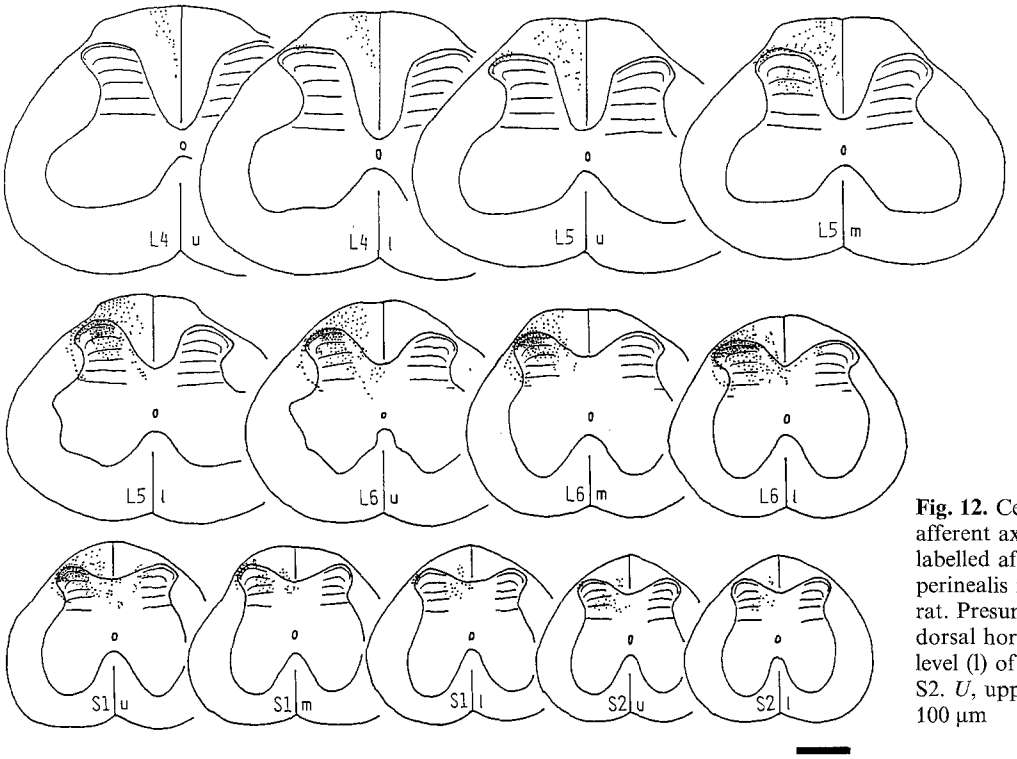

Fig. 12. Central distribution of primary afferent axons of the pudendal nerve (*dots*) labelled after HRP application to the perinealis nerve on the left side of a male rat. Presumed labelled axon terminals in the dorsal horn are distributed from the lower level (l) of the L4 to the lower level of the S2. *U*, upper level; *m*, middle level. Bar = 100 μm

possible existence of preganglionic parasympathetic fibers in the pudendal nerve of the rat (Hulsebosch and Coggeshall 1982).

Taylor et al. (1982) observed labelling of pudendal nerve afferent neurons in the L6 dorsal root ganglia after injection of HRP into the pudendal nerve of the rat. The results of McKenna and Nadelhaft (1986), however, indicated that pudendal nerve afferent neurons of the rat were located in the L6 and S1 dorsal root ganglia. In the present study, pudendal afferent neurons were examined in 12 rats after HRP application to the trunk of the pudendal nerve. Pudendal nerve afferent neurons were labelled in the L6 and S1 dorsal root ganglia in 5 rats; in the L5 and L6 dorsal root ganglia in 5 rats, and in the L5, L6 and S1 dorsal root ganglia in 2 rats. In the present study, the pudendal nerve of the rat was divided into 2 types on the basis of the difference of the segmental composition of the pudendal nerve. The discrepancies among the reported data concerning the segmental distribution of dorsal root ganglion neurons labelled after HRP application to the pudendal nerve might be attributable to the differences in the segmental composition of the pudendal nerve.

The pattern of central distribution of rat pudendal nerve afferents was qualitatively similar to that reported for the cat (Ueyama et al. 1984) and monkey (Roppolo et al. 1985; Ueyama et al. 1985a). As reported previously in the cat (Ueyama et al. 1984), monkey (Roppolo et al. 1985; Ueyama et al. 1985a) and rat (McKenna and Nadelhaft 1986), the dorsal gray commissural and contralateral terminations were observed in pudendal nerve labelling in the present study. In the dorsal commissural gray of the rat, the terminal field of the pudendal nerve afferents appears to overlap more or less the terminal field of primary afferent fibers of the pelvic nerve (Nadelhaft and Booth 1984; McKenna and Nadelhaft 1986), as observed in the cat (Morgan et al. 1981; Ueyama et al. 1984) and monkey (Nadelhaft et al. 1983; Roppolo et al. 1985; Ueyama et al. 1985a). Nahin et al. (1983) reported that neurons in the dorsal gray commissure of the L6 cord segment in the rat responded to noxious somatic stimuli. Thus, the dorsal gray commissure of the L6 cord segment in the rat may be involved in nociception, autonomic regulation of pelvic viscera, and viscerosomatic and somatovisceral interactions.

In the cat, many fibers with enkephalin-like immunoreactivity appear to terminate in the feline homologue of the Onuf's nucleus (Glazer and Basbaum 1980, 1981), and opioids have been shown to have a role in the regulation of micturition at the lumbosacral spinal cord level (DeGroat et al. 1983; Thor et al. 1983; Jubelin et al. 1984; Dray and Nunan 1985). The enkephalin-containing fibers to the Onuf's nucleus have been reported to originate around the central canal and dorsal gray commissure (Konishi et al. 1985). It has also been known in the rat that the dorsal gray commissure and the spinal regions around motoneurons of the dorsolateral and dorsomedial groups are rich in neuropeptides (Gibson et al. 1981, 1984; Hunt et al. 1981; Sasek et al. 1984; Schrøder 1984; Charlton and Helke 1985; Honda and Lee 1985; Romagnano and Hamill 1985; Sasek and Elde 1985, 1986; Micevych et al. 1986).

Primary afferent neurons projecting bilaterally to the spinal cord appear to represent skin near the dorsal and ventral midlines (Culberson et al. 1979; Light and Perl 1979a, b; Koeber and Brown 1980; Smith 1983, 1986). In the dorsal horn, primary afferent terminals from the dorsalis penis (clitoridis) nerve were distributed more medially than those from the perinealis nerve. This arrangement appears to reflect an organization principle described for cutaneous representation in the dorsal horn; dorsal skin is represented laterally and ventral skin medially (Wall 1960; Pomeranz et al. 1968; Brown and Fuchs 1975; Grant and Ygge 1981; Ygge and Grant 1983; Smith 1983; Cervero

and Connell 1984). (For further references about the dorsal gray commissural and contralateral terminations of primary afferent neurons, see Light and Perl 1979a, b; Réthelyi et al. 1979; Morgan et al. 1981, 1986; Neuhuber 1982; Ciriello and Calaresu 1983; Kuo et al. 1983, 1984; Matsushita and Tanami 1983; Nadelhaft et al. 1983; Culberson and Brown 1984; Ueyama et al. 1984, 1985a, b; Kuo and DeGroat 1985; Roppolo et al. 1985; McKenna and Nadelhaft 1986; Neuhuber et al. 1986; Núnez et al. 1986).

The ipsilateral termination of pudendal nerve fibers to the gracile nucleus has been reported in the cat (Ueyama et al. 1984) and macaque monkey (Ueyama et al. 1985a), and the present study confirmed the bilateral termination of pudendal nerve fibers in the gracile nucleus of the rat (Ueyama et al. 1985b). Both dorsalis penis (clitoridis) and perinealis nerves were observed to terminate not only in the spinal cord but also in the gracile nucleus, bilaterally with an ipsilateral predominance. In the gracile nucleus, however, no regional difference was recognized between the terminal field of the dorsalis penis (clitoridis) nerve and that of the perinealis nerve, although somewhat more labelled terminals were seen in the gracile nucleus after HRP application to the perinealis nerve than after HRP application to the dorsalis penis (clitoridis) nerve. Some fibers in the pelvic nerve have also been reported to terminate within the gracile nucleus in the cat (Morgan et al. 1981), but it still remains to be ascertained if the terminal fields of the pelvic nerve to the gracile nucleus overlap with those of the pudendal nerve.

Núnez et al. (1986) reported that labelled possible axon terminals were observed in the spinal gray from the Th13 to S2 cord segments after applying HRP to the dorsal penile nerve of the rat. On the other hand, in the present study, presumed axon terminals of pudendal afferent fibers were observed to be distributed in the spinal gray from the L4 to the S2 cord segments, although some pudendal afferent fibers could be traced rostrally to the gracile nucleus. This obvious discrepancy in the segmental distribution of pudendal afferent fibers between the report of Núnez et al. (1986) and that of the present study might be ascribable to the difference of the survival time of the animals after application of HRP.

Nadelhaft and Booth (1984) observed that afferent fibers of the pelvic nerve in the rat constituted the longitudinal fiber bundle concentrated directly beneath the central canal, which they designated as the medial afferent bundle. This fiber bundle is also known to extend rostrally beyond the sacral region and to contain sympathetic afferent fibers in the upper cord segments (L7–Th11) (Neuhuber 1982). In the present study a few labelled axons were often observed in the regions ventral to the central canal, but it was not confirmed if these fibers were components of the medial afferent bundle.

In a recent light and electron microscopic study in the cat, Mawe et al. (1986) provided evidence indicating that some fibers in the dorsal root make synaptic contacts upon neurons in the sacral parasympathetic nucleus. Monosynaptic contact onto the sacral parasympathetic preganglionic neurons by primary afferent fibers of the pudendal nerve has been assumed to exist in the cat (Ueyama et al. 1984) and monkey (Roppolo et al. 1985), and the present data indicate that a small number of primary afferent fibers of the pudendal nerve terminate bilaterally in the intermediolateral nucleus at the levels of the L6 cord segment. On the other hand, Núnez et al. (1986) presumed that primary afferent fibers in the dorsalis penis nerve of the rat terminated directly onto motoneurons, as well as onto autonomic preganglionic neurons. In the present study, some dendrites of motoneurons in the dorsomedial group were seen to extend into the dorsal gray commissure and spinal regions around the central canal where primary afferent neurons of the pudendal nerve sent many axon terminals. However, no confirmatory evidence showing monosynaptic contact onto motoneurons by primary afferent fibers of the pudendal nerve was obtained.

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References

Abercrombie M (1946) Estimation of nuclear population from microtome sections. Anat Rec 94:239–247

Breedlove SM, Arnold AP (1980) Hormone accumulation in a sexually dimorphic motor nucleus in the rat spinal cord. Science 210:564–566

Breedlove SM, Arnold AP (1981) Sexually dimorphic motor nucleus in the rat lumbar spinal cord: response to adult hormone manipulation, absence in androgen-insensitive rats. Brain Res 225:297–307

Breedlove SM, Arnold AP (1983) Sex differences in the pattern of steroid accumulation by motoneurons of the rat lumbar spinal cord. J Comp Neurol 215:211–216

Breedlove SM, Jacobson CD, Gorski RA, Arnold AP (1982) Masculinization of the female rat spinal cord following a single neonatal injection of testosterone propionate but not estradiol benzoate. Brain Res 237:173–181

Breedlove SM, Jordan CL, Arnold AP (1983) Neurogenesis of motoneurons in the sexually dimorphic spinal nucleus of the bulbocavernosus in the rats. Develop Brain Res 9:39–43

Brown PB, Fuchs JL (1975) Somatotopic representation of hindlimb skin in cat dorsal horn. J Neurophysiol 38:1–9

Cervero F, Connell L (1984) Distribution of somatic and visceral primary afferent fibers within the thoracic spinal cord of the cat. J Comp Neurol 230:88–98

Ciriello J, Calaresu FR (1983) Central projections of afferent renal fibers in the rat: an anterograde transport study of horseradish peroxidase. J Auton Nerv Syst 8:273–285

Charlton CG, Helke CJ (1985) Autoradiographic localization and characterization of spinal cord substance P binding sites: high densities in sensory, autonomic, phrenic, and Onuf's motor nuclei. J Neurosci 5:1653–1661

Culberson JL, Brown PB (1984) Projections of hindlimb dorsal roots to lumbosacral spinal cord of cat. J Neurophysiol 51:516–528

Culberson JL, Haines DE, Kimmel KL, Brown PB (1979) Contralateral projections of primary afferent fibers to mammalian spinal cord. Exp Neurol 64:83–97

De Araujo CG, Schmidt RA, Tanaglio EA (1982) Neural pathways to lower urinary tract identified by retrograde axonal transport of horseradish peroxidase. Urology 19:290–295

DeGroat WC, Booth AM (1980) Physiology of the urinary bladder and urethra. Ann Intern Med 92:312–315

DeGroat WC, Nadelhaft I, Milne RJ, Booth AM, Morgan C, Thor K (1981) Organization of the sacral parasympathetic reflex pathways to the urinary bladder and large intestine. J Auton Nerv Syst 3:135–160

DeGroat WC, Kawatani M, Hisamitsu T, Lowe I, Morgan C,

Roppolo J, Booth AM, Nadelhaft I, Kuo D, Thor K (1983) The role of neuropeptides in the sacral autonomic reflex pathways of the cat. J Auton Nerv Syst 7:339–350

Dray A, Nunan L (1985) Opioid inhibition of reflex urinary bladder contractions: dissociation of supraspinal and spinal mechanisms. Brain Res 337:142–145

Fishman RB, Breedlove SM (1985) The androgenic induction of spinal sexual dimorphism is independent of supraspinal afferents. Dev Brain Res 23:255–258

Gibson SJ, Polak JM, Bloom SR, Wall PD (1981) The distribution of nine peptides in the rat spinal cord with special emphasis on the substantia gelatinosa and on the area around the central canal (lamina X). J Comp Neurol 201:65–79

Gibson SJ, Polak JM, Allen JM, Adrian TE, Kelly JS, Bloom SR (1984) The distribution and origin of a novel brain peptide, neuropeptide Y, in the spinal cord of several mammals. J Comp Neurol 227:78–91

Glazer EJ, Basbaum AI (1980) Leucine enkephalin: localization in and axoplasmic transport by sacral parasympathetic preganglionic neurons. Science 208:1479–1481

Glazer EJ, Basbaum AI (1981) Immunohistochemical localization of leucine-enkephalin in the spinal cord of the cat: enkephalin-containing marginal neurons and pain modulation. J Comp Neurol 196:377–389

Grant G, Ygge J (1981) Somatotopic organization of the thoracic spinal nerve in the dorsal horn demonstrated with transganglionic degeneration. J Comp Neurol 202:357–364

Hayes KJ (1965) The so-called "levator ani" of the rat. Acta Endocrinol (Copenh) 48:337–347

Honda CN, Lee CL (1985) Immunohistochemistry of synaptic input and functional characterization of neurons near the spinal central canal. Brain Res 343:120–128

Hulsebosch CE, Coggeshall RE (1982) An analysis of the axon populations in the nerves to the pelvic viscera in the rat. J Comp Neurol 211:1–10

Hunt SP, Emson PC, Gilbert R, Goldstein M, Kimmel JR (1981) Presence of avian pancreatic polypeptide-like immunoreactivity in catecholamine and methionine-enkaphalin-containing neurones within the central nervous system. Neurosci Lett 21:125–130

Jordan CL, Breedlove SM, Arnold AP (1982) Sexual dimorphism and the influence of neonatal androgen in the dorsolateral motor nucleus of the rat lumbar spinal cord. Brain Res 249:309–314

Jubelin B, Galeano C, Ladouceur D, Lemaire S, Elhilali MM (1984) Effect of enkephalin on the micturition cycle of the cat. Life Sci 34:2015–2027

Katagiri T, Gibson SJ, Su HC, Polak JM (1986) Composition and central projections of the pudendal nerve in the rat investigated by combined peptide immunohistochemistry and retrograde fluorescent labelling. Brain Res 372:313–322

Koeber HR, Brown PB (1980) Projections of two hindlimb cutaneous nerves to cat dorsal horn. J Neurophysiol 44:259–269

Konishi A, Sato M, Mizuno N, Itoh K, Nomura S, Sugimoto T (1978) An electron microscope study of the areas of the Onuf's nucleus in the cat. Brain Res 156:333–338

Konishi A, Itoh K, Sugimoto T, Yasui Y, Kaneko T, Takada M, Mizuno N (1985) Leucine-enkephalin-like immunoreactive afferent fibers to pudendal motoneurons in the cat. Neurosci Lett 61:109–113

Kuo DC, DeGroat WC (1985) Primary afferent projections of the major splanchnic nerve to the spinal cord and gracile nucleus of the cat. J Comp Neurol 231:421–434

Kuo DC, Nadelhaft I, Hisamitsu T, DeGroat WC (1983) Segmental distribution and central projections of renal afferent fibers in the cat studied by transganglionic transport of horseradish peroxidase. J Comp Neurol 216:162–174

Kuo DC, Oravitz JJ, DeGroat WC (1984) Tracing of afferent and efferent pathways in the left inferior cardiac nerve of the cat using retrograde and transganglionic transport of horseradish peroxidase. Brain Res 321:111–118

Kuru M (1965) Nervous control of micturition. Physiol Rev 45:425–494

Kuzuhara S, Kanazawa I, Nakanishi T (1980) Topographical localization of the Onuf's nucleus innervating the rectal and vesical striated sphincter muscles: a retrograde fluorescent double labelling in cat and dog. Neurosci Lett 16:125–130

Light AR, Perl ER (1979a) Reexamination of the dorsal root projection to the spinal dorsal horn including observations on the differential termination of coarse and fine fibers. J Comp Neurol 186:117–132

Light AR, Perl ER (1979b) Spinal termination of functionally identified primary afferent neurons with slowly conducting myelinated fibers. J Comp Neurol 186:133–150

Mannen T, Iwata M, Toyokura Y, Nagashima K (1977) Preservation of a certain motoneurone group of the sacral cord in amyotrophic lateral sclerosis: its clinical significance. J Neurol Neurosurg Psychiatr 40:464–469

Mannen T, Iwata M, Toyokura Y, Nagashima K (1982) The Onuf's nucleus and the external anal sphincter muscles in amyotrophic lateral sclerosis and Shy-Drager syndrome. Acta Neuropathol (Berl) 58:255–260

Matsushita M, Tanami T (1983) Contralateral termination of primary afferent axons in the sacral and caudal segments of the cat, as studied by anterograde transport of horseradish peroxidase. J Comp Neurol 220:206–218

Mawe GM, Bresnahan JC, Beattie MS (1986) A light and electron microscopic analysis of the sacral parasympathetic nucleus after labelling primary afferent and efferent elements with HRP. J Comp Neurol 250:33–57

McKenna KE, Nadelhaft I (1986) The organization of the pudendal nerve in the male and female rat. J Comp Neurol 248:532–549

Mesulam M-M (1978) Tetramethyl benzidine for horseradish peroxidase neurohistochemistry: a non-carcinogenic blue reaction-product with superior sensitivity for visualizing neural afferents and efferents. J Histochem Cytochem 26:106–117

Micevych PE, Coquelin A, Arnold AP (1986) Immunohistochemical distribution of substance P, serotonin, and methionine enkephalin in sexually dimorphic nuclei of the rat lumbar spinal cord. J Comp Neurol 248:235–244

Morgan C, Nadelhaft I, DeGroat WC (1981) The distribution of visceral primary afferents from the pelvic nerve to Lissauer's tract and the spinal gray matter and its relationship to the sacral parasympathetic nucleus. J Comp Neurol 201:415–440

Morgan C, DeGroat WC, Nadelhaft I (1986) The spinal distribution of sympathetic preganglionic and visceral primary afferent neurons that send axons into the hypogastric nerves of the cat. J Comp Neurol 243:23–40

Nadelhaft I, Booth AM (1984) The location and morphology of preganglionic neurons and the distribution of visceral afferents from the rat pelvic nerve: a horseradish peroxidase study. J Comp Neurol 226:238–245

Nadelhaft I, Roppolo J, Morgan C, DeGroat WC (1983) Parasympathetic preganglionic neurons and visceral primary afferents in monkey spinal cord revealed following application of horseradish peroxidase to pelvic nerve. J Comp Neurol 216:36–52

Nagashima T, Beppu H, Uono M, Yamada H (1979) Demonstration of neuronal localization in Onufrowicz's group-X in rabbit by double labelling method. Acta Histochem Cytochem (Japan) 12:409–415

Nahin RL, Madsen AM, Giesler GJ Jr (1983) Anatomical and physiological studies of the gray matter surrounding the spinal cord central canal. J Comp Neurol 220:321–335

Nakagawa S (1980) Onuf's nucleus of the sacral cord in a South American monkey (Saimiri): its location and bilateral cortical input from area 4. Brain Res 191:337–344

Neuhuber W (1982) The central projections of visceral primary afferent neurons of the inferior mesenteric plexus and hypogastric nerve and the location of the related sensory and preganglionic sympathetic cell bodies in the rat. Anat Embryol 164:413–425

Neuhuber WL, Sandoz PA, Fryscak T (1986) The central projections of primary afferent neurons of greater splanchnic and intercostal nerves in the rat. A horseradish peroxidase study. Anat Embryol 174:123–144

Núnez R, Gross GH, Sachs BD (1986) Origin and central projections of rat dorsal penile nerve: possible direct projection to autonomic and somatic neurons by primary afferents of non-muscle origin. J Comp Neurol 247:417–429

Onuf (Onufrowicz) B (1899) Notes on the arrangement and function of the cell groups in the sacral region of the spinal cord. J Nerv Ment Dis 26:498–504

Onuf (Onufrowicz) B (1900) On the arrangement and function of the cell groups of the sacral region of the spinal cord in man. Arch Neurol Psychopathol 3:387–412

Petras JM, Cummings JF (1978) Sympathetic and parasympathetic innervation of the urinary bladder and urethra. Brain Res 153:363–369

Pomeranz B, Wall PD, Weber WV (1968) Cord cells responding to fine myelinated afferents from viscera, muscle and skin. J Physiol (Lond) 199:511–532

Réthelyi M, Trevino DL, Perl ER (1979) Distribution of primary afferent fibers within the sacrococcygeal dorsal horn: an autoradiographic study. J Comp Neurol 185:603–622

Romagnano MA, Hamill RW (1985) Spinal parasympathetic enkephalin fibers: patterns and projections. Brain Res 335:174–181

Roppolo JR, Nadelhaft I, DeGroat WC (1985) The organization of pudendal motoneurons and primary afferent projections in the spinal cord of the rhesus monkey revealed by horseradish peroxidase. J Comp Neurol 234:475–388

Rose RD, Collins WF III (1985) Crossing dendrites may be a substrate for synchronized activation of penile motoneurons. Brain Res 337:373–377

Sasek CA, Elde RP (1985) Distribution of neuropeptide Y-like immunoreactivity and its relationship to FMRF-amide-like immunoreactivity in the sixth lumbar and first sacral spinal cord segments of the rat. J Neurosci 5:1729–1739

Sasek CA, Elde RP (1986) Coexistence of enkephalin and dynorphin immunoreactivities in neurons in the dorsal gray commissure of the sixth lumbar and first sacral cord segments in rat. Brain Res 381:8–14

Sasek CA, Seybold JS, Elde RP (1984) The immunohistochemical localisation of nine peptides in the sacral parasympathetic nucleus and the dorsal grey commissure in rat spinal cord. Neuroscience 12:855–873

Sato M, Mizuno N, Konishi A (1978) Localization of motoneurons innervating perineal muscles: a HRP study in cat. Brain Res 140:149–154

Schrøder HD (1980) Organization of the motoneurons innervating the pelvic muscles of the male rat. J Comp Neurol 192:567–587

Schrøder HD (1981) Onuf's nucleus X: a morphological study of a human spinal nucleus. Anat Embryol 162:443–453

Schrøder HD (1984) Somatostatin in the caudal spinal cord: an immunohistochemical study of the spinal centers involved in the innervation of pelvic organs. J Comp Neurol 223:400–414

Schrøder HD (1985) Anatomical and pathoanatomical studies on the spinal efferent systems innervating pelvic structures. 1. Organization of spinal nuclei in animals. 2. The nucleus X-pelvic motor system in man. J Auton Nerv Syst 14:23–48

Senegelaub DR, Arnold AP (1986) Development and loss of early projections in a sexually dimorphic rat spinal nucleus. J Neurosci 6:1613–1620

Smith CL (1983) The development and post-natal organization of primary afferent projections to the rat thoracic spinal cord. J Comp Neurol 220:29–43

Smith CL (1986) Sensory neurons supplying touch domes near the body midlines project bilaterally in the thoracic spinal cord of rats. J Comp Neurol 245:541–552

Streit P, Reubi JC (1977) A new and sensitive staining method for axonally transported horseradish peroxidase (HRP) in the pigeon visual system. Brain Res 126:530–537

Taylor DCM, Korf H-W, Pierau Fr-K (1982) Distribution of sensory neurones of the pudendal nerve in the dorsal root ganglia and their projection to the spinal cord. Horseradish-peroxidase studies in the rat. Cell Tissue Res 226:555–564

Thor KB, Roppolo JR, DeGroat WC (1983) Naloxone induced micturition in unanesthetized paraplegic cats. J Urol 129:202–205

Ueyama T, Mizuno N, Nomura S, Konishi A, Itoh K, Arakawa H (1984) Central distribution of afferent and efferent components of the pudendal nerve in cat. J Comp Neurol 222:38–46

Ueyama T, Mizuno N, Takahashi O, Nomura S, Arakawa H, Matsushima R (1985a) Central distribution of efferent and afferent components of the pudendal nerve in macaque monkey. J Comp Neurol 232:248–556

Ueyama T, Arakawa H, Mizuno N (1985b) Contralateral termination of pudendal nerve fibers in the gracile nucleus of the rat. Neurosci Lett 62:113–117

Wall PD (1960) Cord cells responding to touch, damage, and temperature of skin. J Neurophysiol 23:197–210

Wan XST, Trojanowski FQ, Gonatas JO, Liu CN (1982) Cytoarchitecture of the extranuclear and commissural dendrites of hypoglossal nucleus neurons as revealed by conjugates of horseradish peroxidase with cholera toxin. Exp Neurol 78:167–175

Weiss HD (1972) The physiology of human penile erection. Ann Intern Med 76:793–799

Yamamoto T, Satomi H, Ise H, Takatama H, Takahashi K (1978) Sacral spinal innervations of the rectal and vesical smooth muscles and the sphincter-ic striated muscles as demonstrated by the horseradish peroxidase method. Neurosci Lett 7:41–47

Ygge J, Grant G (1983) The organization of the thoracic spinal nerve projection in the rat dorsal horn demonstrated with transganglionic transport of horseradish peroxidase. J Comp Neurol 216:1–9

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