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Functional Characteristics of Lumbar Spinal Neurons Projecting to Midbrain Area in Rats

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=ABSTRACT=

The present study was carried out to characterize the functional properties of spinomesencephalic tract (SMT) neurons in the lumbar spinal cord of urethane anesthetized rats. Extracellular single unit recordings were made from neurons antidromically activated by stimulation of the midbrain area, including the deep layers of superior colliculus, periaqueductal gray and midbrain reticular formation. Recording sites were located in laminae I -VII of spinal cord segments of L2-L5. Receptive field properties and responses to calibrated mechanical stimulation were studied in 78 SMT cells. Mean conduction velocity of SMT neurons was 19.1±1.04 m/sec. SMT units were classified according to their response profiles into four groups: wide dynamic range (58%), deep/tap (23%), high threshold (9%) and low threshold (3%). A simple excitatory receptive field was found for most SMT neurons recorded in superficial dorsal horn (SDH). Large complex inhibitory and/or excitatory receptive fields were found for cells in lateral reticulated area which usually showed long after-discharge. Most of SMT cells received inputs from Aδ and C afferent fiber types. These results suggest that sensory neurons in the rat SMT may have different functional roles according to their location in the spinal cord in integrating and processing sensory inputs including noxious mechanical stimuli.

Key Words: Spinomesencephalic tract, Midbrain, Spinal cord, Mechanosensitivity

INTRODUCTION

Since the first demonstration of spinal neurons projecting to the midbrain using anterograde degeneration technique following cordotomies (Collier & Buzzard, 1903), spinomesencephalic tract (SMT) has been described in a variety of species, including man (Bowsher, 1957; Antonetty & Webster, 1975; Menétrey et al, 1982; Wiberg & Blomqvist, 1984; Yezierski, 1988). Mesencephalic terminal area of this projection includes th following structures: periaqueductal gray (PAG), nucleus intercollicularis, deep layers of the superior colliculus, external nucleus of the inferior colliculus, nucleus of Darkschewitsch, nucleus cuneiformis, anterior and posterior pretectal nuclei, and the lateral part of the central gray (Yezierski, 1988; Blomqvist and Craig, 1991).

The cells of origin of the spinomesencephalic tract have been mapped using the horseradish peroxidase (HRP) technique. Menetrey et al

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(1982) found spinal neurons projecting to the rat midbrain in the marginal zone, the neck of the dorsal horn and dorsal gray commissure. Also in the rat, Liu (1983) observed labeled somata in lamina I, III, V, VII and X following injections of HRP in the ventrolateral PAG. The laminar distribution of spinomesencephalic tract cells in the primate was found to be similar to that in the rat but included also laminae VI-VIII (Willis et al, 1979). The majority of SMT cells in the cat were found in the lateral part of lamina I with only a small fraction in laminae IV-V (Wieberg & Blomquist, 1984).

In contrast to what is known about the origin and termination of the SMT, relatively little is known about the physiology of this pathway (Willis & Coggeshall,1991). Early studies (Morin, 1953; Collins & O'Leary, 1954) have shown that evoked potentials can be recorded in the midbrain tegmentum and superior colliculus in response to stimualtion of ipsilateral or contralateral cutaneous, muscle or joint nerves. Single-unit studies have shown that cells in different midbrain regions are responsive to innocuous as well as noxious somatic stimuli and have large, often bilateral, receptive fields (Barnes, 1976; Nagata & Kruger, 1979; Tawil et al, 1983). The involvement the spinomesencephalic projection in transmission of somatosensory information was also supported by the result of studies related to the cells of origin of this pathway. Fields et al (1977) described that cells projecting to the cat midbrain receive convergent inputs from cutaneous as well as deep receptors with some cells responding maximally to noxious stimuli. Responses to thermal and non-noxious mechanical stimuli, applied to different parts of the body, have also been described (Yezierski & Schwartz, 1986; Yezierski & Broton, 1991). However, most previous electro-physiological investigation were made on SMT neurons in a restricted area of spinal cord such as dorsal horn (Menétrey et al, 1980) and laminar I (Hylden et al, 1986). In the rat, although prominent SMT projections arising from the ventral half of spinal gray matter were confirmed in the histological study, functional characteristics of these neurons have not been clearly studied. The present study was designed to evaluate the functional properties of SMT cells according to their location in the spinal gray matter.

METHODS

Animal preparation

Experiments were performed on 23 male Sprague-Dawley rats weighing between 300 and 400 g. Following an intraperitoneal injection of atropine bromide to reduce tracheal secretions, the animals were anesthetized with urethane (1.0-1.25g/kg, i.p.). Tracheotomy and cannulations of the external jugular vein and carotid artery were performed and the animals were artificially ventilated after an intravenous injection of pancuronium bromide to minimize movements of spinal cord due to reflexive movements. Arterial blood pressure and end-tidal CO_2 concentration were monitored continuously and kept within normal limits. Core temperature was monitored by a rectal thermometer and thermostatically maintained at preset temperature (37°C). Following the holding of the animals on the stereotaxic apparatus, laminectomy was performed between T11 and L2 vertebra, and the cord dorsum potentials evoked by electrical stimulation of the ipsilateral hindpaw were checked to localize the area receiving maximum peripheral input to the cord. The dura was opened over this area and a mineral oil pool was formed around the spinal cord by retracting the skin flap and fixing it to the stereotaxic frame. Copper coils connected to a circulating water bath were used to keep the temperature of mineral oil at 37°C throughout the experiment. After craniotomy near lambda on the contralateral parietal bone, the ipsilateral sciatic nerve was exposed and placed intact on a

pair of silver hook electrodes.

Stimulation and recording

Units directly projecting to the midbrain structures were characterized by antidromic activation (0.1 msec duration, 2-3Hz, 500 μA). An antidromic stimulating electrode (Stainless steel; monopolar; tip diameter 0.1 mm; tip exposure 0.2 mm) was positioned in the midbrain at anteroposterior levels of intercollicular region (anterior 0-3 mm, lateral 0.5-2 mm, depth 3-5 mm) according to the atlas of rat brain (Paxino & Watson,1986). The following criteria were used to identify an antidromic activation: 1)constant latency of spike to midbrain stimulation, 2)ability to follow a high frequency (333 Hz) stimulus without any modification in latency, 3)collision with spontaneous or evoked orthodromic impulses, and 4)discrete threshold (Fig. 1). Spinal single cell units activated by antidromic stimulation were recorded at the spinal cord level of L2-L5 through carbon filament electrodes (tip resistance, 1-4 MΩ). It was necessary to make small holes in the pia to allow smooth penetration by the glass micropipettes into the spinal cord. The recorded signal was amplified with AC differential amplifier (DAM-80, WPI), monitored on oscilloscope (5113, Tektronix) and fed into window discriminator (WPI) and laboratory interface (CED 1401) stored in a personal computer for further analysis.

The responses of neurons to mechanical stimulation of their cutaneous receptive field were characterized by applying graded intensity of von Frey filament during extracellular recording. Neurons were classified as wide dynamic range(WDR) cells if they presented a graded response to innocuous tactile stimuli and noxious pinch, as low-threshold (LT) cells if they responded maximally to innocuous tactile stimuli, as high-threshold (HT) cells if they responded only to noxious mechanical stimuli, and as deep/tap (Deep) cells if they responded not to subcutaneous stimuli but to tap, joint movement or probing of subcutaneous structures such as muscles (Fig.4). The responsiveness to the electrical stimulation of sciatic nerve with Aδ (0.1 msec, 0.5-1 mA) and C intensity (0.5 msec, 5 mA) was characterized.

Histology

After completing study of the cell, electrolytic lesions were made (DC current of 100-200 μA, 20-30 sec duration) for histological identification of recording site. At the end of the experiment, the antidromic stimulation site in midbrain was marked by passing DC current through the stimulating electrode and depositing the ferrite ion. And the animals were perfused transcardially with 1% solution of potassium ferrocyanide in 10% formalin. Then the brain and spinal cord were removed and post-fixed for 3-5 days. Frozen sections were cut at 50 μm and stained with cresyl-violet.

Statistical analysis

Statistical comparisons were performed using Student's t-test, chi-square test and Newman-Keuls test and $p<0.05$ was used for all tests of significance. Mean values are presented with their standard errors.

RESULTS

Stimulating and recording sites

A total of 78 lumbar units were activated by contralateral midbrain stimualtion. All 4 antidromic criteria were met for 63/78 cells. Collision could not be demonstrated for 15 cells. The location of antidromic stimulating sites at five different midbrain levels and the distribution of recording sites at L2-L5 spinal cord levels are shown in Fig. 2. According to the location of recording sites in different regions of the spinal gray matter (Fig. 2C based on Burstein et al, 1990), cells were classified into

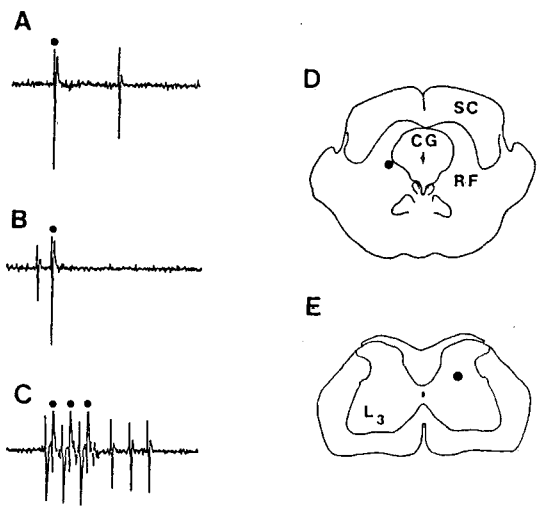

Fig. 1. An example of spinomesencephalic tract neurons identified by antidromic stimulation of midbrain. Dicrete threshold and constant latency of spike to stimulation (A), collision with spontaneous or evoked orthodromic impulses (B), and ability to follow a high frequency (333 Hz) stimulus without any modification in latency (C) were considered as criteria. D and E represent the location of stimulating and recording sites of these cells. SC, superior colliculus; CG, central gray matter; RF, reticular formation.

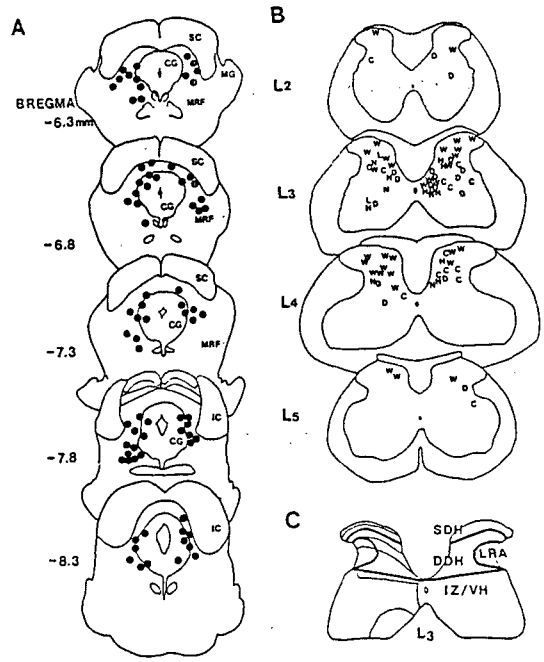

Fig. 2. Histological reconstruction of antidromic stimulation sites (A) and recording sites of SMT cells (B). Division of spinal cord gray matter (C) was based on Burstein et al (1990). Abbreviations: SC, superior colliculus; CG, central gray; MG, medial geniculate; MRF, midbrain reticular formation; IC, inferior colliculus; W, simple wide dynamic range cell; C, complex wide dynamic range cell; H, high threshold cell; L, low threshold cell; D, deep/tap cell; N, non-responsive; SDH, superficial dorsal horn; DDH, deep dorsal horn; LRA, lateral reticulated area; IZ/VH, intermediate zone and ventral horn.

four groups: superficial dorsal horn (SDH), deep dorsal horn (DDH), lateral reticulated area (LRA), and intermediate zone and ventral horn (IZ/VH). As shown in Table 1, most of the WDR cells (32/45) were located in SDH and DDH. In SDH group, 10 of 11 cells were simple WDR. The 12 of 18 Deep Cells were found in laminae V, VI, VII, and VIII.

Conduction velocity

The frequency distribution of conduction velocities for the 78 cells in this study is illustrated in Fig. 3A. Conduction velocities ranged from 4.9 to 41.4 m/sec with a mean of 19.1±1.04 m/sec. The antidromic threshold for these cells was 314±23 μA (Fig. 3B). Most cells (44/78) were activated with the stimulation strength less than 250 μA. The conduction velocities of neurons recorded in SDH (15.8±1.2 m/sec, n=11) were significantly slower (t-test, $p<0.05$) than those recorded in IZ/VH (24.2±2.4 m/sec, n=19).

Response profiles

Seventy-two SMT units were tested in response to peripheral stimulation. Forty five cells were classified as WDR cells, 18 as Deep, 7 as HT, and 2 as LT cells. Typical responses of

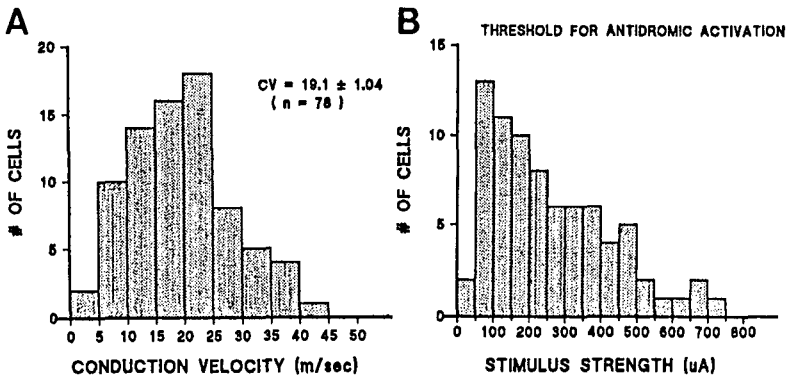

Fig. 3. Histograms showing conduction velocity (A) and threshold for antidromic activation (B) of SMT cells.

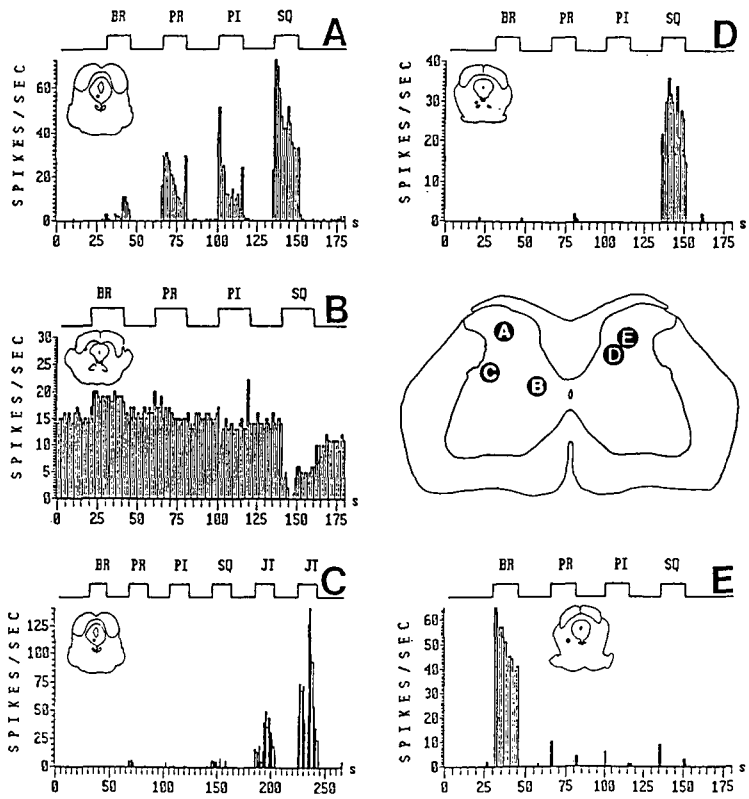

Fig. 4. Response profiles of SMT cells. A, simple WDR cell; B, complex WDR cell; C, deep/tap cell; D, high threshold cell; E, low threshold cell; BR, brush; PR, pressure; PI, pinch; SQ, squeeze; JT, joint movement.

each cell group are shown in Fig. 4. WDR cells were divided into two subclasses based on receptive field (RF) location. Thirty-one cells with excitatory RFs restricted to the ipsilateral hindlimb were classified as simple WDR cells. Fourteen cells with large excitatory and/or

Table 1. Summary of response characteristics and cell location in spinal cord of spinomesencephalic tract neurons

	SDH	DDH	LRA	IZ/VH	Total
Simple WDR	10	18	3		31
Complex WDR	1	3	5	5	14
LT		1		1	2
HT		5		2	7
Deep		7	3	8	18
NR		2	1	3	6
	11	36	12	19	78

See text for abbreviations

inhibitory RFs that included the ipsilateral hindlimb and other parts of the body were classified as complex WDR cells. In addition to RF size, complex WDR cells differ from simple WDR cells in after-discharge. After-discharges lasting longer than 20 seconds after the cessation of stimulation were shown in 9/13 complex WDR group and 6/21 simple WDR group, on which chi-square test indicated a significant difference between two groups ($x^2=3.841$, $p<0.05$).

Von Frey test in WDR cells

Responses to the mechanical stimulation with calibrated von Frey filaments were examined in the 21 WDR cells. Most cells revealed excitatory responses to stimulation with the threshold between 0.3 and 7 g. Firing rate of the cell increased in proportion to the stimulus strength (Fig. 5).

Receptive field size

Receptive field sizes of 72 cells were compared according to their recording sites (Fig. 6). The RFs of LRA group cells were significantly greater than those of DDH cells ($p<0.05$, Newman-Keuls test). There was no significant difference between SDH and DDH group.

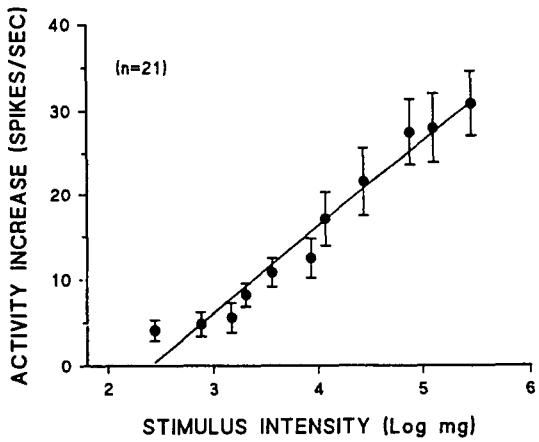

Fig. 5. Stimulus intensity-response relationship for 21 WDR cells determined with von Frey filaments applied to the most sensitive glaborous skin on the ipsilateral foot.

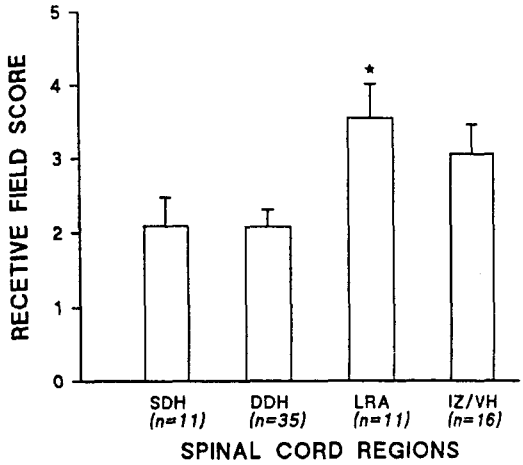

*Fig. 6. Comparison of the receptive field (RF) size of the SMT units according to their location, based on the following RF scores: 1, Ipsilateral foot only; 2, Ipsilateral hindlimb; 3, Scrotum or tail in addition to ipsilateral hindlimb; 4, Ipsilateral and contralateral hindlimbs; 5, Other body parts in addition to both hindlimbs. * Indicates the significant difference from DDH at $p<0.05$.*

After-discharge

After-discharges of SMT units, spikes firing

Table 2. Incidence and firing rates of afterdischarges

	SDH (n=11)	DDH (n=33)	LRA (n=11)	IZ/VH (n=14)
# of afterdischarging cells[1)]	7	11	8	4
Firing rates at 10 seconds after stimulation	12.8±4.5	17.0±4.26	42.0±6.4[2)3)]	19.2±2.8

1) Chi-square test shows significant difference between groups at $p<0.05$
2) Significantly different from IZ/VH at $p<0.05$
3) Significantly different from SDH and from DDH at $p<0.01$

Table 3. Primary afferent inputs to spinomesence phalic tract neurons

	Aδ	Aδ+C	C
Simple WDR	16	20	
Complex WDR	5	2	
Deep	5	1	
HT	2	2	1
LT	1		
	29	25	1

even after the cessation of stimulation with the 100 g strength of von Frey filament for 10 seconds, were compared between groups with different location . The incidence and the firing rate of afterdischarge were significantly higher for the cells in LRA (Table 2).

Afferent nerve fibers

In 55 cells, attempts to identify the types of afferent nerve fibers were made. Spinomesencephalic tract neurons appeared to receive afferent inputs from both Aδ and C type fibers (Table 3).

DISCUSSION

The results of this electrophysiological study provide further evidence supporting the arguement that spinomesencephalic tract (SMT) is made up of multiple neurons with different functional properties as well as different pattern of projection. Spinomesencephalic tract neurons were found in laminae I-VIII in this study. This result is consistent with the distribution of SMT cells in the rat (Menétrey et al, 1982; Liu, 1983), cat (Yezierski & Schwartz, 1986) and primate (Willis et al, 1979). The distribution of recording sites (Fig 2B) is comparable to that observed for fluorescent dye-labeled cells following midbrain injections of this retrograde tracer (Yezierski & Mendez, 1991). Compared with spinoreticular tract neurons (Menétrey et al, 1980), relatively more SMT neurons were found in medial part of intermediate zone and ventral horn, most of which (13/19) were Deep or complex WDR cells.

The four functional classes of SMT cells in this study are similar to those reported for the cells of origin of other ascending spinal pathways (Fields et al, 1977; Carstens & Trevino, 1978; Menétrey et al, 1980; Burstein et al, 1990). The finding that more than 50% of SMT units (WDR and HT, 52/78) were solely or maximally driven by noxious stimuli strongly emphasizes the involvement of this pathway in the transmission of nociceptive signals. This is further supported by the observation that PAG in midbrain plays the major role in the descending inhibitory control of pain (Basbaum & Fields, 1984). Other types of spinomesencephalic neurons were solely driven either by nonnoxious cutaneous stimuli (LT, 2 cells) or by tapping deep structures such as muscles and joints (Deep, 18 cells). The pres-

ence of these type cells shows the possible role of SMT in transmission of nonnoxious information. Deep type cells were usually found in laminae V-VIII. The response profiles of complex WDR cells appeared different from those of simple WDR cells. Complex WDR cells, usually found in the deeper part of gray matter, showed a higher rate of spontaneous firing and after-discharges. About half of these cells had inhitory receptive fields. As shown in Fig.4B, some complex WDR cells showed both excitatory respose to weak mechanical stimulation and inhibitory response to stronger stimulation applied to the same area. Two complex WDR cells were only inhibited by stimulation of their receptive fields. This kind of WDR cell with inhibitory response was also reported in rat spinoreticular tract neurons (Menetrey et al, 1980) and cat SMT neurons (Yezierski & Schwartz,1986). Even though a small population of SMT neurons could be assumed to transmit inhibitory sensory signals, the physiological significance of this inhibitory input to midbrain reticular formation remains unclear. The response and receptive-field properties of rat SMT neurons were almost same as those of cat SMT neurons. Considering that the histological distribution of SMT neurons maintains a phylogenetic constancy across several species (Yezierski, 1988), their functional characteristics could be also regarded as very similar between species. However, the conduction velocity of rat SMT (19.1 ± 1.04 m/sec) was slower than that of cat SMT (45.2 ± 21.4 m/sec) reported by Yezierski & Schwartz (1986).

In the present study, antidromic activation was used to identify neurons at the origin of lumbar spinomesencephalic tract in the rat. Since there are several ascending pathways from the spinal cord to the brain, attempts were made to preferentially activate the spinomesencephalic tract neurons. First, midbrain stimulation sites were chosen mainly at the intercollicular level to avoid the activation of spinocerebellar tract. Second, the depth of stimulating electrode was selected to be between 3.5-4.5 mm below the cerebral cortex, which was dorsal to superior cerebellar peduncle. Third, at midbrain sites, stimulating electrode was placed as medially as possible to reduce the possibility of activating spinothalamic tract(STT). Giesler et al (1981) described that spinothalamic tract passed the lateral part of midbrain reticular formation. Yezierski (1988) found that the strongest projection of spinomesencephalic tract was to the medial part of midbrain surrounding ventral periaqueductal gray (PAG) at intercollicular region and caudal midbrain contralateral to injection sites of wheat-germ agglutinin conjugated tohorse-radish peroxidase-in the spinal cord of rat. However, because only a single stimulating electrode was used in midbrain sites for antidromic activation, SMT cells projecting to bilateral midbrain area and those projecting to both midbrain and thalamus could not be completely ruled out. Additional studies will be needed to further clarify the discrepancies between the distribution of SMT cells determined by antidromic stimulation and that by retrograde tracing methods.

Midbrain areas receiving SMT inputs have been shown to be important in the descending control of spinal neurons (Liebeskind et al, 1973; Basbaum & Fields, 1984), locomotor (Sinnamon, 1984), sexual (Hansen & Gummesson, 1982) and defensive behaviors (Bandler & Depaulis, 1988). Efferent projections from the midbrain have been shown to influence hypothalamic, diencephalic, and cortical neurons (Barone et al, 1981; Barbaresi et al, 1982). Therefore, the SMT neurons providing afferent inputs to midbrain areas are considered important in the motivational affective dimensions of pain as well as in the negative feedback control of spinal sensory neurons.

The electrophysiological properties and conduction velocities of SMT cells closely parallel those reported in spinothalamic (Giesler et al, 1976), spinoreticular (Menétrey

et al, 1980) and spinohypothalamic tract neurons (Burstein et al, 1990). However, SMT cells differ from spinothalamic (STT) and spinohypothalamic tract (SHT) by having larger receptive fields extending to proximal parts of the limb. Most of STT and SHT cells recorded in the lumbar enlargement showed their receptive field localized mainly in ipsilateral foot. Many SMT units, especially those in the lateral part of deep dorsal horn (LRA) showed larger receptive fields frequently extending to scrotum, contralateral hindlimb and other parts of body. This is in agreement with the findings obtained by Brown & Fuchs (1975) where, in the cat, the size increase and proximal extension of receptive fields correlated with increasingly lateral location of the units in the dorsal horn. In addition to the difference in receptive field size, the cells in lateral reticulated area (LRA) showed the higher incidence (9/12 cells) of spontaneous activity, compared with DDH cells (10/36). Most of SMT units in LRA showed also higher rates of greater after-discharge, which lasted longer than 20 seconds after the stimulation. Therefore, it is assumed that the cells in LRA could play a different role in transmitting the sensory signal.

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