A Comparative Study on the Electrophysiological Properties of Medial and Lateral Spinoreticular Tract Cells in Cats

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ABSTRACT

Antidromically activated spinoreticular tract (SRT) cell units in the lumbosacral enlargement of α-chloralose anesthetized cats were classified as medial and lateral SRT units according to the location of their axonal termination. Identified SRT units were tested for antidromic conduction velocity, laterality of their axonal projection, the location in spinal gray, peripheral receptive field, the response pattern to graded mechanichal stimulation and the responsiveness to Aδ and C volley of the peripheral nerve.

1) The 59% of 34 medial SRT units were recorded in ipsilateral side to the antidromic stimulation site, but 60% of the 47 lateral SRT units projected to contralateral side.

2) Most of the medial SRT cells and rostral ventrolateral medulla (RVLM)-projecting lateral SRT cells were recorded in lamina VII & VIII. The LRN (lateral reticular nucleus)-projecting SRT cells, however, distributed through all the laminae except superficial ones (I & II).

3) The identified SRT units were classified as low theshold (LT), deep, high threshold (HT), wide dynamic range (WDR) cells, based on the response patterns to graded mechanical stimuli. The proportion of SRT units which receive noxious input was 37.5%, 25% and 75% in the medial, LRN-projecting and RVLM SRT group, respectively.

4) There was no significant difference in the mean conduction velocities between the 3 groups. But the deep cells had significantly higher velocity than that of the HT cells.

The above results show that the peripheral inputs to the SRT units are different in the 3 groups: medial, LRN & RVLM SRT group. Especially in case of the SRT cells projecting to RVLM which is a probable candidate for the integration center of various pressor reflexes such as somatosympathetic reflex, the noxious informations occupy higher proportion of input to them than in other groups. Therefore the noxious information transmitted through the lateral SRT destined for RVLM is expected to play a role in somatosympathetic reflex.

Key Words: Lateral spinoreticular tract, Rostral ventrolateral medulla, Somatosympathetic reflex

INTRODUCTION

Spinoreticular tract (SRT) is known as the main

pathway from the spinal gray matter to the pontomedullary reticular formation (PMRF), and it passes through the anterolateral funicular white matter. Anatomical studies revealed that the axons of SRT cells, except the fibers to the precerebellar nucleus,

chiefly terminate below the rostral pole of the inferior olivary complex and the medial two thirds of the brain stem (Brodal & Rossi, 1957; Bowsher, 1976). And the single anatomical structure in brain stem, with the most concentrated distribution of the SRT fiber terminals, is known to be nucleus reticularis gigantocellularis (NGC). These anatomical findings led the last two decades' electrophysiological studies on the SRT to be dedicated to the SRT fibers projecting to the medial RF including NGC, namely the medial SRT cells (Albe-Fessard et al, 1974; Fields, 1975, 1977; Maunz et al, 1978; Haber et al, 1982).

Most medial SRT cells have been reported to have little modality specificity and little topographic organization of their inputs, and to show the polymodal sensory convergence (Fields, 1977). Most cells in NGC were reported to respond maximally to the peripheral nerve stimulation with $A\delta$ intensity (Casey, 1969) and a component of their afferent limbs, medial SRT cell, was known to adapt rapidly to the repeated peripheral nerve stimulations (Peterson et al, 1976; Maunz et al, 1978). These results suggest that the cells in NGC have a wide receptive field with polymodal sensory convergence and they are activated in response especially to newly arrived input. These characteristics of the NGC cells correspond to their plausible physiological functions, such as the maintenance of awakeness and the induction of escape behavior (Brodal, 1958; Casey, 1971; Foreman & Blair, 1988).

On the other hand, most of lateral SRT fibers, which transmit the information to the lateral PMRF, terminate in the lateral reticular nuclus (LRN) but some of their terminals are distributed in the rostral ventrolateral medulla (RVLM) such as paragigantocellular nucleus (NPGCL) and rostral pole of LRN including ventral area to facial nucleus (Brodal & Rossi, 1957). We are intersted in this anatomical finding because the recent studies revealed that the RVLM is important to maintaining the vascular tone and mediating the various sympa-

thetic reflexes.

We investigated the electrophysiological properties of the SRT cells to the LRN and RVLM, which are regarded as a potent candidate for the integration center of the somatosympathetic reflex, and also compared them with the properties of the medial SRT cells. Ciriello (1977), Thomas (1977) and Iwamoto (1982) suggested that LRN should be a specific site of mediation of somatosympathetic reflex for the following reasons. First, the neurons in LRN respond to the activation of group II & III cutaneous and muscle affrents, which are afferent path of the late component of somatosymapathetic reflex. Second, a discrete bilateral lesion of the LRN abolishes the late component of somatosymathetic reflex (Ciriello & Calaresu, 1977). Third, the pressor response to the stimulation of vasomotor area is maintained, after the bilateral lesion of LRN (Iwamoto, 1982).

On the contrary, from their experimental results in which the caudal VLM had been stimulated electrically and chemically, Janss et al. (1987) indicated a possibility that the stimulated component might be a passing fiber, for the pressor response had been induced by electrical stimulation but the depressor response by glutamate injection into the same site. Stornetta et al. (1989) reported that the ablation of LRN did not affect the somatic pressor reflex and this reflex was affected only by the electrolytic or chemical (kainic acid) lesion of the ventral part to the contralateral retrofacial nucleus and this area overlapped with the C1 area. The latter two reports conflict with the former in the experimental results. The C1 area, which is also called as rostral ventrolateral medulla, glycine sensitive area (Feldberg & Guertzenstein, 1976) & subretofacial nucleus (McAllen, 1987) and functions as a decending limb of the sympathetic baroreflex (Granata et al, 1985), contains population of cells which project their axon to the intermediolateral cell column (IML) and provide tonic excitatory drive to the preganglionic sympathetic neurons (Amendt et al, 1979; Gebber &

Barman, 1985). And their distribution overlap with medullary pressor area where pressor response can be elicited by electrical stimulation (Caverson et al, 1983). Anatomically this area corresponds to the rostral LRN, retrofacial portion of the NPGCL or the mediocaudal region of facial nucleus.

On the other hand, dorsolateral funiculus and dorsolateral sulcus area was reported as a afferent pathway of somatosympathetic reflex when peripheral myelinated and unmyelinated nerve fibers were stimulated, respectively. Kozelka & Wurster (1985), however, indicated that there is another reflex pathway for excercise pressor reflex. And the SRT is noticed as a possible candidate for this afferent pathway (Mitchell et al, 1983; Thies, 1985).

In this study, therefore, we attempted to classify the SRT neurons according to the distribution of their axon terminals, and to compare their electophysiological properties. We selected nucleus gigantocellularis for the antidromic stimulation of the medial SRT cell, and LRN & RVLM for stimulation of the lateral SRT cells. Considering the fact that functions of LRN is related to the autonomic regulation, especially to somatosympathetic reflex and exercise pressor reflex, besides the relay of motor imformation to cerebellum, and the role of RVLM is critical to various pressor reflex, we hope this elucidation of the electrophysiolgical properties of the lateral SRT, which is main afferent pathway to this medullary area, to contribute to clarifying the mechanism of somatosympathetic reflex.

METHODS

Preparation of the experimental animal

Cats weighing 1.8~3.3 kg, were used for experimental animal. Anesthesia was induced with ketamine HCl (Ketalar, 20 mg/kg, i.m.) and maintained with single intraperitoneal injection of α-chloralose (60 mg/kg, Sigma). Trachea, jugular vein and carotid artery were cannulated and used for artificial ventilation, intravenous injection and blood pressure monitoring respectively. All animals were paralyzed by intermittent intravenous administration of pancuronium bromide (Mioblock, Organon) and ventilated artificially. Blood pressure was monitored from the carotid artery and maintained above 80 mmHg. The body temparature was maintained at 37 ± 1℃ using a heating blanket (Animal blanket condition unit, Havard). Laminectomy was done on L4-S1 vertebrae and the lumbosacral enlargement of spinal cord was exposed. Occipital craniectomy was performed and the cerebellum was removed by suction to expose the 4th ventricular floor. An incision was made on the back skin of hind limb. The sciatic, common peroneal and tibal nerves were isolated and exposed for electrical stimulation.

After the operation, the cat was mounted on the stereotaxic apparatus and we used the incised skin to set up mineral oil pool in the exposed region by operation.

Stimulation and recording procedure

After the recovery interval of about 1 hour, we executed the following procedures in order to select the antidromic stimulation site in brain stem. Insulated concentric bipolar electrodes (tip diameter: 100 μ m) were introduced into the the medial medullary RF, rostral VLM and obex-level LRN respectively, in order to record the single cell activity induced by the natural stimulation such as tapping applied to the left hindlimb. If we regard the median line and the obex as a origin, the coordinates of the MRF, RVLM & obex-level LRN was (1.5, 4), (3.5, 4) & (3.5, 0) respectively, expressed as the distances in millimeter lateral to the median line and rostral to the obex. We adjusted the depth of the stimulating electrode where we could obtain the maximal amplitude of evoked response.

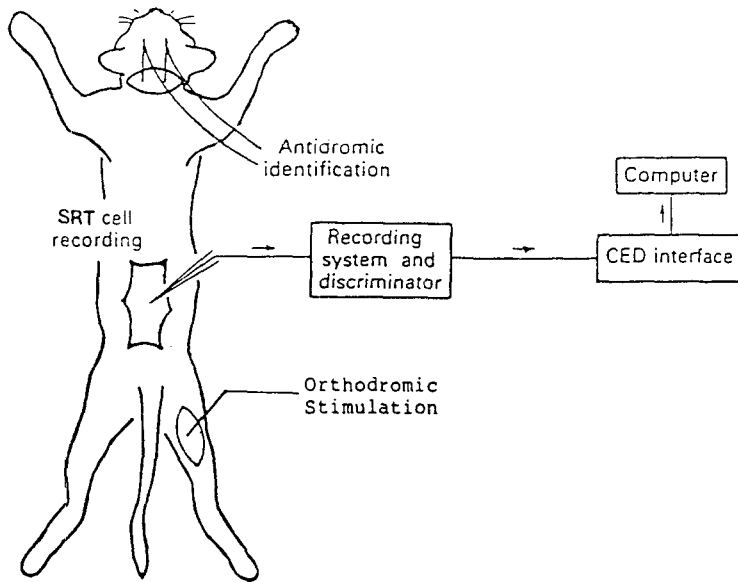Spinal single cell units activated by antidromic stimulation of the brain stem, were recorded at the

Fig. 1. A schematic diagram of experimental set-up. To stimulate brain stem antidromically, stainless bipolar concentric electrode was placed where the RF unit was activated maximally by natural stimulation of hindlimb. The site of the orthodromic stimulation through the tripolar platinum electrode was common peroneal nerve and tibial nerve. The signals which recorded through the glass micropipett electrode with carbon filament core was amplified and was fed to the window discriminator and oscilloscope. The isolated SRT units' activities were led to CED1401 and processed. The processed signal was displayed and stored in the computer.

spinal level of lumbosacral enlargement through carbon filament electrode (tip resistance: $1 \sim 2 \, M\Omega$, diameter: $6 \sim 7 \, \mu m$). The recorded signal was amplified with an AC differential amplifier (DAM-80, WPI), monitored on oscilloscope and through the window discriminator (Fredrick Haer & Co) and laboratory interface (CED 1401), was stored in a personal computer for further analysis (Fig. 1). The four criteria were used to determine whether or not the recorded units were activated antidromically. These include the following items: 1) a constant latency of the spike from the stimulus, 2) a discrete threshold, 3) the ability to follow high frequency train of antidromic stimuli (333 Hz), and 4) collision of antidromic spike with orthodromically evoked spikes. For the antidromic SRT unit, we characterized the following items.

1) The depth of the SRT in the spinal gray.

2) The projection laterality of the axon terminal.

3) Latency and conduction velocity of the SRT unit activated by antidromic stimulation.

4) Peripheral receptive field.

5) Classification of the SRT cells as low threshold cell (LT), high threshold cell (HT), wide dynamic range cell (WDR), and Deep cell according to the responsiveness to the graded mechamical stimulation applied to their cutaneous and deep receptive field.

6) The responsiveness to the electrical stimulation of peripheral nerve, i.e. common peroneal nerve and tibial nerve, with $A\delta$ and C intensity. The $A\delta$-intensity (0.1 ms, $0.5 \sim 1$ mA) and C-intensity (0.5 ms, 5 mA) corresponds to the $10 \sim 50$ times and to the $500 \sim 1000$ times of the $A\alpha$-intensity.

Histology

After completing study of the cell, electrolytic

Table 1. Classification of SRT cells by responses to the mechanical stimulation applied to their receptive fields.

The Axonal Termination	No. of Cells		Response Type to Natural Stim.						Proj. Ltralty		
	Total	Full-Def.*	Deep	LT	HT	WDR	LT+HT^	IO	bi	cont	ipsi
MRF	34	8	4 (50)	1 (13)	1 (13)	—	2 (25)	4	2 (6)	20 (59)	12 (32)
RVLM	14	8	2 (25)	—	4 (50)	2 (25)	—	—	1 (1)	4 (36)	9 (61)
LRN	33	14	7 (50)	4 (29)	2 (14)	1 (7)	—	—	1 (7)	12 (29)	20 (64)

The numbers in the parentheses are the proportions expressed in percentage.; *: fully defined cell means the SRT units that satisfy all the criteria of antidromic stimulation, especially 4th item.^: Cells of this type was difficult to classify, since responded to both brushing and squeezing but not to pressure and pinch.; Abbreviations, LT: low threshold cell, HT: high threshold cell, WDR: wide dynamic range cell, IO: inhibitory only, Proj. Latrlty: Projection laterality, bi: bilateral, cont: contralateral, ipsi: ipsilateral;

lesions were made (DC current of $100 \sim 200$ μA, $20 \sim 30$ sec duration) for histological identification of recording site. At the end of the experiment, the antidromic stimulation site in brain stem was marked by passing DC current through the stimulating electrode and depositing the ferrite ion. And the brain stem and spinal cord were removed and fixed in a 10% formalin solution containing potassium ferrocyanide. After at least a week, the spinal cord and brain stem were frozen and cut every thickness of 40 μm.

RESULTS

In 23 cats, 69 presumable and 32 definite SRT units were identified. The "presumable" SRT units mean the ones which we could not activate orthodromically because they had no spontaneous activity or their receptive fields were not found. The identified SRT units were calssified as MRF (medial reticular formation) group, RVLM group, and obex-level VLM or LRN group according to where the unit was activated antidromically. We further classified the same cell as LT, HT, WDR and deep cell according to the response pattern to the graded

mechanical stimuation applied to their receptive field.

The average conduction velocity in MRF, RVLM and LRN group was 39.0 ± 0.5 (mean $\pm$ S.E.), 31.2 ± 1.3 and 33.7 ± 0.5 m/sec respectively, showing no significant difference in conduction velocity between the 3 groups. Generally these conduction velocoties are slower than those reported previously in papers on SRT but the order is consistent (Fields, 1975; Ammons, 1989; Thies, 1985). On the other hand, the average conduction velocities in deep, LT, HT and WDR group was 41.0 ± 1.5, 43.7 ± 3.8, 24.0 ± 2.8 and 27.1 ± 5.5 m/sec respectively. The conduction velocities of SRT cell groups which receive the noxious input were significantly slower than those of innocous cells (Table 1, student t-test, $p < 0.05$). The relative slower conduction velocity in RVLM group may attribute to the high occupancy of HT cell in this group (Table 1).

Fig. 2 shows the laminar locations of SRT cells in spinal gray (right) and the distribution of their axon terminals in the medulla (left). These are the camera lucida representations reconstructed for the SRT cells whose sites of recording and antidromic stimulation had been marked by DC lesion after completing

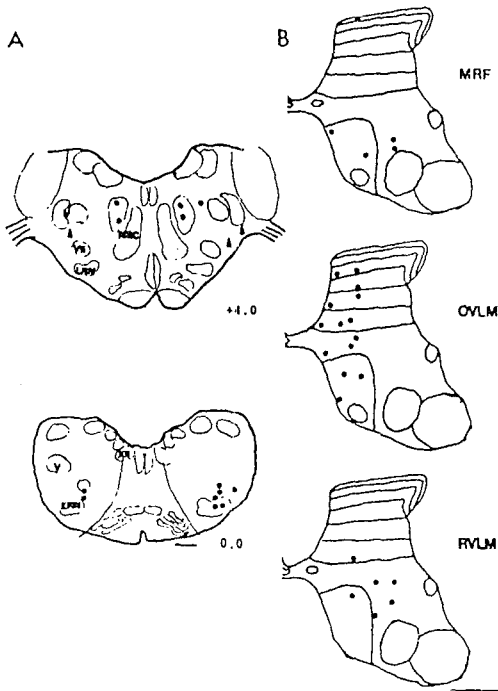## DISTRIBUTION OF SRT UNITS
FIBER TERMINAL   CELL BODY

Fig. 2. A. Locations of antidromic stimulation sites in medial reticular formation (*upper*, circle), rostral ventrolateral medulla (*upper*, triangle), and lateral reticular nucleus (*lower*, circle). The right lower number indicates the rostral distance from obex in millimeter. Calibration 1 mm. B. Location of SRT units which are antidromically activated by stimulation of medial RF (*upper*), LRN (*middle*), rostral VLM (*lower*) in spinal gray of lumbosacral enlargement. Calibration, 1 mm.

study of the cell. The spinal distributions of the SRT cells projecting to MRF and RVLM mostly overlap each other, and they were mainly located in lamina VII (intermediate zone) and deep dorsal horn. In case of the SRT cells projecting to LRN, however, their distributions were diffuse through all the laminae except the superficial ones (I & II). But the majority of the cells were located in the medial part of spinal gray.

The size and properties of receptive fields of the SRT cells were dependent on their locations in spinal gray rather than their axonal termination sites. Although homogenous sensory convergence and restricted receptive fields were observed in superficially located SRT cells, the cells in deep dorsal or ventral horn showed polymodal sensory convergence and vague-bordered wide receptive fields. Especially, ten of the thirteen deep cells which responded only to the subcutaneous stimulation such as tapping were found in the intermediate zone or ventral horn deeper than 3000 μm from dorsal surface of spinal cord.

An example of medial SRT cell is shown in Fig. 3. In spite of its spinal level (lumbosacral enlargement), this cell has a wide receptive field through the almost whole body. As the cell responded only to the tapping, and its activity was inhibited by pressure or pinch, it was classified as deep cell. It was located in lamina VII as others in this group and had a rapid antidromic conduction velocity, 82.5 m/s. Interestingly, the bursting spontaneous cell activity every 3 second was induced after the electrical stimulation of common peroneal nerve with C intensity (Fig. 3, E (b)).

In the only 8 of 34 medial SRT cells, we could find their peripheral receptive fields. Compared with the lateral SRT group whose receptive fields were found in 46%, high proportion of medial SRT cells had no cutaneous or subcutaneous receptive fields for the graded mechanical stimulation. The receptive fields of medial SRT cells were characterized by the polymodal sensory convergence with complicated border and coexistence of the receptice fields which had different response characteristics (Table 1).

When the stimulation of medial medullary reticular formation, orthodromic units were found more frequently than antidromic units. The former may contribute to the formation of the field potential more than the latter does. Usually the spinal field potential began to be detected at 2700 μm, peaked at 3500 μm and disappeared at 4500 μm. The baseline
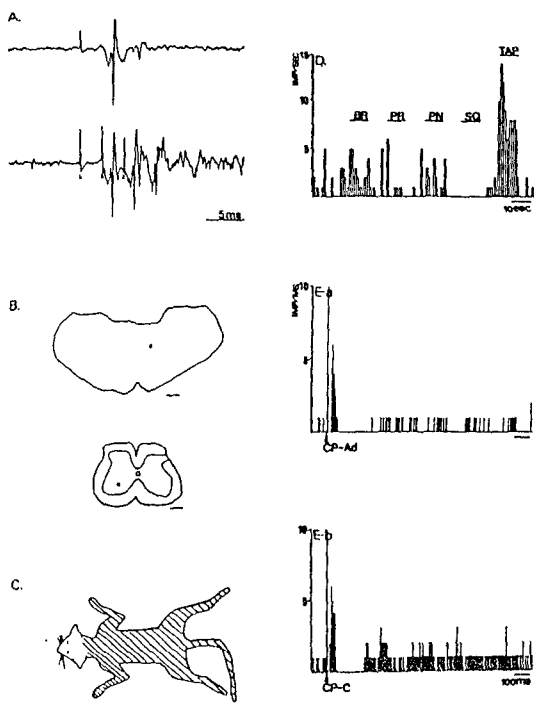
Fig. 3. A. The SRT unit activated by antidromic stimulation of medial reticular formation, NGC. 10 times-signal averaged strip by single (upper) and triple pulse stimulation of MRF for high frequency following test (lower) at the time indicated by arrows. Calibration, 1 ms. B. The location of the antidromic stimulation site in brain stem 4.0 mm rostral to obex, and recording site in spinal gray. Calibration, 1 mm. C. This unit receives sensory input from entire body except the head and part of neck. D. Single-pass time histogram with bin width of 1 sec. The graded natural stimuli were applied at the time indicated by horizontal bar. BR: brush, PR: pressure with large arterial clamp, PN: pinch with small arterial clamp, SQ: squeez with forceps, TAP: tapping. The only adequate excitatory mechanical stimulus was tapping. E. a) This poststimulus time histogram (PSTH) shows response to the single pulse stimulus of common peroneal nerve with $A\delta$-strength (0.1 ms, 1 mA). b) PSTH of response to C-strength (0.5 ms, 5 mA). This stimulation initiates the spontaneous bursting activity in this SRT cell. Each PSTH was built from 20 trials using electrical stimulation at 100 ms (indicated by arrow).
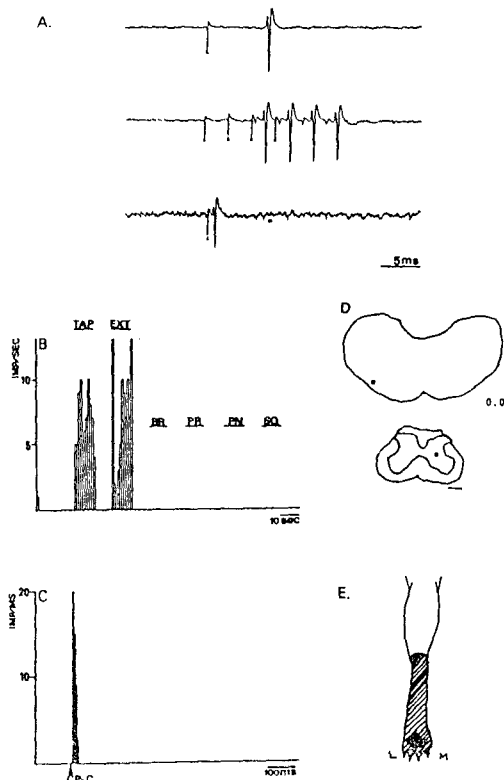
Fig. 4. Example of the typical SRT unit projecting to obex-level LRN. A. This unit satisfied all the criteria: high frequency following test (upper), constant latency, 8 ms (middle), collision test (lower, Antidromic unit disappeared by collision with spontaneous cell activity and failed to occur at the time of filled circle. The fist two strips were obtained by averaging the signals from 10-times trial. The arrows indicate antidromic stimulation time. The antidromic threshold current was 5 μ A. B, E. This cell had bilateral receptive fields and responded to the tapping on plantar surface and hyperextension of the ankle. Other mechanical stimulus was inadequate to activate this cell. C. This cell responded to the peripheral nerve stimulation with $A\delta$ and C intensity in similar fashion. This PSTH was obtained from 20-times stimulation of common peroneal nerve with C-strength. D. This unit was activated by antidromic stimulation of contralateral obex-level LRN (upper), and recorded in laminar VII (lower, 2800 μm from dorsal surface of spinal cord) Calibration 1 mm.
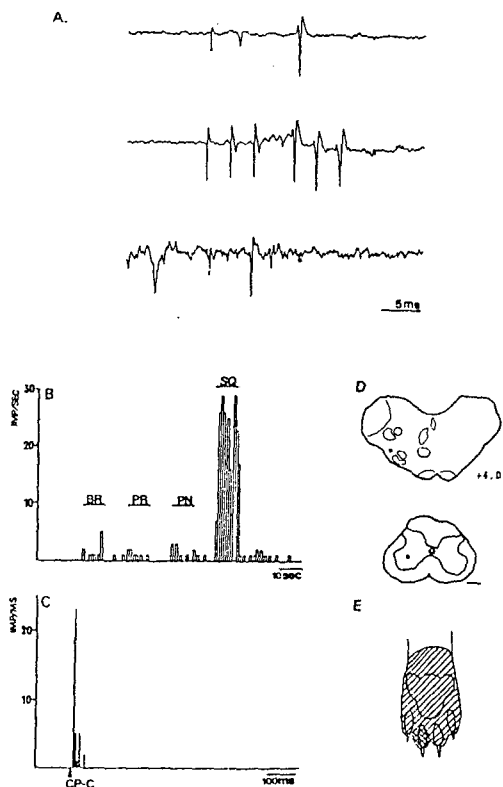
Fig. 5. The antidromic spikes recorded extracellularly is shown in A. The response pattern to the graded mechnical stimuli applied to the receptive field (E) is shown in B. This cell classified as high threshold cell since it was activated exclusively by high intensity mechanical stimuli such as squeezing. C shows the response to the C-intensity stimulation of common peroneal nerve. The PSTH of similar profile to this was obtained for Aδ-stimulation. The location where recorded this unit was lamina VII, as shown in D (lower), and the site for antidromic stimulation was ipsilateral rostral ventrolateral medulla, D (upper).

instability of Fig. 3(A), in spite of the 10 times-averaged signal, was due to the field potential formed by many spinal cells activated orthodromically.

The typical example of the SRT cell projecting to LRN is shown in Fig. 4. This cell was activated by antidromic stimulation of the LRN, with threshold 5 μA. It had a bilateral receptive fields and responded
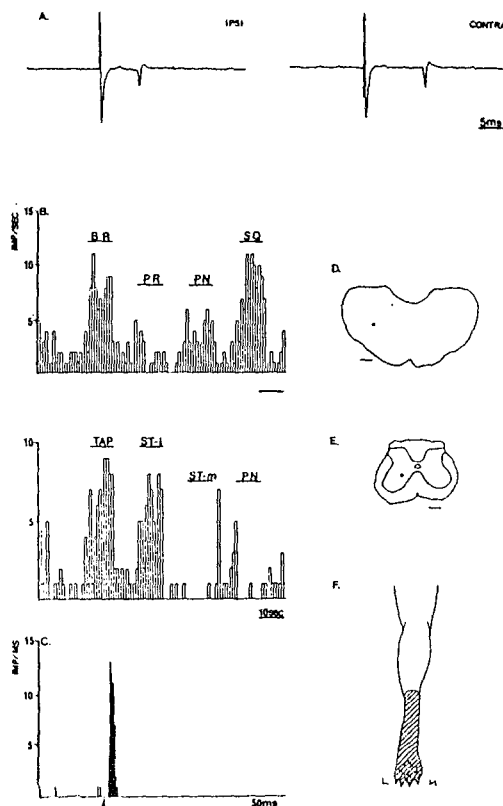

Fig. 6. An example of the antidromic SRT unit activated bilaterally. A. antidromic unit of SRT neuron by stimulation in ipsilateral (right) and contralateral (left) rostral VLM of the same rostrocaudal level. The latent period was 8 ms when ipsilateral stimulation, and 5 ms when contralateral stimulation. This unit satisfied the 4 criteria (not shown). B. *upper*: single-pass time histogram with bin width, 1 sec. *lower*: single-pass time histogram to test the responsiveness to stimulus of other modalities, TAP: tapping foot pad, ST-1: stroke of lateral margin of the left foot, ST-m: stroke of medial margin, PN: pinching foot pad. C. This poststimulus time histogram was obtained by 20 consecutive stimulation of the ipsilateral common peroneal nerve with C-strength (0.5 ms, 5 mA) at 100 ms. bin width, 1 ms. D & E. Camera lucida representation of the location of the antidromic stimulation and SRT unit in the spinal gray. Calibration 1 mm. F. Receptive field of this unit was ipsilateral (left) plantar surface.
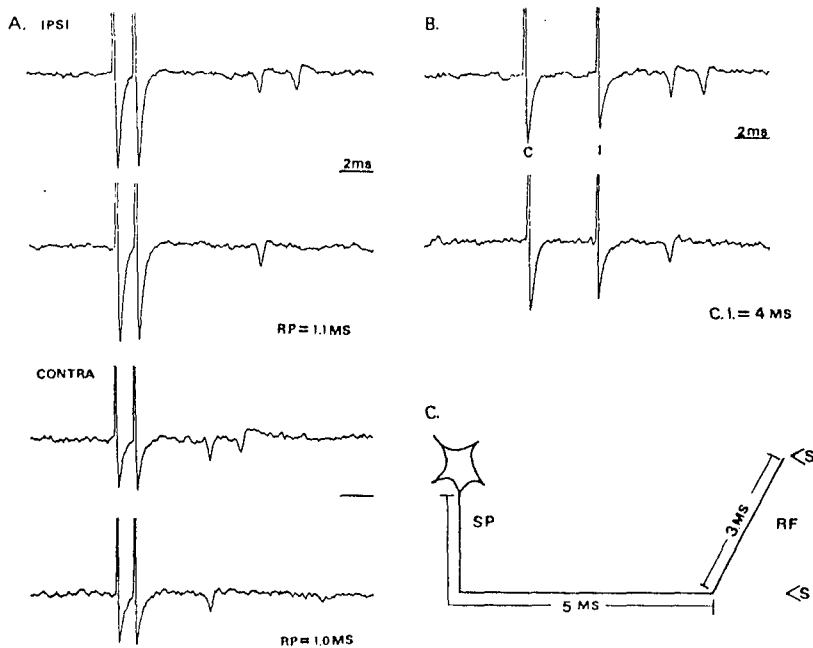
Fig. 7. A. Estimation of the axonal refractory period by two subsequent antidromic pulses in the same unit described in Fig. 6. The refractory period of ipsilateral side was longer than that of contralateral side by 0.1 ms. The horizontal scale at the bottom is 1 ms per division B. Time controlled collision test. Collision interval was measured by paired stimuli, ipsilateral side (I) and contralateral side (C). The measured collision interval was 4 ms. Calibration, 5 ms. C.I.: collision interval. C. The possible axonal projection pattern of this SRT unit with conduction time. SP: spinal gray RF: reticular formation S: antidromic stimulation site

only to the tapping and hyperextension of ankle joint so that it was classified as deep cell. The deep cells with similar properties occupied one half of the SRT cells which were activated antidromically by the stimulation of the obex-level LRN or the MRF.

Fig. 5 represents the antidromic SRT unit activated by the stimulation of RVLM. The cell was classified as high threshold cell, since activated exclusively by high intensity mechanical stimuli such as squeezing. One half of SRT cells projecting to RVLM were classified as HT cell because of the similar response patterns to graded mechanical stimulation.

The 59% of 34 medial SRT cells were located in spinal gray ipsilateral to antidromic stimulation site. More than half (60%) of lateral SRT cells, however, projected to the contralateral to where the units were recorded, and there was almost no difference

between the projection lateralities of RVLM & LRN group. For lateral SRT cells, these relsults agree with others (Thies, 1985) but not for the medial ones (Fields et al, 1975). But the projection lateralities of medial SRT cells are not definite because others reported that ipsilateral projections were found more frequently (Maunz et al, 1978).

About 5% of SRT cells were activated by the antidromic stimulation of both sides of medullary RF. An example of bilaterally projecting SRT cells is shown in Fig. 6 & 7. This unit was activated by the stimulation in ipsilateral and contralateral RVLM of same rostrocaudal level, ventral to the retrofacial nucleus. The recording site of this unit was lamina VII in spinal gray and its reactivity to the mechanical stimulation was difficult to determine due to polymodal sensory convergence. The antidromic

threshold of this unit was 300 μA at ipsilateral side and 750 μA at contralateral one. The latency and refractory period of this unit was measured as 8 ms & 1.1 ms at ipsilateral and 5 ms & 1.0 ms at contralateral side respectively (Fig. 7, A). The collision interval between two sides was measured as 4 ms by time controlled collision test (Fig. 7, B). These values satisfied the following equation.

$$C.I. = Li - Lc + Rc$$

(C.I.: collision interval, Li: latency measured at ipsilateral side, Lc: contralateral latency, Rc: refractory period measured by contralateral stimulation)

From the above results, it was indicated that the ipsilateral stimulation site may be a main axon terminal rather than the branch from contralateral (Shinoda et al, 1976; Barman & Gebber, 1985; Jankowska et al, 1972). Therefore this result may be a indirect evidence that there is a crossover in the pathway of the SRT. There is little possibility that one electrode stimualted the other side, as effective stimulaion area was reported as 10 μm/μA when monopolar electrode used and the distance between two electrodes was 7 mm (Abzug, 1974; Ranck, 1971).

The SRT groups classified according to the distributions of their axon terminals, have different reactivity to the graded mechanical stimulation applied to their peripheral receptive fields (Table 1). The proportion of cells responsive to natural nociceptive stimulation was 37.5%, 21% and 75% in medial SRT cells, LRN projecting cell and SRT cells projecting to RVLM respectively (Table 1). From this result, it may be concluded that the SRT cells to RVLM receive high proportion of nocicptive information from periphery, compared with other groups of SRT cells.

For all the SRT cells identified, we tested the response to electrical peripheral nerve stimulation with Aδ and C intensity. Almost all the cells have not shown any difference in responses to Aδ & C intensity. But this result is not consistent with those report-

ed by others. For the medial SRT cells, it is difficult to compare our data with others directly because there were no available data about the reponsiveness to peripheral nerve stimulation.

DISCUSSION

The spinoreticular and spinothalamic tracts have been regarded as the main pathways which transmit pain sense. It has been well known that the two pathways transmit the two aspects of the pain, namely motivational affective component of the pain and sensory discriminative information respectively. The papers that surveyed the responses of the neurons located in NGC to the peripheral stimulation, however, reported that the neurons responded not only to the noxious stimuli applied to skin or subcutaneous tissue, enough to cause escape behavior, but also to the mechanical stimuli which were regarded as innocuous one, for example the brusque tapping (Casey, 1969; Bowsher, 1968, 1976; Segundo et al, 1967). These papers suggest that the medial SRT transmits informations other than pain sense. Also the present study shows that more than 60% of medial SRT cells responded only to the innocuous stimuli such as phasic hairy movement or brusque tapping. Considering the fact that the medial reticular formation has the role of maintaining the awakeness and induce the escape behavior, we can conjecture that the medial SRT cells will transmit the information concerning the above-mentioned role of NGC (Brodal, 1958; Casey, 1971).

All the medial SRT cells which responded to the noxious stimuli were HT cell, but WDR cell was not detected. Then the WDR cells funtion as a encoder of intensities of the stimuli but the HT cells can not. The STT cells of which more than half is WDR cells in primate (Willis et al, 1974), therefore, will be concerned with transmission of the sensory discriminative component of the pain. On the other hand, the WDR cells occupy very low proportion of the medial

SRT cells. This results indicate that the medial SRT cell receive the motivational affective component of pain necessary to the activity of the autonomic nervous system, rather than discriminative one. But considering that the SRT is not the only afferent pathway to the medial RF from spinal gray and the other multisynaptic pathway exist, the information transmitted monosynaptically through the medial SRT which we surveyed will contribute only a part of the many functions of the medial RF and this functions will be the one which require rapid processing such as arousal or the escape behavior.

Compared with other groups, most medial SRT cells we recorded had no cutaneous or subcutaneous receptive fields for mechanical stimulation. The following possible causes for this result would be considered. First, many medial SRT cells may receive input from the intramuscular or temparature receptors which we have not studied in this experiment. Second, many medial SRT cell activity may be inhibited reciprocally by the reticulospinal neronal activity induced by orthdromic stimulation used for searching the axon terminal of the SRT cell (Haber et al, 1982). Third, the continuous repetitive stimulation of the medullary reticular formation for antidromic searching may give rise to adaptation of medial SRT cells in cellular level (Maunz et al, 1978). Fourth, the extent of peripheral receptive field may be distorted by the different states of anesthesia or the orthodromic stimulation of retiular formation (Bowsher, 1976). At present time, however the main cause of this result is not clear.

The two lateral SRT groups, namely RVLM & LRN-projecting SRT group, have different compositons of their transmitting information. In compare with the SRT cells projecting to RVLM, the deep cell, which responded to proprioceptive stimuli such as tapping, hyperflexion & hyperextension, composed higher proportion of SRT cells projecting to obex-level LRN. This result suggests that the lateral SRT projecting to LRN, which is the one of

precerebellar nuclei, constitute the afferent limb of the pathway which relay informations concerned with the motor function of cerebellum. In additon, as progression of a electrode into ventral directon, the receptive fields of cells in LRN moved toward caudal direction. This is considered to be the indirect evidence of the somatotopic organization of the LRN (Künzle, 1973). Generally our results showed that the infomations to LRN coincide with the function of it as a precerebellar relay nucleus which transmit the discriminative motor information to cerebellum. On the other hand, the number of noxious information transmitting cells, that are HT & WDR cell, composed more than 70% of lateral SRT cells to RVLM or rostral pole of LRN. Therefore this area will be related to the processing of the noxious information.

Because of the following reasons, however, it may look too hasty to relate the noxious informations transmitted by SRT toward RVLM to the somatosympathetic reflex directly. First, we could not determine the medullary localization of the axon terminals of the lateral SRT cells whose responses to C-intensity peripheral nerve stimulation, by which the somatic pressor reflex is induced, were different from that to Aδ intensity. But this may not be the case, for Huh et al. (1989) reported that 3-train pulses with C-intensity was more effective to elicit these C-responses, but the single pulse was used in this study. Second, as we did not investigated the responsiveness of SRT neuron to stimulation of the intramuscular afferent fiber, we can not deny the existence of the bias caused by the examination of only a part of the afferent limb from cutaneous and subcutaneous receptive field. Third, Maunz et al. reported that the responses of the medial SRT neurons decline during period of repetitive stimulation. This adaptation phenomena contradict the somatic pressor response which give rise to the steady increment of the blood pressure. The investigation into the response of lateral SRT neuron to the repetitive C-intensity stimulation will permit the further specu-

lation. Though the data size is too small and restricted to the SRT neuron to LRN, we investigated the responsiveness of the SRT cell to the repetitive peripheral stimulation of Aδ-intensity in two cases. The two SRT neurons responded maximally at 5 Hz and the responses began to decrease at 10 Hz. At the higher frequency, even spontaneous activities were inhibited. These responses resemble the profile of somatic pressor response to the stimulation of various frequencies. But the two profiles are not identical, because the reflex sympathetic activity decreases at 0.3 Hz stimulation in somatosympathetic reflex (Sato & Schmidt, 1973). Consequently the further study is necessary to answer the question, whether the lateral SRT is the afferent limb of the somatosympathetic reflex or not.

Though results of this experiment suggest that the quality of the information transmitted by SRT cells depend patially on the destination of the axon terminal of SRT cell, we can not deny there are many pitfalls in this experiment. First of all, the sample size is too small to assert the uneven localization of input informations to reticular formation. Second, we didn't verified whether the antidromic stimulation sites were axon terminal or the fiber tract passing by it, especially when the site was the lateral reticular formation where many fibers such as ventral spinocerebellar tract, spinotectal tract, spinothalmic tract, and medial spinoreticular tract pass. In order to minimize the stimulated area, however, we used concentric bipolar electrode and threshold current to identify the single SRT unit. And the anatomical and electrophysiological results supplement the pitfalls. In most sensory pathways, except lemniscal system, their collaterals branch out vertically to the axis of their main axons. Especially, the STT are the longest pathway of the spinoreticulothalmic system (Scheibel, 1984; Bowsher, 1976). And in animals except the primate, the number of STT is considerably small in compare with SRT (Albe-Fessard, 1974; Blair et al, 1984).

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== 국문초록 ==

고양이의 내측 및 외측 척수망상로 세포의 전기생리학적 비교연구

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Vasomotor area로 알려져 있던 외측연수망상체는 최근 rostral ventrolateral medulla로 불리면서 sympathoexcitatory neuron이 집중적으로 분포하는 연수내 부위로서, 체성교감신경반사에 중요한 역할을 하는 것으로 알려지고 있어 이 부위로의 입력정보가 그동안 많은 연구가 되어온 내측 척수망상로 세포와 어떤 차이를 보이는가를 규명하고자 하였다.

1) Medial SRT 세포는 34 cell중 약 60%가 동측으로 향하였으나, lateral SRT cell의 경우 47 cell의 약 60%가 반대측으로 향하였다.

2) 각 군의 세포를 말초자극에 대한 반응성에 따라, LT cell, Deep cell, HT cell 및 WDR cell로 나누었으며 유해자극을 전달하는 세포를 HT와 WDR cell이라 하고, 무해자극을 전달하는 세포와 유해자극을 전달하는 세포의 비율로 볼 때, 다른 부위에 비하여 rostral VLM에 유해자극정보가 비교적 많이 전달됨을 볼 수 있었다.

3) 평균 전도 속도는 각 군간에 유의한 차이가 없었으나, Deep cell은 HT cell보다 유의하게 빠른 전도속도를 보였다.

4) Medial SRT 세포는 척수 회백질 내에서 Rexed laminae VII 및 VIII에 주로 분포하며, LRN projecting SRT cell의 경우엔 전 lamina에 걸쳐 고루 분포하였다.

이상의 결과는 내측 및 외측 망상체간의 말초 입력 정보의 차이를 보여주고 있으며, 연수 망상체의 세 부위중 특히 rostral ventrolateral medulla로 많은 동통정보가 입력되고 있어 RVLM의 기능중 하나인 체성교감반사의 통합과 연관된 역할을 하리라 기대된다.