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The Electrophysiological Characteristics of Medullospinal Tract Cells in Cat Ventrolateral Medulla

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= ABSTRACT =

Although the existence of nerve cells which determine the activity of sympathetic nervous system in ventrolateral medulla is advocated recently, there are wide varieties on the location and function of them according to authors. Present study aimed to identify and characterize the medullospinal tract cells in rostral and caudal medulla of cats which branch to the lateral horn of the upper thoracic spinal cord.

Cats were anesthetized with α-chloralose. The upper thoracic spinal cord and floor of the IVth ventricle were exposed. Medullospinal tract cells in rostral and caudal medulla were identified by antidromic stimulation of the intermediolateral nucleus in the upper thoracic cord and then the location and physiological characteristics of these cells were studied.

A total of seventy cells in medulla had constant latency and responded to high frequency stimulation to thoracic cord. Among them fifty-six cells were identified as medullospinal tract cells either by collision with spontaneous activities or activities evoked by sciatic nerve stimulation(27/56), or by determining the refractory period (29/56). Thirty-one of these cells branched to the contralateral thoracic spinal cord, twenty-one cells to the ipsilateral side and remaining four cells branched to both sides. The conduction velocity of cells branching to the contralateral side was 29±2.9 m/sec and that of cells to the ipsilateral side was 39.1±6.0 m/sec. When medulla was devided into two by a horizontal plane at 3 mm rostral to the obex, fifty-one among seventy cells were in the rostral medulla and nineteen were in the caudal medulla. The conduction velocities of these two groups were 27.6±1.0 and 33.3±3.9 m/sec, respectively.

In this study, we confirmed the existence of two groups of medullospinal tract cells in rostral and caudal ventrolateral medulla, which branch to the lateral horn of thoracic cord and these cells have relatively few spontaneous activities and rapid conduction velocity, so we concluded that these cells are different from the previously known sympatho-related cells in ventrolateral medulla.

Key Words: Medullospinal tract cell, Rostral and caudal ventrolateral medulla, Thoracic spinal cord, Antidromic stimulation.

INTRODUCTION

Somatosympathetic reflex pathway is one of the several parallel pathway processing the nociceptive inputs in the central nerv-

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ous system. For the nociceptive inputs to evoke sympathetic responses, the peripheral nocicpetive afferent inputs should be carried at least to the spinal and/or medullary sympathetic areas. Although the intermediolateral, intermediomedial and intercalated nuclei are known to be the seats of preganglionic cells, the final common pathway of the sympathetic nervous system, it is doubtful whether the peripheral afferent inputs are conducted to these nuclei in physiological condition(Stokes et al, 1983). Since the spinal sympathetic activities are dependent on medullary sympathetic areas, the peripheral nociceptive afferent inputs should be carried to the medulla, be processed there and then the output should be carried to the spinal sympathetic areas.

The afferent inputs evoking the somatosympathetic depressor response are mediated by Aδ-fibers and ascend in the spinal dorsolateral funiculus bilaterally, while those evoking somatosympathetic pressor response are mediated by C-fibers and ascend in the dorsolateral sulcus area bilaterally (Chung & Wurster, 1976; Chung et al, 1979; Kozelka et al, 1981; Mitchell et al, 1983). Since noxious stimuli are the most effective ones to evoke the somatosympathetic reflexes, we can not rule out the possibility that the spinothalamic and spinoreticular tract also mediate the somatosympathetic reflexes.

During the past two decades the role of rostral ventrolateral medulla (RVLM) in the regulation of arterial blood pressure has been studied extensively. Topical application of glycine or glutamate to the ventral surface of medulla produces depressor or pressor response respectively and electrical stimulation of it produced pressor responses (Guertzenstein, 1973; Guertzenstein & Silver, 1974; Feldberg & Guertzenstein, 1976). More accurate localization of the vasopressor cells in the RVLM has been done recently (Dampney et al, 1985 & 1987; McAllen, 1986). After applying the horseradish peroxidase to the lateral horn of the thoracic spinal cord, cells containing HRP granules were identified in the RVLM (Dahlstrom & Fuxe, 1964; Amendt et al, 1979; Ross et al, 1984). Immunohistochemical studies have revealed epinephrine containg C1 cells in the RVLM (Ross et al, 1983; Goodchild et al, 1984; Reis et al, 1984 & 1986).

Vasomotor cells in the RVLM receive various kinds of inputs. They receive baroreflex inputs through the solitary tract nucleus, inputs from the defense-areas in midbrain and hypothalamus (Dampney et al, 1982; Hilton et al, 1983; Ciriello et al, 1985; Lowey, 1986; Sun & Guyenet, 1986; Urbanski & Sapru, 1988; Cassell & Gray, 1989) and also inputs from the spinothalamic tract and spinoreticular tract (Ammons, 1988; Lee et al, 1990). All these inputs are closely related to the sympathetic activity and play important roles in arterial blood pressure regulation (Gebber & Barman, 1981; Barman & Gebber, 1985; Granata et al, 1985; Guyenet et al, 1986; Lebedev et al, 1986; Haselton & Guyenet, 1989; Somogyi et al, 1989; Stein et al, 1989).

For a medullary neuron to be involved in determining the sympathetic tone it should send their excitatory signals to the spinal sympathetic centers. Such sympathetic related medullospinal tract cells have been identified in cat and rat medulla (Barman & Gebber, 1985; Dampney et al, 1987; Sun & Guyenet, 1987; Morrison et al, 1988). However, medullospinal tract cells are not homogenous functionally. In present study we aimed to identify medullospinal tract cells in ventrolateral medulla of cat and analyze their electrophysiological properties concerning their possible roles in mediation of the somatosympathetic reflex.

METHODS

Preparation of animal

Thirty adult cats of either sex (2-3 kg, bo-

dy weight) were used. After sedation with single doses of ketamine (Ketalar, 20 mg/kg, i.m.), animal was anesthetized with α-chloralose (60 mg/kg, i.p.). Trachea, femoral artery and vein were cannulated and used for artificial ventilation, blood pressure monitoring and intravenous injection of drugs, respectively. Animal was paralyzed by intravenous administration of pancuronium bromide (Mioblock, Organon, initial dose 0.4 mg, maintaining dose 0.4 mg/hour). End-expiratory CO_2 concentration was maintained at 3-4% and rectal temperature was maintained at 37 ± 1°C. Hartmann solution was infused continuously throughout the experiment (10-15 ml/hour).

The upper thoracic spinal cord was exposed by a laminectomy on T1-T3 vertebrae. An occipital craniectomy was performed. To expose the floor of the fourth ventricle, the cerebellum was removed by suction. The sciatic, common peroneal and tibial nerves were isolated and exposed for electrical stimulation in the left hindlimb.

After the operation the animal was mounted on a stereotaxic apparatus and mineral oil pools were made with incised skin flaps over exposed areas. A water circulating heating coil was used in the thoracic pool to prevent heat loss through exposed area.

Stimulation and recording (Fig. 1)

Electrodes set-up: After a recovery period of at least an hour, exposed thoracic dura mater was opened and bipolar tungsten stimulating electrodes (0.5 mm diameter and 0.1 mm tip diameter) were placed at the dorsolateral sulcus bilaterally. Electrodes were lowered ventrally to the depth (usually 1.5-2.0 mm) where the largest arterial pressor response to brief square pulse stimulation was observed, where the intermediolateral nucleus of sympathetic preganglion cell was assumed to exist. Tripolar platinum electrodes were placed under the exposed peripheral nerves for stimulating them.

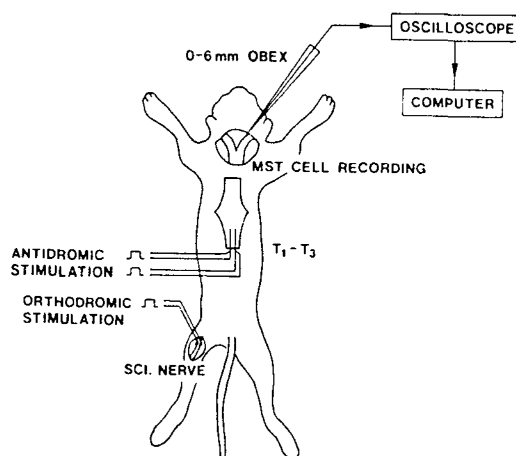

Fig. 1. A diagram showing the experimental set-up. The medullospinal tract cells were identified antidromically by stimulation of the T1-T3 spinal lateral horn. Collisions with either spontaneous or orthodromically evoked activities were tested. MST, medullospined tract cell.

Single cell activity in the ventrolateral medulla was recorded with carbon filament recording electrodes (tip resistance: 1-2 MΩ). A recording electrode was positioned at the dorsal surface of the medulla, 0-6 mm rostral to the obex, and 3-4 mm from midline. Electrode was lowered down step by step with micromanipulator until single cell activities were descernible. Usually single cell activities were picked up at depth between 3-7 mm from the dorsal surface. Each track was separated by 0.25-0.5 mm.

Recordings: For the identification of a medullospinal tract cell with conventional criteria of antidromic activation, brief square pulses (0.1 msec, 500 μA, 2-3 Hz) were applied through the concentric electrodes to thoracic spinal cord. The electrical activities were amplified and displayed on oscilloscopes as usual, then stored and analyzed in a personal computer using interface (CED 1401).

Histology: At the end of the experiment electrolytic lesions were made to mark the

recording site in the medulla as well as the stimulating sites at the spinal cord. DC currents of 100-200 μA were applied for 20 seconds through the recording and stimulating electrodes. The brainstem and the spinal cord were taken out and fixed in a 10 % formalin solution for at least a week. After then the tissues were frozen, cut and stained for histological identification.

Statistics

Statistical comparisons were performed by the use of Student's t-test. P-values <0.05 were considered significant. Mean values are expressed with their standard errors (S. E.).

RESULTS

Identification of medullospinal cells

The conventional criteria of antidromic activation for a neuron branching to some separated area are: 1) constant latency, 2) faithful follo-wing high frequency stimulation and 3) collison with either a spontaneous or a orthodromically activated impulse. One such an example was shown in Fig. 2. Coordinates of this cell were: 4.0-3.0-3,280 (4 mm rostral to the obex, 3 mm lateral from midline and 3,280 μm in depth from the dorsal surface). The cell was antidromically activated by the stimulation of T2 spinal cord of contralateral side (threshold: 460 μA at 0.1msec duration). The latency was 2.4 msec and followed a triple stimuli of 333 Hz faithfully, and collided with a spontaneous activity. The conduction velocity was 41.2 m/sec.

The majority of ventrolatral medullary cells showing constant latency and following high frequency antidromic stimulation, however, did not have any spontaneous activities. Some of these cells could be activated orthodromically by stimulation of the sciatic nerve to confirm collisions. For example the cell shown in Fig. 3 was identified as a medullospinal tract cell with above criteria. The coordinates were: 4.0-3.0-5,190 and activated by ipsilateral stimulation (threshold: 680 μA at 0.1 msec). The

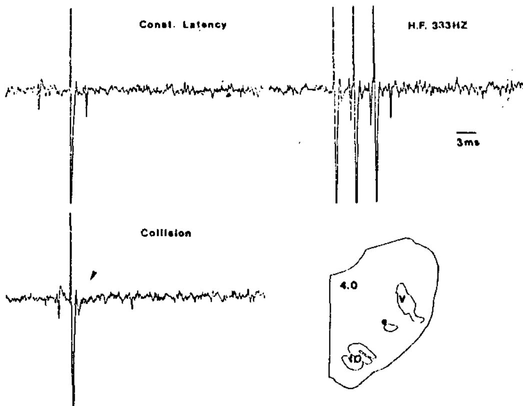

Fig. 2. An example of medullospinal tract cells identified by collision with spontaneous activity. In lower right the recorded site of the cell was shown. Arrow-head indicates the time of expected action potential which was missed due to collision with spontaneous activity appeared just before the stimulus artifact. H.F. high frequency stimulation.

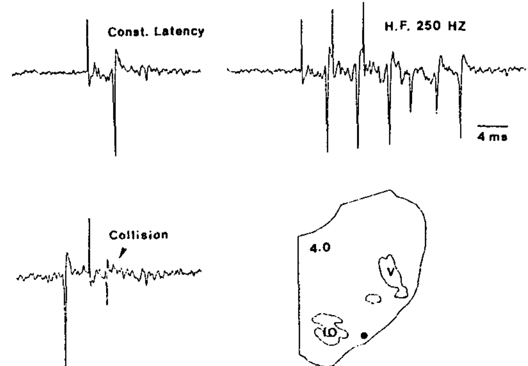

Fig. 3. An example of medullospinal tract cells identified by collision with evoked activity. Contralateral sciatic nerve was stimulated to evoke responses on medullospinal tract cells orthodromically. Abbreviations are the same as Fig. 2.

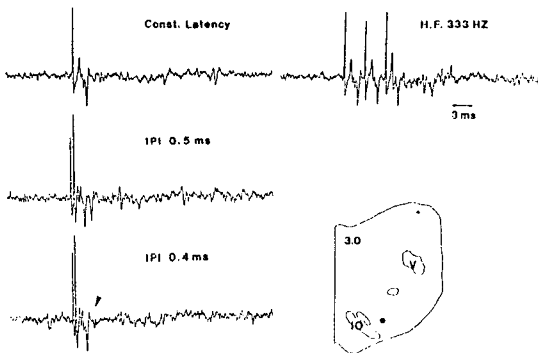

Fig. 4. An example of medullospinal tract cells identified tentatively by refractory period. Left lower two traces show that refractory period of this cell was 0.4 msec. IPI, interpulse inteells.

Table 1. Number of medullospinal tract cells identified by antidromic stimulation of the T1-T3 spinal segments

Identifying method		Number of identified units
Collision	Spontaneous Activity	8
	Sciatic N. Stimulation	19
Refractory Period		29
Total		56

latency was 3.22 msec and followed a triple stimuli of 250 Hz. The conduction velocity was 34.2 m/sec.

The remaining cells did show neither spontaneous activity nor evoked response to the peripheral nerve stimulation, although they could be activated antidromically with constant latency and followed high frequency stimulation faithfully. For these cells, the refractory periods were examined using two consecutive pulses with variable interpulse intervals and determined as medullospinal

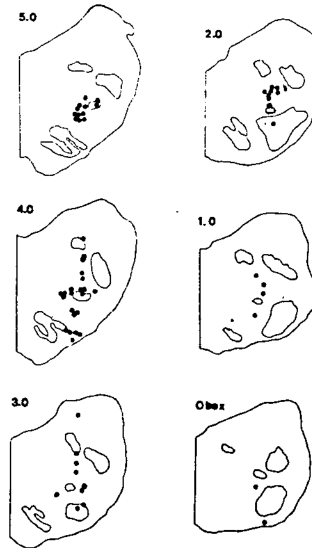

Fig. 5. Location of medullospinal units which were antidromically activated by stimulation of T1-T3 spinal lateral horn. Sections were redrawn after Reinoso-Suarez (1961).

tract cells temporarily. The intensity of the first stimulus was two times that of threshold intensity and that of the second stimulus was four to five times the threshol intensity. Fig. 4 shows one example. The coordinates of this cell were: 3.0-2.5-4,470. The cell was activated antidromically by ipsilateral stimulation (threshold: 510 μA at 0.1 msec duration) and the latency was 1.98 msec, followed a triple pulse of 333 Hz, the refractory period was 0.5 msec and the conduction velocity was 42.9 m/sec.

In present study a total of seventy cells showed constant latency and followed high frequency stimulation faithfully. Among them fifty-six cells were determined as medullospinal cells using the above mentioned criteria. They are summarized in Table 1. Eight cell showed collision with spontaneous activities and nineteen collided with orthodromically evoked activities. The assumed recording sites of them were reconstructed on the stereotaxic map of Reinoso-Suarez in Fig. 5.

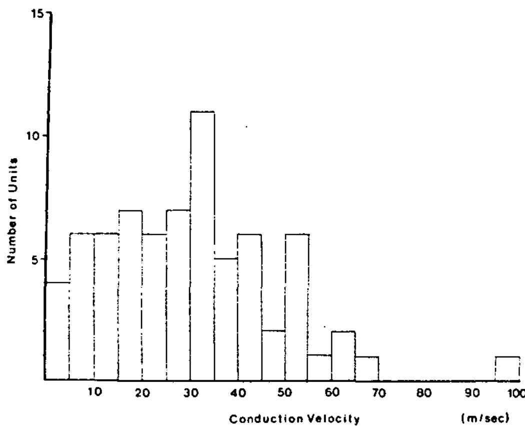

Fig. 6. A histogram showing the distribution of conduction velocity of the identified medullospinal tract cells.

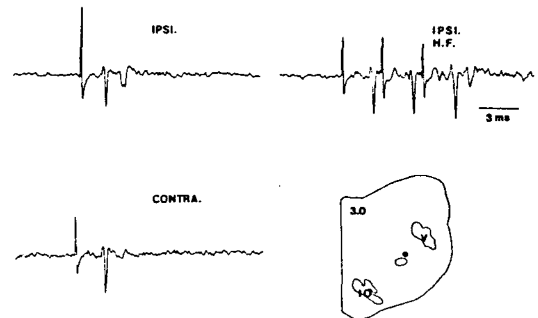

Fig. 7. An example of medullospinal tract cells which were projecting bilaterally to T2 spinal lateral horn. ipsi, ipsilateral; contra, contralateral side.

Table 2. Comparision of conduction velocity of medullospinal cells according to their spinal projections (m/sec)

Inputs	Number of units	Conduction velocity*
Ipsilateral	21	39.1±6.0
Contralateral	31	29.0±2.9
Both	4	30.3±4.0

Table 3. Comparision of conduction velocities between rostral and caudal medullospinal tract cells (m/sec)

	Number of units	Conduction velocity*
Rostral Medullospinal cell	51	27.6+1.1
Caudal Medullospinal cell	19	33.3+3.9

A histogram showing distribution of the conduction velocity of the medullospinal tract cells identified in this experiment was shown in Fig. 6. The majority of them belonged to Aδ- (10-40 m/sec) or Aβ-group (40-70 m/sec) and only four cells belonged to the C (<4 m/sec)-group. Twenty-one cells among fifty-six were activated ipsilaterally and their conduction velocity was 39.1 ± 6.0 m/sec. Thirty-one cells sent their terminals to the contralateral T2 spinal cord and their conduction velocity was 29.0±2.9 m/sec, which significantly differed from that of ipsilaterally activated cells ($0.025 < p < 0.05$). Four cells sent their terminals to ipsi- as well as contralateral side. These results were summarized in Table 2. Fig. 7 shows an example of the medullospinal cells sending their terminals bilaterally. The coordinates of this cell were: 3.0-3.5-3,190 and the threshold for ipsilateral spinal cord stimulation was 180 μA and the latency was 2.31 msec, while the contralateral threshold was 70 μA and the latency was 1.98 msec.

A total of seventy cells which had a constant latency and followed high frequency stimulation faithfully, were divided into two groups: the rostral group (above 3 mm from the obex) and the caudal group (0-3 mm from the obex). In Table 3 the conduction velocities of these two groups were compared. Conduction velocity of the fifty-

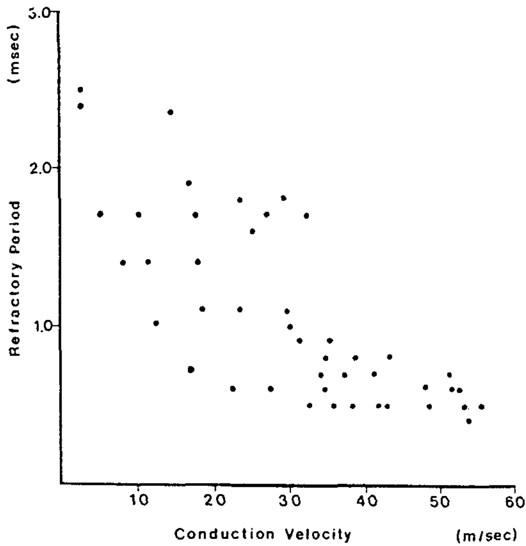

Fig. 8. Relationship between the conduction velocity and the refractory period of the medullospinal tract cells.

one cells belonged to the rostral group was 27.6±1.1 m/sec, while that of the nineteen caudal group cells was 33.3±3.9 m/sec ($0.01 < p < 0.025$). Relationship between the conduction velocity and the refractory periods of fourty-five cells identified as medullospinal cells was shown in Fig. 8. As the conduction velocity becomes larger, the refractory period becomes shorter and the shortest refractory period was in the range of 0.4-0.5 msec.

The peripheral inputs to the medullospinal tract cells

It was not easy to find the peripheral receptive field of the medullospinal tract cells and only four cells had peripheral receptive fields. Fig. 9 shows one example. Coordinates of the cell were: 5.0-3.0-5,360. The cell was activated by contralateral sti-

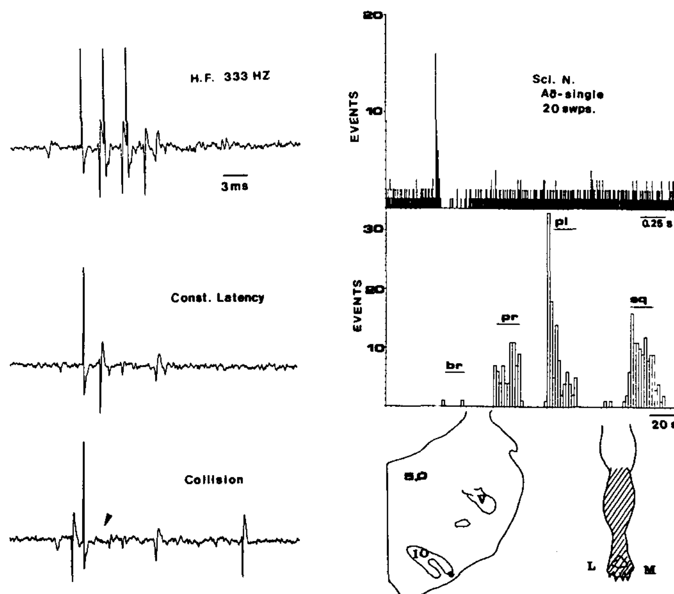

Fig. 9. An example of medullospinal tract cells of which peripheral receptive field was identified and characterized by graded mechanical stimuli applied to its receptive field. Br, brushing; PR, pressure; PI, pinch; SQ, squeeze; L, lateral; M, medial.

mulation (threshold: 85 μA at 0.1 msec, latency 2.36), followed triple pulse of 333 Hz, collided with spotaneous activities and its conduction velocity was 42.4 m/sec. It was determined as a high-threshold cells and received Aδ-peripheral nerve inputs. the receptive field was in lower hindlimb and also received deep somatic inputs.

DISCUSSION

Although it has been known for a long time that the medulla plays a key role in regulation of the arterial blood pressure, only recently the exact location of the cells mediating such a function became elucidated. In special reference to the somatosympathetic reflex, the rostral ventrolateral medulla (RVLM) and the lateral reticular nucleus (LRN) have been concerned with arterial blood pressure regulation (Ciriello & Calaresu, 1977; Iwamoto et al, 1982; McAllen, 1985; Lebedev et al, 1986; Stornetta et al, 1989). Among them the sympathetic-related medullospinal tract cells are located in the RVLM (Barman & Gebber, 1985). They have spontaneous and tonic discharge and the impulse discharge are closely related to the cardiac cycle (Barman & Gebber, 1985; Dampney et al, 1987; Sun & Guyenet, 1987; Morrison et al, 1988).

Summary of the electrophysiological characteristics of the medullospinal tract cells identified in the present study is: 1) The majority of the cells (their coordinates: 0-5 mm from the obex, 3-4 mm from the midline and 3-6 mm in depth from the dorsal surface) did not show any spontaneous discharges and sent their branch to the contralateral thoracic spinal cord. 2) The conduction velocity of rostral VLM (>3 mm from the obex) was different from that of the caudal VLM (0-3 mm from the obex). These results are somewhat different from those of sympathoexcitatory cells in the RVLM reported by other research groups. This might be originated from the contention that the RVLM cells are subdivided into functionally different groups as well as from the differences in species and methods.

First of all the term, "rostral ventrolateral medulla", has been used differently among different groups. Feldberg' group used the term "glycine sensitive area" or "glutamate sensitive area" for the ventrolateral surface of cat medulla after they applied these substances to the area to evoke changes in the arterial blood pressure and single cell activities (Guertzenstein, 1973; Guertzenstein & Silver, 1974; Feldberg & Guertzenstein, 1976). Using the immunohistochemical method, Reis' group defined the C1 cell containing region which is ventral to the ambiguus nucleus, caudal to the facial nucleus, and rostral to the inferior olive in rat medulla (Reis et al, 1989). In cat, Barman & Gebber designated the area 3.5-6.0 mm rostral to the obex, 3-4 mm from the midline and 5-6 mm in depth ventrally as the RVLM (Barman & Gebber, 1985). And Dampney et al (1985) defined the subretrofacial nucleus in rabbit as the RVLM Among the above, Barman & Gebber's method and animal species are very similar to the present study.

Barman & Gebber (1985) identified one hundred and two reticulospinal cells by antidromic stimulation to the second thoracic spinal cord. Two-thirds among them were related to the sympathetic rhythms and their conduction velocity was slower than 3.5 m/sec. Such slowly conducting and sympathetic-related reticulospinal tract cells were also reported in rat (Sun & Guyenet, 1987; Morrison et al, 1988). On the contrary, the cellular activity of the one-third of Barman & Gebber's cells were not related to the sympathetic rhythms and had relatively faster conduction velocity (24.4 m/sec). The rostral medullary group in present study has similar conduction velocity

(27.6~1.1 m/sec) as the latter group.

Only four cells were categorized as C cells by conduction velocity in our study, while the results of Barman & Gebber's study revealed that two-thirds of the cells they recorded were C-cells. The discrepancy between two studies is not clear. One possibility is the slight difference in the recording sites. If one took a careful look at the Fig. 2 of Barman & Gebber's, their reconstructed recording sites were in the area 2.5-3 mm lateral to the midline and ours were in 3-4 mm range from midline and we studied only upto 5 mm rostrally from the obex which is somewhat caudal to the already reported as RVLM. Rather our recording sites seem to be in the lateral tegmental field. Another possibility is that the differences in anesthesia and other methodology might result in the discrepancy.

For a medullospinal cell to be a sympathetic-related cell, it should show spontaneous discharge of impulses and its activities be closely correlated with the sympathetic nerve discharges. The majority of the presently reported cells did not show any spontaneous activity, although they were activated by antidromical stimulation to T2 spinal cord. Such a result implies the existence of a medullospinal tract system which originates from RVLM but is not involved in the generation of sympathetic discharge.

One-third of our cells were in the range of 0-3 mm rostral to the obex and their conduction velocity (33.3 m/sec) was faster than those of remaining two-thirds which are more rostral cells (27.6 m/sec). This location is the area ventral to the lateral reticular nucleus and is known to be involved in mediation of the exercise pressor reflex which is one example of the somatosympathetic reflexes (Ciriello & Calaresu, 1977; Iwamoto et al, 1982; Bauer et al, 1989). This area, however, does not play a key role in the maintainance of sympathetic tone and arterial blood pressure. For example no sympathetic related medullo-spinal tract cells could be sampled in this area (Barman & Gebber, 1985) and even after a lesion was made in the area there was no changes in the resting arterial blood pressure and also pressor response was evoked by the peripheral nerve stimulation. In the latter study a microinjection of glutamate into the area elicited a pressure response before making a lesion (Park, 1990).

In conclusion we identified two subpopulations of medullospinal tract cells in the ventrolateral medulla and they may not belong to the known medullospinal tract system involved in the regulation of arterial blood pressure.

REFERENCES

Amendt K, Czachurski J, Dembowsky K & Seller H (1979) Bulbospinal projection to intermediolateral cell column: a neuroanatomical study. *J Auto Nerv Syst* **1**, 103, 117

Ammons WS (1988) Renal and somatic input to spinal neurons antidromically activated from the ventrolateral medulla. *J Neurophysiol* **60**, 1967-1981

Barman SM & Gebber GL (1985) Axonal projection patterns of ventrolateral medullospinal sympathoexcitatory neurons. *J Neurophysiol* **53**, 1551-1566

Bauer RM, Iwamoto GA & Waldrop TG (1989) Ventrolateral medullary neurons modulate pressor reflex to muscular contraction. *Am J Physiol* **257**, R1154-1161

Cassell MD & Gray TS (1989) The amygdala directly innervates adrenergic (C1) neurons in the ventrolateral medulla in the rat. *Neuro Sci Letts* **97**, 163-168

Chung JM, Webber CL & Wurster RD (1979) Ascending spinal pathway for the somatosympathetic A and C reflexes. *Am J Physiol* **237**, 342-347

Chung JM & Wurster RD (1976) Ascending pre-ssor and depressor pathways in the cat spinal cord. *Am J Physiol* **231**, 786-792

Ciriello J & Calaresu FR (1977) Lateral reticu-

lar nucleus: a site of somatic and cardiovascular integration in the cat. *Am J. Physiol* **233**, R100-109

Ciriello J, Caverson MM & Calaresu FR (1985) Lateral hypothalamic and peripheral cardiovascular afferent inputs to ventrolateral medullary neurons. *Brain Res* **347**, 173-176

Dalhlstrom A & Fuxe K (1964) Evidence for the existence of monoamine containing neurons in the central nervous system. I. Demonstration of monoamines in the cell bodies of brainstem neurons. *Acta Physiol Scand* **62** (Suppl 232), 1-55

Dampney RAL, Goodchild AK, Robertson LG & Montgomery W (1982) Role of ventrolateral medulla in vasomotor regulation: a correlative anatomical and physiological study. *Brain Res* **249**, 223-235

Dampney RAL, Goodchild AK & Tan E (1985) Vasopressor neurons in the rostral ventrolateral medulla of the rabbit. *J Auto Nerv Sys* **14**, 239-254

Feldberg W & Guertzenstein PG (1976) Vasodepressor effects obtained by drugs acting on the ventral surface of the brainstem. *J Physiol (London)* **258**, 337-355

Gebber GL & Barman SM (1981) Sympathetic-related activity of brainstem neurons in baroreceptor-denervated cats. *Am J Physiol* **240**, R348-355

Goodchild AK, Moon EA, Dampney RAL & Howe PRC (1984) Evidence that adrenaline neurons in the rostral ventrolateral medulla have a vasopressor function. *Neurosci Letts* **45**, 267-272

Granata AR, Ruggiero DA, Park DH, Joh TH & Reis DJ (1985) Brainstem area with C1 epinephrine neurons mediates baroreflex depressor responses. *Am J Physiol* **248**, H547-567

Guertzenstein PG (1973) Blood pressure effects obtained by drugs applied to the ventral surface of the brainstem. *J Physiol (London)* **229**, 395-408

Guertzenstein PG & Silver A (1974) Fall in blood pressure produced from discrete regions of the ventral surface of the medulla by glycine and lesions. *J Physiol (London)* **242**, 489-503

Haselton JR & Guyenet PG (1989) Electrophysiological characterization of putative C1 adrenergic neurons in the rat. *Neurosci* **30**, 199-214

Hilton SM, Marshall JM & Timms RJ (1983) Ventral medullary relay neurons in the pathway from the defence areas of the cat and their effect on blood pressure. *J Physiol (London)* **345**, 149-166

Iwamoto GA, Kaufmann MP, Botterman BR & Mitchell JH (1982) Effects of lateral reticular nucleus lesions on the exercise pressor reflex in cats. *Circ Res* **51**, 400-403

Kozelka JW, Chung JM & Wurster RD (1981) Ascending spinal pathways mediating somato-cardiovascular reflexes. *J Auto Nerv Sys* **3**, 171-175

Lebedev VP, Krasyukov AV & Nikitin SA (1986) Electrophysiologic study of sympathoexcitatory structures of the bulbar ventrolateral surface as related to vasomotor regulation. *Neurosci* **17**, 189-203

Lee SH, Jun JY, Park CO, Goo YS, Kim J & Sung HK (1990) A comparative study on the electrophysiological properties of medial and lateral spinoreticular tract cells in cats. *Kor J Physiol* **24**, 181-194

McAllen RM (1986) Location of neurones with cardiovascular and respiratory function at the ventral surface of the cat's medulla. *Neurosci* **18**, 43-49

Morrison SF, Milner TA & Reis DJ (1988) Reticulospinal vasomotor neurons of the rat rostral ventrolateral medulla: relationship to sympathetic nerve activity and the C1 adrenergic cell group. *J Neurosci* **8**, 1286-1301

Reis DJ, Morrison SF & Ruggiero DA (1988) The C1 area of the brain stem in tonic and reflex control of blood pressure. *Hypertens* **11** (Suppl I), I 8-13

Reis DJ, Ross CA, Ruggiero DA, Granata AR & Joh TH (1984) Role of adrenaline neurons of ventrolateral medulla (the C1 group) in the tonic and phasic control of arterial pressure. *Clin Exp Hyperten* **A6**, 221-241

Reis DJ, Ruggiero DA & Granata AR (1986) Brainstem mechanisms governing the tonic and reflex control of the circulation. In: Stokes T et al (eds), *Central Nervous System Control of the Heart*, Martinus Nijhoff, Boston, pp 19-36

Ross CA, Ruggiero DA, Joh TH, Park TH & Reis DJ (1983) Adrenaline synthesizing neurons in the rostral ventrolateral medulla: a possible role in tonic vasomotor control. *Brain Res* 273, 356-361

Ross CA, Ruggiero DA, Park TH, Joh TH & Reis DJ (1984) Rostral ventrolateral medulla: selective projections to the thoracic autonomic cell column from the region containing C1 adrenaline neurons. *J Comp Neurol* 228, 168-184

Somogyi P, Minson JB, Morilak D, Llewellyn-Smith I, McIlhinney RAJ & Chalmers J (1989) Evidence for an excitatory amino acid pathway in the brainstem and for its involvement in cardiovascular control. *Brain Res* 496, 401-407

Stein RD, Weaver LC & Yardley CP (1989) Ventrolateral medullary neurones: effects on magnitude and rhythm of discharge of mesenteric and renal nerves in cats. *J Physiol (London)* 408, 571-586

Stocks G, Schmelz M, Knuepfer MM & Forssmann WG (1983) Functional and anatomic aspects of central nervous cardiovascular regulation. In: Ganten D and Pfaff D (eds), *Central Nervous Cardiovascular Control,* Springer-Verlag, Bèrlin, pp 1-30

Stornetta RL, Morrison SF, Ruggiero DA & Reis DJ (1989) Neurons of rostral ventrolateral medulla mediate somatic pressor reflex. *Am J Physiol* 256, R448-462

Sun M-K, Guyenet PG (1986) Hypothalamic glutamatergic input to medullary sympathoexcitatory neurons in rats. *Am J Physiol* 251, R798-810

Urbanski RW and Sapru A (1988). Evidence for a sympathoexcitatory pathway from the nucleus tractus solitarii to the ventrolateral medullary pressor area. *J Auto Nerv Sys* 23, 161-174