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Physiological Properties of the Spinal Dorsal Horn Cells Receiving Ventral Root Afferent Inputs in the Cat†

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= Abstract = Spinal dorsal horn neurons receiving ventral root afferent inputs were studied in cats anesthetized with α-chloralose. The L7 and S1 spinal ventral roots were stimulated electrically, and after identifying the evoked single cell activities, their receptive fields, cell types and peripheral nerve inputs were determined. Followings are the results obtained.

1. A total of 43 cells receiving ventral root afferent inputs were identified. These were located in lamina IV-VI of the spinal cord. More than half of them were silent or showed spontaneous discharge less than 5 Hz during the resting period. The remaining units discharged spontaneously in the range of 10-20 Hz.

2. In 23 cells, the cell types were determined according to the responses to graded mechanical stimulation applied to receptive fields. Eleven cells were HT cells and seven were WDR cells.

3. All these cells were activated by C-intensity stimulation but not by Aδ-stimulation of the ventral roots, while their main peripheral nerve inputs were Aδ-inputs.

4. Intravenous morphine inhibited the reponses of these cells to VR stimulation, and naloxone reversed the morphine effect.

From the above results it was concluded that afferent inputs carried by the VRA fibers might be associated with still unknown pain pathways.

Key words: ***Ventral root afferent, High threshold cell, Wide dynamic range cell, Peripheral nerve inputs, Morphine***

INTRODUCTION

According to Bell-Magendie's law, afferent nerves are contained in the mammalian dorsal root, while motor and preganglionic nerves are in the ventral root. Recent electron microscopic studies, however, have revealed that a significant number of afferent nerve fibers exist in the spinal ventral root (Coggeshall *et al.*, 1974, 1975; Clifton *et al.*, 1976; Coggeshall, 1980; Risling *et al.*, 1987). Some authors reported that these ventral root afferent (VRA) fibers might enter the spinal cord directly through the ventral root (Maynard *et al.*, 1977; Light & Metz, 1978; Hosobuchi, 1980; Longhurst *et al.*, 1980), but others insisted that these fiber eventually entered the spinal cord through the dorsal root, although they existed in the ventral root (Risling & Hildebrand, 1982; Risling *et al.*, 1984).

The number of afferent fibers in the ventral root composed 20-30% of the total nerve fibers in the ventral root (Coggeshall *et al.*, 1974; Applebaum *et al.*, 1976). Their physiological role, however, is completely unkown. A series of physiological studies revealed recently that: 1) some

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neurons in the dorsal horn could be excited by the activation of ventral root afferent fibers (Chung *et al.*, 1983; 1985), 2) EPSPs with long latency could be recorded in the spinal motor neuron responding to VRA stimulation (Endo *et al.*, 1985), 3) flexion reflex could be demonstrated in the proximal stump of the cut ventral root while stimulating the distal stump of the cut ventral root of the same segment (Shin *et al.*, 1985), 4) a pressor response was elicited to the VRA activation (Chung *et al.*, 1986; Kim *et al.*, 1989), and 5) the proportion and location of spinal neurons receiving the VRA inputs (Kim *et al.*, 1988) were studied. All these findings were the results of stimulating the distal stump of the cut VR and hence suggest that functional VRA inputs enter the spinal cord through the dorsal root. Reports revealing the existence of nerve fibers connected between the dorsal and ventral roots (Kim & Chung, 1985) and that many of the VRA fibers were third branches of dorsal root ganglion cells (Kim *et al.*, 1987) further support the above contention.

All these data, however, do not explain the exact nature and role of the VRA system. Since the major population of VRA fibers belonged to the C-groups, which were related to nociceptive transmission, some authors suggested that the VRA system plays a role in mediating nociceptive information from the pia mater and/or nearby surrounding tissues (Dalsgaard *et al.*, 1982; Risling *et al.*, 1984). Others reported that the number of VRA fibers decreased when they were accessing the spinal cord and increased with age (Risling & Hildebrand, 1982) or increased after neonatal sciatic nerve injuries (Risling *et al.*, 1984; Nam *et al.*, 1989; Oh *et al.*, 1989).

So far we don't have the direct means of measuring the physiological role of the VRA system. Since the initial stage of the study of the VRA system, it was known that they had receptive fields in the periphery (Clifton *et al.*, 1976; Coggeshall & Ito, 1977) and that the spinal dorsal horn cells receiving the VRA inputs also had peripheral receptive fields (Chung *et al.*, 1983, 1985; Kim *et al.*, 1988). We attempted in the present study to investigate the physiological nature of the spinal neurons receiving VRA inputs.

MATERIALS AND METHODS

Adult cats of either sex (1.8-3.0 kg) were used in the present experiment. Each animal was anesthetized with ketamine (15 mg/kg, i.m.) and α-chloralose (60-70 mg/kg, i.p.) and the trachea was cannulated. Pancuronium bromide (initial dose of 0.4 mg, maintained by a dose of 0.4 mg every hour) was injected for generalized muscle relaxation, and the animal was artificially ventilated. Arterial blood pressure was monitored throughout the experiment with a pressure transducer connected to a carotid arterial catheter, and drugs or infusion solutions were given through a jugular venous catheter. The body temperature was maintained at 37 $\pm$ 1°C using a heated blanket (Animal blanket condition unit, Harvard).

A laminectomy was done on the L4-S1 vertebrae, and lumbosacral enlargement of the spinal cord was exposed. The L7 and/or S1 spinal roots were traced intradurally, and the VRs were cut near the spinal cord. Thoracotomies were done in the intercostal spaces bilaterally. An incision was made at the back skin of the left hind limb. The sciatic, common peroneal and tibial nerves were isolated and exposed. After completion of the surgery, the animal was mounted on a spinal animal apparatus, and mineral oil pools with a water-circulating heating coil were made over the exposed area.

Figure 1 represents a schematic diagram for the experimental setup used. The distal stump of the cut VR was placed on a tripolar platinum stimulating electrode, of which the most distal lead was grounded to prevent the current-spread. Square pulses generated from a stimulator (SEN-7103, Nihon Kohden) were applied through an isolator (WPI, 850A). The peripheral nerves exposed in the hind limb were also placed on tripolar electrodes. The intensity and duration of the stimuli were determined such that Aδ-stimulation means 10-50 times that of the Aα-nerve activation (0.1 msec, 500-1000 μA), and C-stimulation means 500-1000 times (0.5 msec, 5-10 mA).

Single cell activities from the spinal dorsal horn cells were recorded with a carbon filament microelectrode (tip resistance: 1-2 MΩ). The distance between the searching tracks was 200 μm. The recorded signals were amplified with

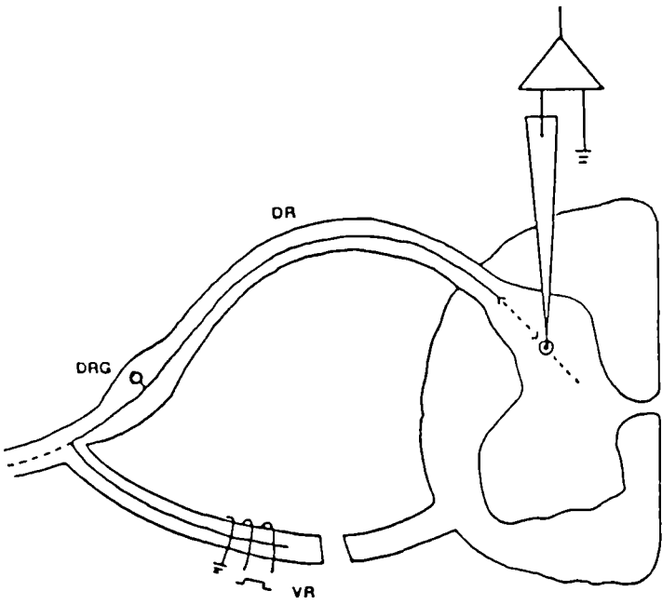

Fig. 1. A schematic drawing of the stimulation and recording setup. The L7 ventral root was cut near the spinal cord, and the distal stump was placed on a tripolar stimulation electrode, the most distal lead was grounded. Single cell activities were recorded with a carbon filament microelectrode. DR, dorsal root; DRG, dorsal root ganglion; VR, ventral root.

an AC differential amplifier (DAM-80, WPI), monitored on oscilloscopes and through a window discriminator (Frederick Haer & Co) and laboratory interface (CED 1401) stored in a personal computer for further analysis.

When a single-cell activity receiving VRA inputs was isolated sufficiently, its peripheral receptive fields, response pattern to natural stimulation and peripheral nerve input were characterized. After completion of the recording, electrolytic lesions were made (a DC current of 100-200 μA, 20-30 sec duration) for histological identification of the recorded site.

RESULTS

A total of 43 dorsal horn cells receiving VRA inputs were identified in 25 cats. Figure 2 shows an example of the responses of a dorsal horn cell to the stimulation of the distal stump of the cut VR. When 3-train pulses (20 msec interpulse interval) of C-intensity (0.5 msec, 5 mA) stimuli were applied to the L7 VR, the cellular discharge rate increased for about 200 seconds with a latency of 40 msec. These responses were not

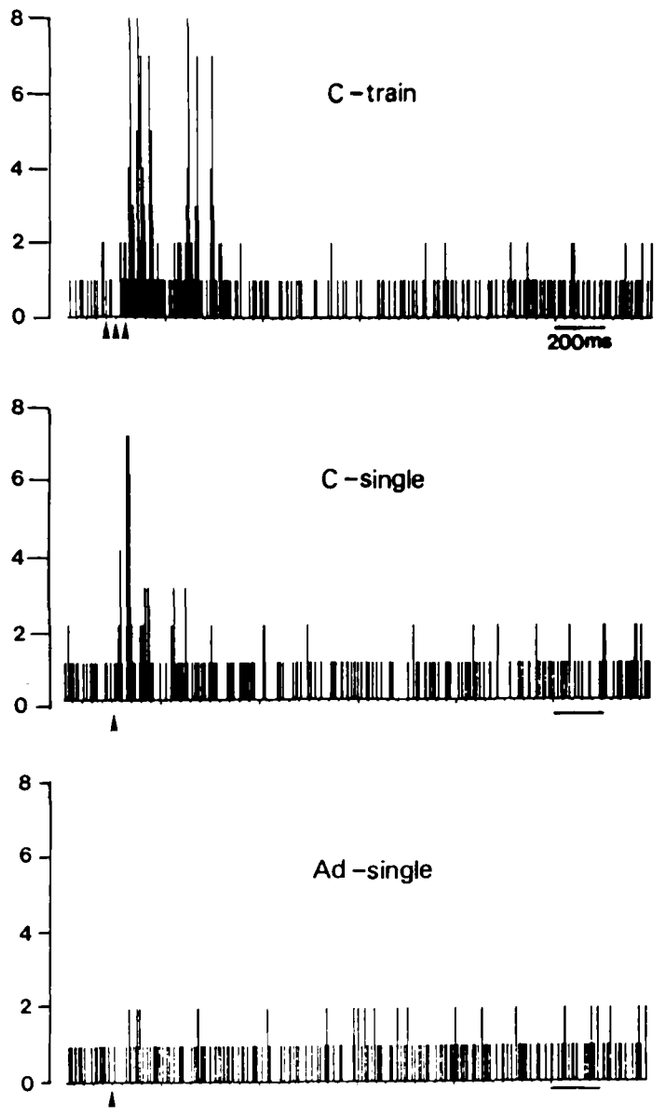

Fig. 2. Responses of a dorsal horn cell to stimulation of the ventral root. In A, responses were recorded while stimulating the L7 ventral root with C-strength, 3-train pulses (20 msec interpulse interval, 0.5 msec, 5 mA). In B, the ventral root was stimulated with C-strength, single pulse and in C, stimulated with Aδ-strength, single pulses (0.1 msec, 0.5 mA). All the peristimulus time histograms (bin width, 1 msec) were compiled from 20 consecutive stimulations (at arrowheads).

elicited by 3-train pulses with Aδ-intensity, and train pulses were more effective than single pulses when C-intensity stimuli were applied. Recorded cells were distributed mainly in lamina IV-VI in the L6-S1 spinal segments, and only two cells were identified in lamina I & II. More than half of them (23/43) were silent or at most spontaneous dischargers (less than 5 Hz).

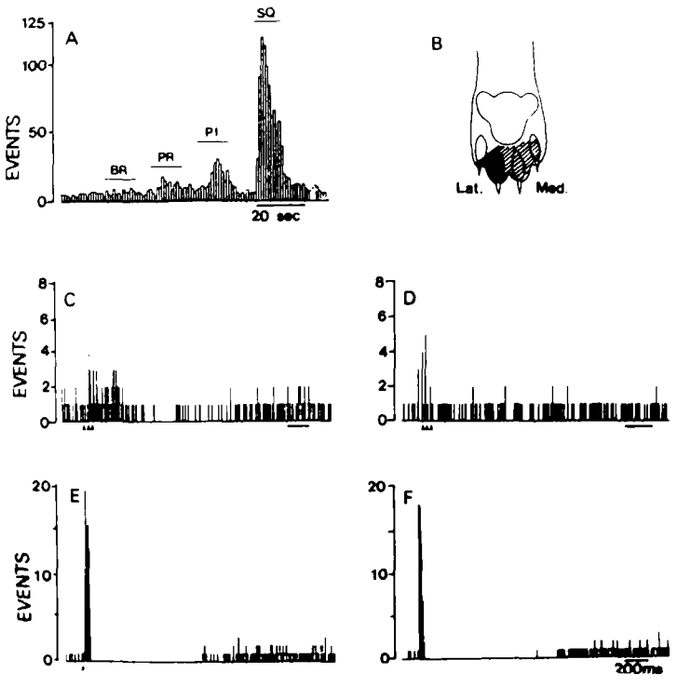

Fig. 3. An example of a high-threshold dorsal horn cell receiving the ventral root afferent inputs. In A, responses of the cell to graded mechanical stimulation applied to the receptive field are shown. The recetptive field is shown in B. In C and D, responses of the cell to stimulation of the L7 ventral root with 3-train, C- and Aδ-strength stimuli are shown, respectively. Reponses to common peroneal nerve stimulation with C- and Aδ-intensity stimulation are shown in E and F, respectively. The single-pass histogram (A) was formed while brushing the skin with a camel's hair brush (BR), application of a large arterial clip (PR), a small arterial clip (PI), or squeezing a fold of skin with serrated forceps (SQ) for 10 seconds as indicated by the lines at the top of the histogram (bin width, 1 sec).

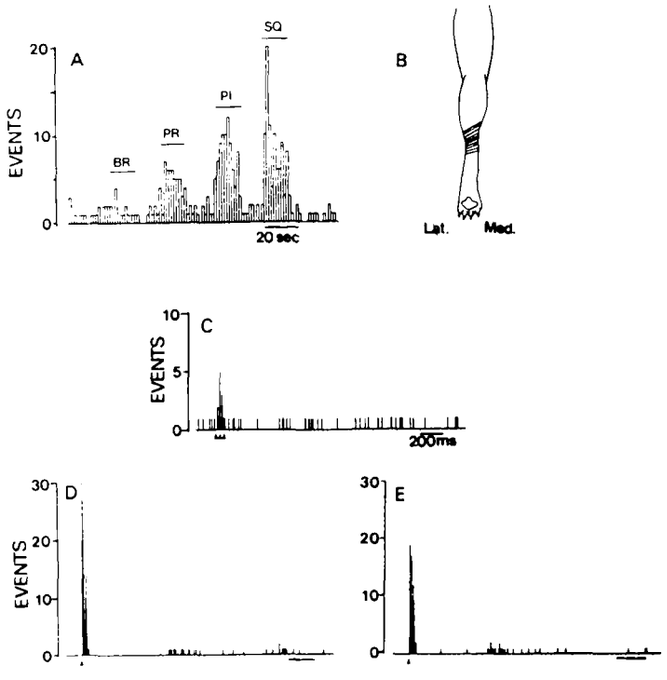

Fig. 4. An example of wide-dynamic range dorsal horn cell receiving the ventral root afferent inputs. In A, responses of the cell to graded mechanical stimulation applied to the receptive field (B) are shown. Responses to stimulation of the L7 ventral root with 3-train, C-intensity pulses are shown in C. Responses to tibial nerve stimulation with C- and Aδ-intensity stimuli are shown in D and E.

Others showed a spontaneous discharge of impulses in 10-20 Hz.

Twenty-three of the 43 cells were classified according to their responses to graded natural mechanical stimulation applied to the peripheral receptive fields. Eleven were belonged to high-threshold (HT) cells. Figure 3 represents a typical example of such HT cells. The cell shown in figure has a small receptive field in and between the lateral toes. It did not respond to non-noxious mechanical stimulation such as brushing with camel's hair or pressing with a large arterial clip, but responded to pinching with a small arterial clip and to squeezing with a serrated forceps. It received both common peroneal and tibial nerve inputs, but the Aδ-stimulation to the peripheral nerves was sufficient to activate the cell, contrary to the VR stimulation in which C-strength stimulation was needed.

Seven cells were classified as wide-dynamic range (WDR) cells. Figure 4 shows an example of WDR cell receiving VRA inputs. This cell responded in a graded manner to graded mechanical stimulation as typical WDR cells of spinothalamic tract cells do. Many cells, however, showed atypical responses, for example, responding to brushing to the same extent as pinching or squeezing. The size of the receptive fields was somewhat larger than those of the HT cells as shown in Figure 4.

The remaining cells (5/23) showed inhibitory responses to the activation of VRA, and their receptive fields' characteristics were very complex. For example, the discharge rate of the cell shown in Figure 5 decreased when the distal stump of the cut VR was stimulated, and it had

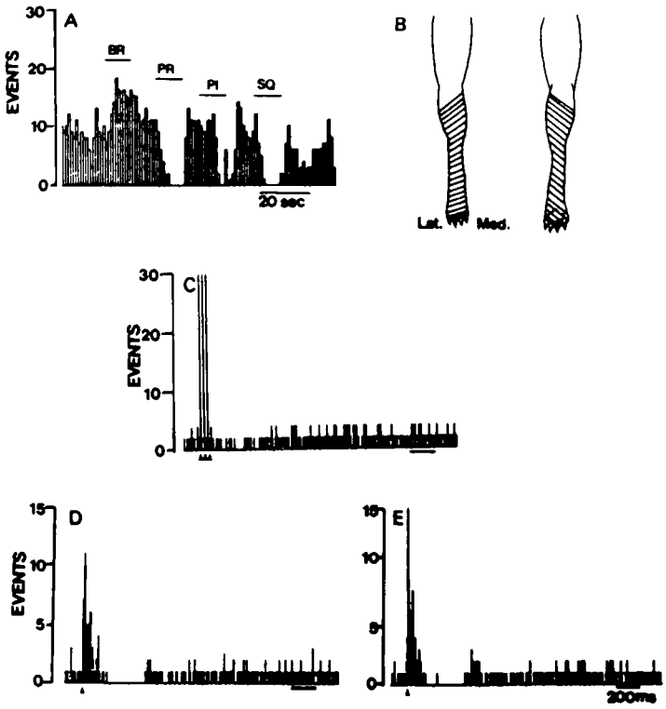

Fig. 5. An example of a dorsal horn cell receiving ventral root afferent inputs, which showed both excitatory and inhibitory responses to the graded mechanical stimulation. The discharge rate was increased by brushing the receptive field (B), while more strong mechanical stimuli decreased the discharge rate as shown in A. C, D and E represent responses of the cell to stimulation of the ventral root with 3-train, C-intensity, and to tibial and peroneal nerve stimulation with single C-intensity stimuli, respectively.

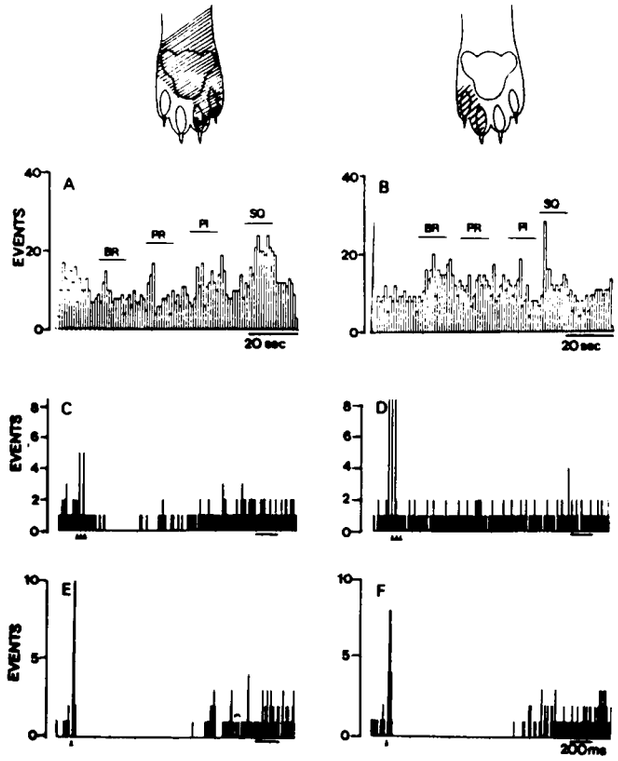

Fig. 6. An example of a dorsal horn cell receiving the ventral root afferent inputs and showing two discrete receptive fields of excitation and inhibition. In A, the mechanical stimulation applied to the receptive field shown in the insert with brush and pressure inhibited the activity of the cell, while pinching and squeezing enhanced the activity. The reverse was true when graded mechanical stimuli were applied in the receptive field shown in the insert figure in B. Responses to the stimulation of the ventral root with C- and Aδ-intensity, 3-train pulses are shown in C & D.

a large receptive field in both legs. To brushing stimulation it responded excitatorily, but to stronger mechanical stimulations it responded inhibitorily in a graded manner, and hence was similar to inversed WDR cells. It received inhibitory input from the common peroneal nerve but received excitatory inputs, followed by inhibitory inputs from tibial nerve. The cell represented in Figure 6 had different characteristics. Activation of the VRA inhibited its discharge rate of impulses. The cell had two separate receptive fields, one in the footpad and lateral toes and the other in the medial toes. When graded mechanical stimuli were applied to the former receptive field, it showed inhibitory responses to brushing, pressure and pinching but excitatory responses to squeezing. The reverse was true when graded mechanical stimuli were applied to the latter receptive field.

In five cells, the effect of morphine on the response of the dorsal horn cell receiving VRA inputs was studied. Figure 7 represents one example. The cell was an HT cell having its receptive field in the lateral two toes. As shown in the figure, stimulation of the VR resulted in an increased firing rate. This response was eliminated by an intravenous injection of morphine HCl (2 mg/kg). Naloxone (0.2 mg, i.v.) rapidly reversed the morphine effect. Other cells responded essentially in the same manner as the cell in Figure 7.

DISCUSSION

The first report of central neurons receiving VRA inputs was done by Chung *et al.* (1983). The

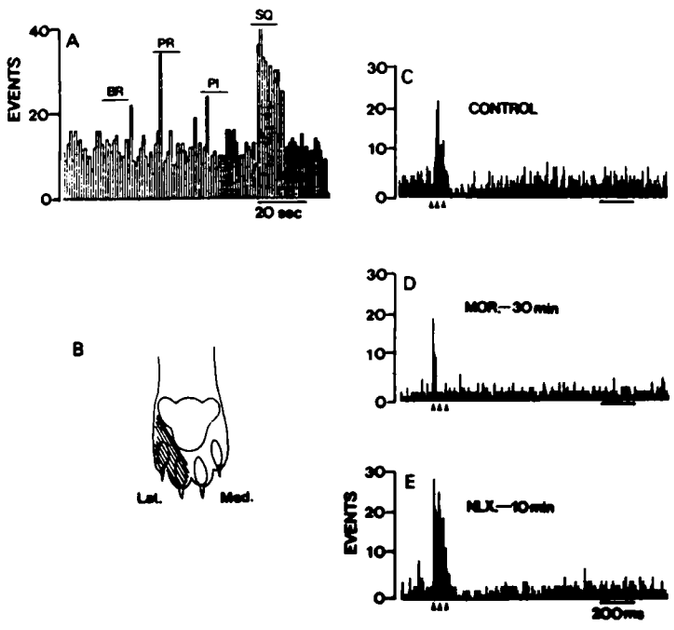

Fig. 7. Effect of intravenous morphine (2 mg/kg) on the responses of the dorsal horn cell activated by stimulation of the L7 ventral root. This cell was a high theshold cell as shown in A and had a narrow receptive field in the lateral two toes (B). Responses of the cell to the activation of ventral root afferent fibers (C) were eliminated after morphine injection (D) and, as shown in E, this effect was reversed by an intravenous injection of naloxone (0.2 mg).

report was a short one demonstrating that central neurons could be activated by stimulation of the distal stump of the cut ventral root and that information carried by the VRA fibers might enter the spinal cord through the dorsal root. Since then, Chung's laboratory has reported on the distribution, peripheral receptive field and peripheral nerve inputs of these cells (Chung *et al.*, 1985; Kim *et al.*, 1988). Followings are the summarized results of those reports: 1) to activate the spinal neurons, the VR should be stimulated with C-intensity, train pulses, 2) the majority of the cells receive both Aδ- and C-peripheral nerve inputs, 3) they are distributed mainly in lamina IV-VI, and one-fifth of the entire spinal neuron population received the VRA inputs, 4) among the cells, 50% were HT cells and 40% were WDR cells, 5) some of them were sending ascending axons, at least to the thoracic spinal cord. Our results were essentially the same. But the proportion occupied by the HT cells was higher, and comparatively more cells showed inhibitory reponses and complex receptive field characteristics.

In general sensory neurons in the spinal cord and higher centers are classified as wide-dynamic range cell, high-threshold cell, low-threshold cell and deep cell according to their responses to the graded mechanical stimulation applied to their receptive fields (Price *et al.*, 1978; Chung *et al.*, 1979; Willis, 1985; Price, 1988). For spinothalamic tract cells, over 60% are WDR cells, HT cells are less than 30% and the remaining are LT or deep cells. However, this classification is too simple, for there are many cells which cannot be classified easily. This becomes more important as the sensory cells come to receive inputs through more and more synapses. So some authors classified sensory cells in the ventral posterior lateral nucleus of the thalamus into six groups based on cluster analysis (Chung *et al.*, 1986; Surmeier *et al.*, 1987). In the present study typical WDR cells were seen in only one or two of the seven cells classified as WDR cells and five cells receiving inhibitory VRA inputs showed variable responses. Generally, cells which had more complex receptive fields were distributed more deeply in the dorsal horn. These results suggest that the spinal afferent processing mechanism of the VRA inputs are more complex than those of the cutaneous nociceptive inputs.

In the present study the proportion of high-threshold dorsal horn cells receiving VRA inputs was 48%. This result agrees with others (Chung *et al.*, 1985; Kim *et al.*, 1988) but differs from those of the STT cells receiving cutaneous nociceptive inputs. It has been said that in spinal lamina IV-VI, more WDR cells are found than HT cells (Wall, 1967; Price, 1988). For the dorsal horn cells receiving VRA inputs, however, the majority was distributed in lamina IV-VI, but were HT cells. One possibility for this discrepancy is that the cells involved in the afferent processing of the VRA inputs are clustered together in lamina IV-VI, and we might have sampled these cells due to the experimental bias resulting from the methodology and object of the study. Throughout the present experiment if a single-cell activity receiving VRA inputs had been identified, then several cells receiving VRA inputs could be identified in the same track or nearby tracks. This might support the above possibility.

Earlier studies cited above reported that dorsal horn cells activated by stimulation of the VR

would receive both Aδ- and C-peripheral nerve inputs (Chung *et al.*, 1985; Kim *et al.*, 1988). But in this study the cells were activated mainly by peripheral Aδ-inputs and not by C-inputs. Since HT cells could be activated by Aδ- and/or C-fiber inputs, whereas WDR cells could be activated by Aβ-, Aδ- and C-fiber inputs (Price, 1988), the main peripheral nerve inputs to HT cells recorded in the present study might be Aδ-inputs although activated by stimulation of the VR with C-intensity stimuli. Our earlier report that many VRA fibers were third branches of the dorsal root ganglion cells and that conduction through the VR was slower than that through the peripheral nerve (Kim *et al.*, 1987) drew essentially the same conclusion as the present results.

The physiological roles that the VRA system is playing are not known. On the basis of the fact that the majority of VRA fibers are unmyelinated (Coggeshall *et al.*, 1974, 1975; Clifton *et al.*, 1976; Coggeshall, 1980; Kim & Chung, 1985; Rislig *et al.*, 1987) and unmyelinated fibers are closely associated with the transmssion of nociceptive information, investigators have vaguely implicated that they are associated with some pain system which is not yet known. For example, nociceptive afferent information arising in the pia mater of the ventral surface or surrounding tissues might take its route to the dorsal root ganglions in the nearby ventral root for convenience, not through the peripheral nerves (Dalsgaard *et al.*, 1982; Risling *et al.*, 1984; Kim *et al.*, 1988), or the recurrent sensibility, which means the recurring pain after dorsal rhizotomy for pain allevation (Coggeshall *et al.*, 1975), might be associated with the VRA system.

The afferent processing mechanisms of the VRA system, however, might differ from those of the cutaneous nociceptive system. As revealed in the present study as well as in others, the distribution and types of dorsal horn cells receiving VRA inputs are different from those of the spinothalamic tract cells. The pressor response to stimulation of the VR differs in its frequency and intensity characteristics, and its ascending pathways through the spinal cord (Kim *et al.*, 1986) from those of peripheral nerve stimulation (Chung & Wurster, 1976; Chung *et al.*, 1979). In the extreme, considering the facts that the number of VRA fibers increases as the animal grows older (Risling & Hildebrand 1982), and after sciatic nerve damage given experimentally (Risling *et al.*, 1984; Nam *et al.*, 1989; Oh *et al.*, 1989), these VRA fibers may not play a significant role in physiologic conditions. Rather, they may be the regenerating sprouts of the damaged peripheral nerves growing into the VR by chance.

Other results, on the contrary, are consistent with the implication that VRA systems are associated with the transmission of nociceptive information. The VRA fibers could be activated by peripheral noxious stimulation (Clifton *et al.*, 1976; Coggeshall & Ito, 1977), their activation could induce flexion reflex (Shin *et al.*, 1985) and activate the HT and WDR cells which receive nociceptive peripheral inputs (Chung *et al.*, 1985; Kim *et al.*, 1988 and present study). The eliminating effect of the morphine on the response of the dorsal horn cells to the stimulation of the VR, along with the reversing effect of naloxone, further support the above contention. In spite of these indirect evidences implicating the association of the VRA system with nociceptive transmission, more effort is needed to elucidate the mechanism and role of the VRA systems in physiological conditions.

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= 국문초록 =

고양이에서 척수전근 구심섬유의 흥분을 받는 척수후각 신경세포의 생리학적 특성

서울대학교 및 조선대학교* 의과대학 생리학교실

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고양이에서 척수전근내 구심섬유의 흥분을 받는 신경세포들의 전기생리학적 특성을 조사하였다. 고양이를 α-chloralose로 마취한 후 L7-S1 척수전근을 노출시키고 자극하면서 척수회질에서 세포활동을 추적하였다. 원하는 세포가 확인되면 말초감수야, 세포의 종류, 말초신경 자극에 대한 반응 등을 관찰하고 이에 대한 morphine의 효과를 관찰하였다.

척수전근 구심섬유의 흥분을 받는 척수신경세포를 모두 43개 확인하였는데 이들은 주로 lamina IV-VI에서 관찰되었으며 안정상태에서 자발적 흥분발사가 적었다. 이중 23 세포에서는 말초에 대한 점진적인 기계적 자극에 대하여 분류하였을 때 HT세포가 가장 많았고 다음이 WDR세포이었다. 이들은 주로 Aδ-말초신경의 흥분을 받았으며 morphine 투여시 전근내 구심섬유를 자극하여 유발되던 척수신경세포들의 반응이 억제되었다.

이상 척수전근내 구심섬유들은 척수내에서 통각정보를 처리하는 HT, WDR세포들을 흥분시키고 또 morphine에 의해서 척수전근 자극에 대한 반응이 억제되는 결과로부터 척수전근내 구심섬유가 아직 알려지지 않은 통각정보의 처리과정과 관련이 있으리라 사료된다.