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CONVERGENCE OF FORELIMB AFFERENT ACTIONS ON C7-TH1 PROPRIOSPINAL NEURONES BILATERALLY PROJECTING TO SACRAL SEGMENTS OF THE CAT SPINAL CORD

P. KRUTKI AND W. MRÓWCZYŃSKI

Department of Neurobiology, University School of Physical Education, 55, Grunwaldzka Str., 60-352 Poznań, Poland

INTRODUCTION

Propriospinal tract neurones connecting cervical and lumbosacral enlargements have been widely investigated in cats in numerous electrophysiological studies (2, 25, 36). These systems have deserved special attention with respect to their essential role in generating complex patterns of muscle activity, underlying spinal reflexes and locomotion and suggesting their contribution to the coordination of movements of the fore- and hindlimbs. Experimental lesions of various parts of the spinal cord in cats have confirmed this point of view. Motor deficits and disruptions of the pattern of limb movements during locomotion have been observed mainly after lesions of dorsolateral (7, 24) or ventral funiculi (34). Other studies have brought the evidence of direct, monosynaptic connections of cervical propriospinal neurones with motoneurones located in the lumbosacral enlargement that innervate hindlimb muscles (22). However, little is known about the type of information processed and conducted to lower spinal segments. Afferent connections from various peripheral receptors and supraspinal centres have been described in details only in short C3-C4 propriospinal neurones projecting to motor centres controlling forelimb muscles (4) and to a some extent in C3-C5 propriospinal neurones with axons descending beyond the Th9 segment (2, 3). Monosynaptic excitation and disynaptic inhibition from muscle and cutaneous forelimb receptors together with monosynaptic actions evoked from several pathways descending from the motor cortex and brain stem centres have been observed in the latter group of cells.

Previous electrophysiological investigations in our laboratory have concerned other type of long descending propriospinal connections: neurones located in C6-C7 segments and projecting as far as to sacral segments of the spinal cord. Bilateral course of branching axons in the spinal white matter has been confirmed in the majority of these cells and collaterals to the gray matter of lumbar segments have been described (25, 27). On the basis of these findings, a possible contribution to the process of motor coordination of all four limbs has been proposed.

Correspondence: Dr. Piotr Krutki, Department of Neurobiology, University School of Physical Education, 55, Grunwaldzka Str., 60-352 Poznań, Poland - Tel. + 48 61 8355435 - Fax: + 48 61 8355444 - E-mail: krutki@awf.poznan.pl

In the present study in the cat we extended our previous findings by determining patterns of afferent connections from various forelimb receptors to this group of neurones. Experiments were based on intracellular recordings of postsynaptic potentials following stimulation of afferent fibres in selected muscular, cutaneous and mixed nerves of the distal forelimb. In individual cells we intended to identify a convergence of excitatory or inhibitory actions from various sources and to define mono-, di- or polysynaptic coupling of various afferents with these neurones.

METHODS

Preparation.

Eleven adult cats of both sexes (weighing between 2.8 and 3.8 kg) were used for experiments. All the experimental procedures were approved by a local ethics committee and followed Polish Law on the Protection of Animals and European Union guidelines of animal care. Anaesthesia was induced with ketamine hydrochloride (25-40 mg kg^{-1}, i.m.) for the initial surgery and maintained during recordings with a-chloralose (supplemented as required, up to 50 mg kg^{-1}, i.v.). The depth of the anaesthesia was controlled by the lack of withdrawal and corneal reflexes before animals were paralyzed and by the diameter of pupils, heart rate and arterial blood pressure during recordings. Additional doses of anaesthetic were given when pupils dilated or the blood pressure rose. The blood pressure was continuously kept between 90 and 130 mmHg, the frequency and volume of artificial ventilation was adjusted to keep the CO_2 level in the expired air around 4%, the body temperature was maintained by heating lamps at 37 ± 1 °C. The detailed description of drugs administration and surgical procedures was described in our previous papers (16, 31).

The experimental arrangement is given in Figure 1. The spinal cord was exposed by laminectomies made over the cervical enlargement, lower thoracic and sacral segments of the spinal cord. The dura mater was cut and removed over cervical and sacral segments but left intact at the thoracic level. Small holes were made in the pia for the insertion of recording micropipettes in C7-Th1 segments and stimulating tungsten electrodes in S1-S2 segments. Exposed areas of the spinal cord were covered with warm paraffin oil. In addition, ipsilateral forelimb nerves: deep radial (DR), superficial radial (SR), median (Med) and ulnar (Uln) were dissected and mounted in cuff electrodes between muscles or under the skin.

Stimulation and recording.

In order to stimulate descending axons in lateral funiculi of the spinal cord bipolar silver ball-tipped electrodes were placed bilaterally on dorsal parts of lateral funiculi at the level of Th13 segment. Rectangular pulses of 0.2 ms duration and strength of 80-800 μA were delivered at a frequency of 3-5 Hz. To stimulate axons or their terminals in the gray matter of sacral segments two varnished tungsten needle electrodes (tip diameter of 5 μm, exposed for 10-20 μm) were introduced bilaterally, perpendicular to the surface of the spinal cord, 1 mm lateral from the mid-line, to a depth of 2.2-2.5 mm. Pulses of 0.2 ms and 35-100 μA were applied at a frequency 3-5 Hz. A stimulus of 100 μA can excite axons within a radius of 0.5-1.0 mm (6, 32), thus it was expected that in each case only axonal branches on the stimulation side were activated. Afferent fibres in forelimb nerves were stimulated with pulses of 0.1 ms duration and strength expressed in multiples of threshold for the most sensitive fibres in a nerve.

Silver ball electrode was placed on the spinal cord surface close to the dorsal root entry area in order to record incoming afferent volleys from the nerves stimulated. Recording glass micropipettes (tips broken under a microscope to 1.5-2.5 μm, resistance 2-10 MΩ) filled with 2 M potassium citrate solution were inserted into the gray matter of the C6-Th1 segments using a stepping micromanipulator. Before afferent actions were recorded intracellularly, antidromic action potentials from descending axonal branches were recorded in order to identify neurons as long propriospinal tract cells (Fig. 1 A-D). Constant latency, amplitude and threshold of stimulation, all-

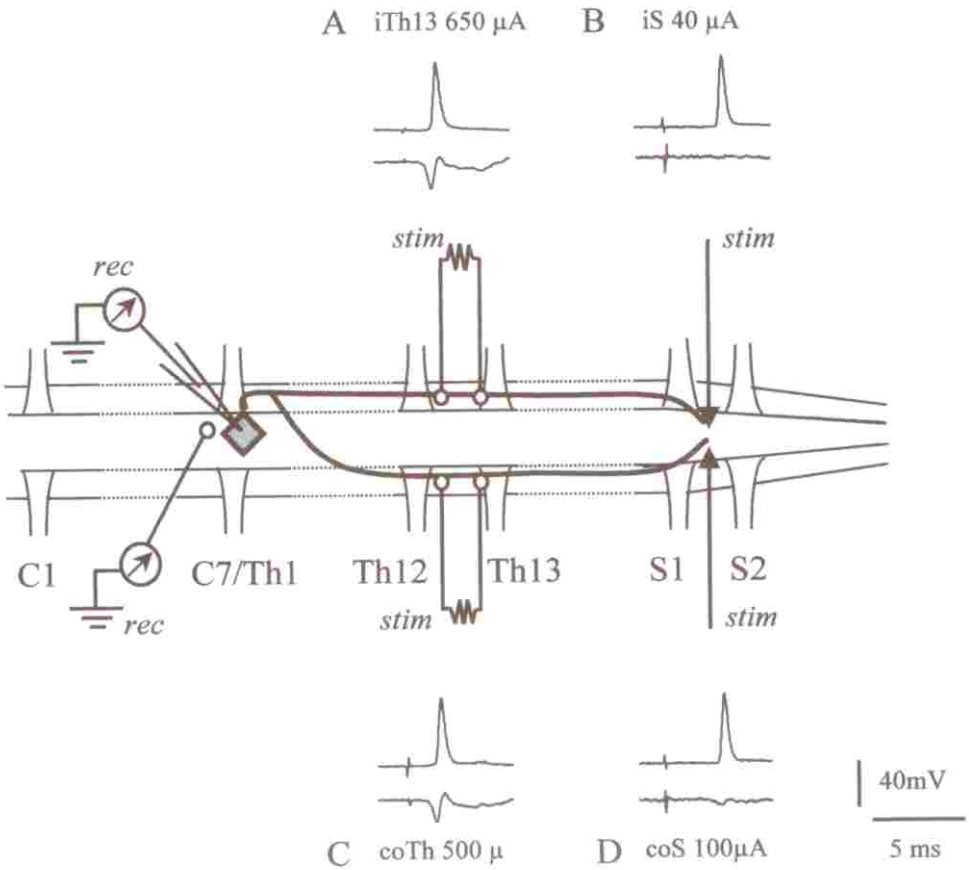

Fig. 1. - *The identification of neurones.*

Schematic drawing of the spinal cord contains an example of a propriospinal neurone located in the cervical enlargement (C7/Th1) and bilaterally projecting to sacral segments (S1, S2). Stimulating (*stim*) and recording (*rec*) sites are indicated. Ball-tipped stimulating electrodes were placed on the surface of lateral funiculi at the Th12-Th13 level and needle tungsten electrodes were inserted into the gray matter of sacral segments. The recording glass microelectrode was used for intracellular recordings from neurones while the ball-tipped metal electrode was used for recording of afferent volleys from the cord dorsum. A-D: Intracellular records of antidromic action potentials (upper traces, five averaged records) from a C7 neurone bilaterally projecting to sacral segments, after stimulation of the ipsilateral and contralateral lateral funiculi at the level of Th13 (A and C, respectively) as well as of the gray matter of sacral segments on ipsi- and contralateral sides of the spinal cord (B and D, respectively). Lower traces are cord dorsum potentials.

or-none appearance, high frequency following (> 200 Hz) and collision between orthodromic and antidromic potentials were used as criteria for recognizing antidromic spikes (28).

All recorded signals were amplified and passed to a computer for storage and further analysis. Either single events or averaged responses (5-10) were recorded.

Data analysis.

Afferents from muscle spindles, Golgi tendon receptors, high threshold group III muscle afferents and cutaneous afferents were stimulated in the nerves. However, thresholds of stimulation for

Ia and Ib muscle afferents could not be differentiated (33) and effects evoked from both types of fibres were analyzed together and classified as group I muscle afferents. Postsynaptic potentials (PSPs) were identified as evoked from group I muscle afferents when a stimulus strength was lower than 1.5 times threshold (< 1.5 T) for the most excitable fibres (14, 20). Potentials were identified as evoked from group II muscle afferents when stimulus strength was 1.5-5.0 times threshold (20, 23). To exclude high threshold group I muscle afferents, only those PSPs increasing in amplitude following stimulation above 2.0 T were classified as evoked from group II muscle afferents. In mixed nerves (Med and Uln) only effects from low threshold muscle afferents could be separated from those evoked from cutaneous fibres. EPSPs and IPSPs from group I muscle afferents often appeared when a stimulus strength did not exceed 1.4-1.5 T and no cutaneous component was visible in the records of afferent volleys. PSPs obtained following stimulation above 5.0 T were identified as evoked from group III muscle afferents or high threshold flexor reflex afferents (FRA). The latter term included also group II and III muscle, joint and cutaneous afferents from mixed nerves (12, 29). Postsynaptic effects of SR stimulation were evoked from low- as well as high-threshold cutaneous afferents (1.1–10 T).

Identification of mono-, di- or polysynaptic potentials was based on central latencies, measured in each case from the fastest component of the incoming afferent volley to the beginning of a postsynaptic potential.

RESULTS

Antidromic action potentials from sacral segments were recorded intracellularly from 51 neurones. Among them, 26 were located in C7, 22 in C8 and 3 in Th1 segments of the spinal cord. Recording sites were located in the medial part of the gray matter, at depths 2.42-5.23 mm, corresponding to Rexed's laminae V-VII and lamina VIII. Bilateral projections to sacral segments were confirmed in 31 cases, ipsilateral projections in 19 neurones, while exclusively contralateral projection was found in one neurone. Axonal conduction velocities ranged from 22 to 120 ms^{-1}, with no significant differences between ipsilateral and contralateral descending branches. These results were consistent with our previous reports, based on extracellular records from long propriospinal neurones projecting to sacral segments (25, 27).

Stimulation of peripheral afferents was effective in evoking PSPs in most of the cells studied, however, in 10 cases no synaptic actions from the periphery could be recorded from any of the nerves activated. Figure 2A shows that the rest of the population studied can be divided into three groups of neurones, depending on excitatory or inhibitory characteristics of postsynaptic effects. In 9 neurones exclusively EPSPs were recorded, in 11 cases IPSPs only, but in the majority of the cells - 21, both EPSPs and IPSPs were evoked by stimulation of peripheral afferents. The most prominent effects were evoked from DR - they were found in 36 neurones (88% of neurones with a peripheral input). PSPs from Med were evoked in 26 (63%), from SR in 19 (46%) and Uln in 19 (46%) cells. Figure 2B shows that synaptic actions from DR were most frequent in the neurones investigated. EPSPs were recorded from 64% while IPSPs from 84% of neurones with excitatory and inhibitory actions, respectively. Excitatory effects from cutaneous receptors conducted by SR nerve were relatively more frequent than inhibitory (43 and 34% of neurones with respec-

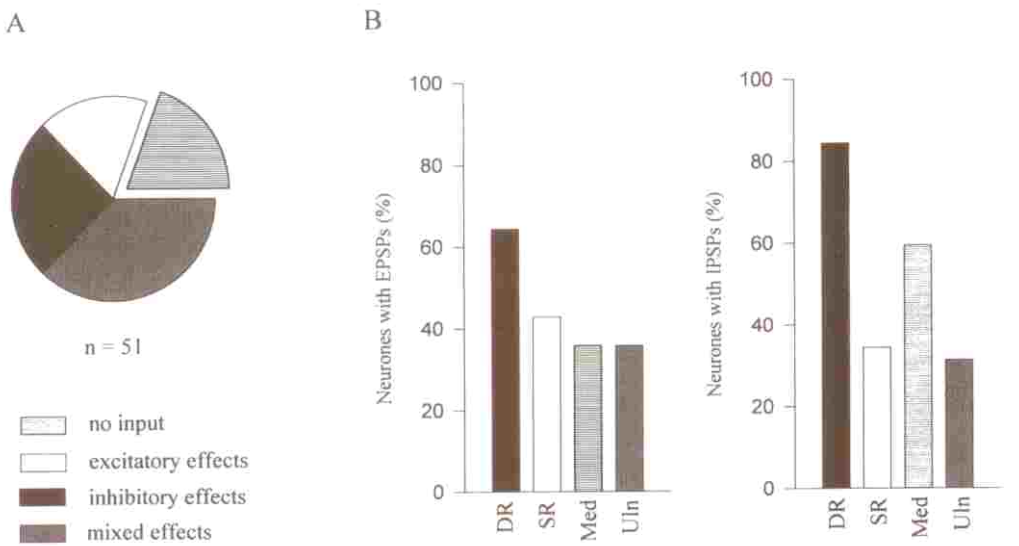

Fig. 2. - *The proportion of neurones excited or inhibited by peripheral afferents and relative contribution of individual nerves in excitatory or inhibitory actions.*

A. Four groups of neurones, divided with respect to the peripheral input from all the nerves studied. B. The number of neurones, expressed in percents, in which excitatory effects (left diagram) or inhibitory effects (right diagram) were evoked from deep radial (DR), superficial radial (SR), median (Med) and ulnar (Uln) nerves.

tive actions). On the other hand, stimulation of Med was relatively more effective in evoking inhibitory actions (59% of cells with IPSPs) than excitatory (36% of cells with EPSPs). Effects from Uln were the weakest with respect to both types of actions (36 and 31% of neurones with EPSPs and IPSPs, respectively). It must be noted that no correlation between the type of peripheral input and the location was found.

Excitatory postsynaptic potentials.

Excitatory actions, present in 30 neurones, were most often evoked from muscle afferents. Their amplitudes were comprised in the range 0.6-3.5 mV. Central latencies of EPSPs from group I muscle afferents were in 14 neurones shorter than 1.2 ms (0.92 ± 0.21 ms, mean ± SD, n = 14), so the connections were recognized as monosynaptic (5, 11). In two cases latencies were 1.4 and 1.7 ms, and in other two cases they were longer than 2 ms. These EPSPs were classified as disynaptic or polysynaptic, respectively. EPSPs from gr. II muscle afferents were found even more often than those from gr. I and they were evoked either mono-, di- or polysynaptically. PSPs from group II muscle afferents were classified as monosynaptic when a central latency was shorter than 1.7 ms, as disynaptic – when it amounted to 1.7-2.3 ms, as polysynaptic – when latency was longer than 2.3 ms (1, 10). Fig. 3A shows an example of a monosynaptic connection from gr. II muscle afferents. Such a monosynaptic effect was recorded from 13 neurones (the mean cen-

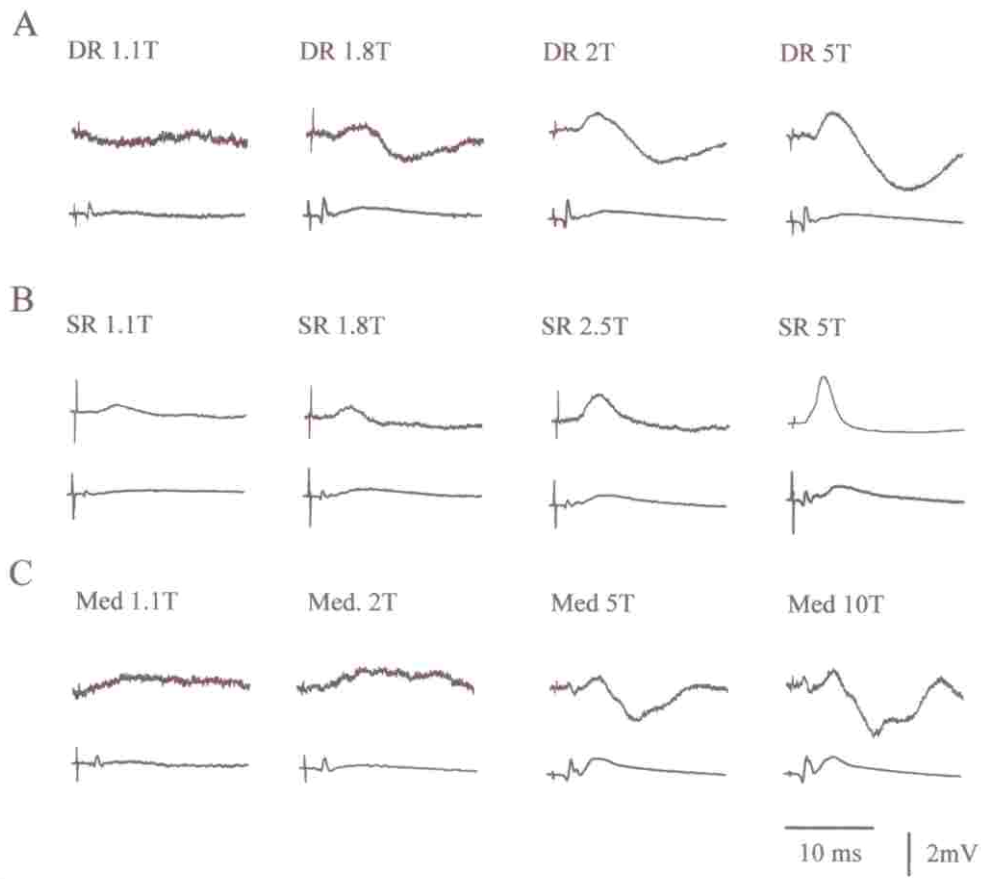

Fig. 3. - *Synaptic actions evoked from muscle, cutaneous and high threshold afferents in thee propriospinal neurones.*

Upper traces in A-C are intracellular records, lower traces are cord dorsum potentials. Five averaged records are presented on each panel. A. A monosynaptic EPSP from gr. II muscle afferents (central latency < 1.7 ms, evoked by a stimulus of 1.8T), followed by a polysynaptic IPSP from the same type of afferent fibres of the deep radial nerve (DR). B. A monosynaptic EPSP from low-threshold cutaneous afferents (central latency < 1.2 ms, evoked by a stimulus of 1.1T) from the superficial radial nerve (SR). C. Polysynaptic IPSPs from high threshold afferents (central latency > 3 ms, evoked by a stimulus of 5T with the amplitude increasing between 5T and 10T) from the median nerve (Med).

tral latency 1.38 ± 0.16 ms, n = 13). In 3 cases EPSPs were found to be evoked disynaptically, while in 19 polysynaptically. In most cases polysynaptic actions from one nerve accompanied mono- or disynaptic EPSPs evoked from the same or another nerve.

EPSPs from low-threshold cutaneous afferents were found less frequently, in 13 neurones. They were classified as monosynaptic in 2 neurones, in which central latencies amounted to 0.8 and 1.0 ms (Fig. 3B), as disynaptic in 7 neurones – with latencies between 1.2 and 1.6 ms, as polysynaptic in 4 neurones – with latencies longer than 2.5 ms (5,11).

Stimulation of flexor reflex afferents within DR, Med or Uln nerves resulted in EPSPs in 6 neurones only. Central latencies were longer than 4 ms and pointed to polysynaptic connections.

Inhibitory postsynaptic potentials.

IPSPs were found in 32 neurones of the total sample and they appeared almost twice more frequently than EPSPs. Their amplitudes amounted to 0.6-4.1 mV. In most cases IPSPs were classified as polysynaptic. Inhibitory actions from gr. I muscle afferents often followed monosynaptic EPSPs. In 8 cases with central latencies between 1.2 and 1.8 ms they were evoked disynaptically, in 16 cases latencies were longer than 2.3 ms what indicated polysynaptic connections. Also IPSPs from gr. II muscle afferents usually followed monosynaptic EPSPs (Fig. 3A) and were evoked di- (10 cases) or polysynaptically (20 cases).

In 24 neurones IPSPs appeared following stimulation of high threshold muscle afferents in DR or flexor reflex afferents in Med or Uln nerves. Usually two or three IPSPs from the same nerve appeared successively following stimulation with high intensity (5-10T). Minimal central latencies were 3.7 ms, but in most cases they were longer than 6 ms, what pointed to a polysynaptic way of afferent impulses, with a relay by at least two interneurones. An example of such IPSPs evoked by stimulation of the median nerve with a stimulus intensity at least 5T is shown in Fig. 3C.

The weakest inhibitory effects in the neurones investigated were recorded from cutaneous afferents. In 4 cases central latencies of IPSPs from SR were between 1.2 and 1.8 ms, thus they were classified as disynaptic. In 7 neurones IPSPs were considered as polysynaptic since their latencies were longer than 2.3 ms for low threshold cutaneous afferents or longer than 6 ms for high threshold cutaneous afferents.

Convergence from forelimb afferents.

Apart from 10 neurones without any peripheral input, eleven different types of convergence from various types of afferent fibres were found in the population studied. As it is shown in Table I, excitatory or inhibitory effects from muscle afferents (gr. I, gr. II or both) were present in all 41 cells in which PSPs were recorded. However, stimulation of gr. I muscle afferents was effective only in 20, while stimulation of gr. II muscle afferents in 37 neurones. In 10 cells out of this sample exclusive input from muscle receptors was present, while in the remaining 31 neurones additional effects from high threshold flexor reflex or cutaneous afferents were recorded. Exclusive effects from FRA or cutaneous afferents were not observed.

DISCUSSION

Forelimb afferent connections to cervical propriospinal neurones have been studied previously in two groups of neurones. Alstermark et al. (4) have described the pattern of convergence onto short C3-C4 propriospinal neurones projecting to forelimb motor

Table 1. - *Patterns of afferent connections from various types of receptors. Plus symbols indicate types of forelimb afferents effective in evoking synaptic actions in 51 propriospinal neurones studied. Bottom line contains numbers of neurones within each group of convergence pattern. Note that in 10 cells postsynaptic effects from none of the forelimb nerves were recorded.*

	Pattern of convergence											
Group I muscle afferents	+	+	+	+	+	+	+					no input
Group II muscle afferents		+		+	+		+	+	+	+	+	
Flexor reflex afferents				+		+	+		+		+	
Cutaneous afferents			+		+	+	+			+	+	
Number of neurones (n = 51)	1	4	2	5	3	1	5	5	6	2	7	10

nuclei. They receive mainly disynaptic inhibitory input from primary and secondary muscle afferents as well as cutaneous and high threshold flexor reflex afferents. Additional monosynaptic EPSPs from gr. I muscle afferents and polysynaptic IPSPs from FRA have been observed in a part of those cells. On the other hand, investigations on long descending propriospinal tract neurones have revealed mostly monosynaptic excitatory connections from muscle and cutaneous afferents and – less often – disynaptic inhibitory effects from the same groups of fibres (2). Responses of these neurones to natural stimuli delivered to the skin, muscles and tendons of the fore limbs have confirmed their sensibility to various types of stimuli (37).

Our study concerned cervical propriospinal neurones with bilateral axonal branches descending as far as to sacral segments that have not previously been investigated with respect to the synaptic input from peripheral receptors. The results appear to be partly consistent with all those cited above. In some neurones of the sample investigated prevailing monosynaptic EPSPs from muscle receptors coexist with di- or polysynaptic IPSPs from muscle, cutaneous and flexor reflex afferents, while in a part of neurones mainly inhibitory di- or polysynaptic actions from muscle receptors dominate. However, the information from muscle fibres (present in all neurones responding to peripheral stimulation) seems to be more important in comparison to effects evoked from other types of afferents. Moreover, it has been revealed that effects from gr. II muscle afferents are even more common than these from gr. I muscle afferents. The latter observation has not been reported for descending propriospinal tract neurones so far.

Apart from neurones responding to stimulation of forelimb afferents, in ten cases, i.e., about one fifth of the sample, no synaptic actions have been recorded. However, these neurones are not different from the rest of the population studied with regard to anatomical location of cell bodies, axonal course, or conduction velocities. The lack of PSPs may be explained in two ways. Firstly, they may form a subpopulation activated by afferents from other forelimb nerves, e.g., innervating a shoulder (8), from supraspinal tracts descending from brainstem centres or motor cortex (3, 18), or from ascending tracts originating from lower segments of the spinal cord (13, 26, 30). Secondly, it cannot be excluded that a proportion of the polysynaptic connections from muscle, skin and joint receptors was not revealed due to a very weak convergence of afferent fibres on interneurones mediating these actions. The described pattern of convergence, limited to nerves from a distal part of the limb is certainly

incomplete and needs to be supplemented in future experiments concerning sensory input from proximal forelimb afferents as well as from descending pathways.

The coordination of movements of fore – and hind – limbs has been postulated for long descending propriospinal neurones (7, 15, 19, 22, 24, 35). Our previous studies on bilaterally descending propriospinal neurones that connect cervical and lumbosacral segments of the spinal cord (16, 25, 27) have suggested that signals from spinal centres controlling forelimbs reach not only ipsilateral motor centres of the hindlimbs, but also motor nuclei on the contralateral side of the spinal cord. In this paper we have revealed that at least part of these neurones indeed receive impulses directly or indirectly from muscle spindles or Golgi tendon receptors. Thus, they process information about the degree and dynamics of muscle stretch or changes in muscle force, generated during contractions of motor units of both flexors and extensors innervated by axons in DR, Med or Uln nerves. The weaker cutaneous and flexor reflex afferent connections suggest supplementary function of information from these receptors, that are activated mainly by mechanical, thermal or nociceptive stimuli. However, it must be stressed that eleven different patterns of convergence from various types of forelimb afferents have been established. Thus, individual neurones process different types of afferent information, originating from various parts of the forelimb at various phases of movements. The divergence of descending axons makes possible to conduct signals in parallel to more than one spinal centre, on both sides of the spinal cord.

In conclusion, neurones in this study obviously form only a part of a more complex system that contributes to the coordination of movements of all four limbs. Other short and long ascending or descending propriospinal tracts as well as segmental interneurones at various spinal cord levels are involved in this process. It must be also noted that the spinal mechanisms of co-operation between centres controlling fore – and hind – limbs are well known in lower vertebrates, rat, cat, and to a certain degree also in monkey. The question arises, whether these results can be useful for understanding the problems of motor coordination in man. The positive answer comes from recent reports based on indirect investigations of neuronal cooperation in the human spinal cord that suggest that propriospinal systems are organized in humans in a similar way (9, 21).

SUMMARY

Propriospinal neurones located in the cervical enlargement and projecting bilaterally to sacral segments of the spinal cord were investigated electrophysiologically in eleven deeply anaesthetized cats. Excitatory or inhibitory postsynaptic potentials from forelimb afferents were recorded following stimulation of deep radial (DR), superficial radial (SR), median (Med) and ulnar (Uln) nerves. 26 cells were recorded from C7, 22 from C8 and 3 from Th1 segments. The majority of the cells were located in the Rexed's laminae VIII and the medial part of the lamina VII. In 10 cases no afferent input from the forelimb afferents was found. In the remaining neu-

rones effects were evoked mostly from DR (88%) and Med (63%), less often from SR (46%) and Uln (46%). Inhibitory actions were more frequent than excitatory. The highest number of IPSPs was evoked from high threshold flexor reflex afferents (FRA) – all connections were polysynaptic. However, inhibitory actions were often evoked from grup I or II muscle afferents (polysynaptic or disynaptic) and, less frequently, from cutaneous afferents (mostly polysynaptic). Di- or polysynaptic IPSPs often accompanied monosynaptic EPSPs from group I or II muscle afferents. Disynaptic or polysynaptic EPSPs from muscle and cutaneous afferents were also recorded in many neurones, while polysynaptic EPSPs from FRA were observed only exceptionally. Various patterns of convergence in individual neuronal subpopulations indicate that they integrate different types of the afferent input from various muscle and cutaneous receptors of the distal forelimb. They transmit this information to motor centers controlling hind limb muscles, forming a part of the system contributing to the process of coordination of movements of fore – and hind – limbs.

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