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Projections of laminae IV-VI neurones located in the S2 segment of the spinal cord to the C6 segment and the cerebellum in the cat

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Abstract. Ascending projections of neurones of the second sacral segment (S2) of the spinal cord to the sixth cervical segment (C6) and to the cerebellum were electrophysiologically investigated in eight adult cats under α-chloralose anaesthesia. Antidromic potentials recorded from 44 neurones following stimulation of their axons in the grey matter of the C6 segment as well as in the contralateral restiform body (coRB) showed evidence of both supraspinal and propriospinal projections. About one third of neurones (15) ascended to the cerebellum through the coRB and gave off collaterals to the C6 segment, while the rest (29) terminated exclusively at the level of the C6 segment. The cell bodies were found mainly in central parts of Rexed's laminae IV, V and VI while axons ran in lateral funiculi. Axonal conduction velocities measured between S2 and C6 segments were in the range of 42-78 m/s. A decrease of conduction velocity above the Th13 and C6 segments was found in most axons suggesting that they give some collaterals at spinal as well as supraspinal levels.

Key words: antidromic identification, spinocerebellar, propriospinal, cat

INTRODUCTION

It has been demonstrated that neurones originating from lower segments of the lumbo-sacral enlargement are the source of many sensory pathways ascending through the spinal cord. Spino-cerebellar tracts (Matsushita and Hosoya 1979, Matsushita et al. 1979, Grant et al. 1982, Xu 1988), spino-thalamic tracts (Trevino et al. 1972, Carstens and Trevino 1978, Jones et al. 1987, Myers and Snow 1982), spino-reticular tracts (Fields et al. 1975, Maunz et al. 1978, Huber et al. 1997), spino-olivary tracts (Armstrong and Schild 1979, Molinari 1984, Matsushita et al. 1992) and spino-cervical tracts (Bryan et al. 1973, Brown 1981) have been described. On the other hand, it has been known that neurones of a long propriospinal tract are also located in this region of the cord (Barilari and Kuypers 1969, Miller et al. 1973, Rustioni et al. 1971, English et al. 1985). Moreover, a similar location in laminae IV-VI of the second sacral segment has been reported for neurones of origin of both spino-cerebellar tracts (Matsushita and Hosoya 1979) and propriospinal pathways reaching cervical segments of the spinal cord (Mrówczyński 1997).

In anatomical studies based on horseradish peroxidase transport it has been described that spino-cerebellar axons from the sacral part of the cord run mainly in the dorsal part of the contralateral lateral funiculus and most of them reach the cerebellar cortex through the restiform body (Kitamura and Yamada 1989). Axons of long propriospinal tracts originating in the S2 segment ascend to the cervical enlargement bilaterally, contralaterally or ipsilaterally in dorsal parts of lateral funiculi as well (Krutki et al. 1997b, Mrówczyński 1997). Moreover, it should be stressed that it has not been cleary established whether all axons of the sacro-cervical connections terminate at the spinal level. It has been supposed that some of them give off collaterals to other neurones in the spinal cord and ascend in parallel to supraspinal structures (Krutki et al. 1997b).

Similarities in the location and axonal courses along the spinal cord suggest that some spino-cerebellar and propriospinal tract neurones form in fact one group. Therefore the aim of this study was to investigate electrophysiologically whether neurones of laminae IV-VI of the S2 segment project both to the C6 segment of the spinal cord and to the cerebellum.

METHODS

Experiments were performed on eight adult cats weighing between 2.1 and 3.2 kg, anaesthetized with several doses of α-chloralose (up to 50 mg/kg, i.v.) and immobilized with gallamine thriethiodide (3 mg/kg/h i.v.). The initial surgical procedures were fully described previously (Huber et al. 1994, Krutki 1997, Krutki et al. 1997b, Mrówczyński 1997).

The spinal cord was exposed at required levels by laminectomies and the craniotomy over the cerebellum was made. A pair of bipolar silver ball-tipped electrodes was placed bilaterally on the surface of the lateral funiculi at the thoracic (Th13) level. The needle varnished tungsten stimulating electrodes (tip diameter of 3-5 μm) were inserted bilaterally into the spinal grey matter of the C6 segment and contralaterally through the cerebellar cortex into the restiform body (coRB) (Fig. 1 A), according to Horsley - Clarke's coordinates: L, 5.6; P, 8.5; H, -3.5 to -4.0 (Berman and Jones 1982). Axons of the investigated neurones were stimulated on their course in the lateral funiculi of the spinal cord, in the grey matter of the C6 and in the restiform body at a rate 3-5 Hz using pulses of 0.2 ms duration and a strength of 0.1-1.2 mA, 0.05-0.2 mA and 0.05-0.15 mA, respectively. Under these conditions most of the axons in the C6 segment and in the inferior cerebellar peduncle were expected to be excited within an area of a diameter less than 1 mm (Ranck 1975, Bagshaw and Evans 1976).

Extracellular and intracellular records of antidromic action potentials from neurones located in the S2 segment were made with glass micropipettes (tips broken up to 1.5-2.0 μm diameter, impedance 3-5 MΩ) filled with 2 M potassium citriate solution. Records were analysed from photographs of 3-5 superimposed single sweeps from the oscilloscope screen.

The recognition of antidromic potentials was based on previously described criteria (Lipski 1981): the constant latency of a spike, its "all-or-none" appearance, high frequency following test (150-300 Hz) and collision at appropriate intervals with synaptically evoked potential (Fig. 1 B).

During the whole experiment the body temperature, arterial blood pressure and the end tidal CO_2 were continously monitored and maintained within physiological limits ($38^{\circ} \pm 1^{\circ}$C, 90 - 120 mmHg and 2-4%, respectively).

RESULTS

Axons of the investigated neurones were stimulated bilaterally at both the Th13 and C6 levels of the spinal cord and contralaterally in the coRB. Antidromic responses were obtained from 44 neurones located in the grey matter of the S2 segment. Intracellular antidromic potentials (Fig. 1 D) were recorded from 12 cells, while exclusively extracellular antidromic potentials were recorded from the remaining 32 neurones (Fig. 1 C).

Pattern of axonal projections

The course of each axon was estimated according to antidromic potentials recorded in the neurone following stimulation at various sites. Considering values of stimulation current used, it was found that axons ascended in the spinal cord within dorsal and lateral parts of the lateral funiculi.

In 21 neurones antidromic potentials were evoked by bilateral stimulation of both Th13 and C6 segments (Fig. 2 - group 1). Most neurones from this group (13/21) terminated at the cervical level, with no response after coRB stimulation (Fig. 2 - type 1B). In the remaining 8 neurones from group 1 antidromic potentials were additionally recorded after the coRB stimulation (Fig. 2 - type 1A).

In the next 11 cells antidromic potentials appeared following contralateral stimulation at the Th13 and C6 segments (Fig. 2 - group 2), with no antidromic activation from the ipsilateral C6 segment. These neurones showed only contralateral axonal projections to the C6 segment,

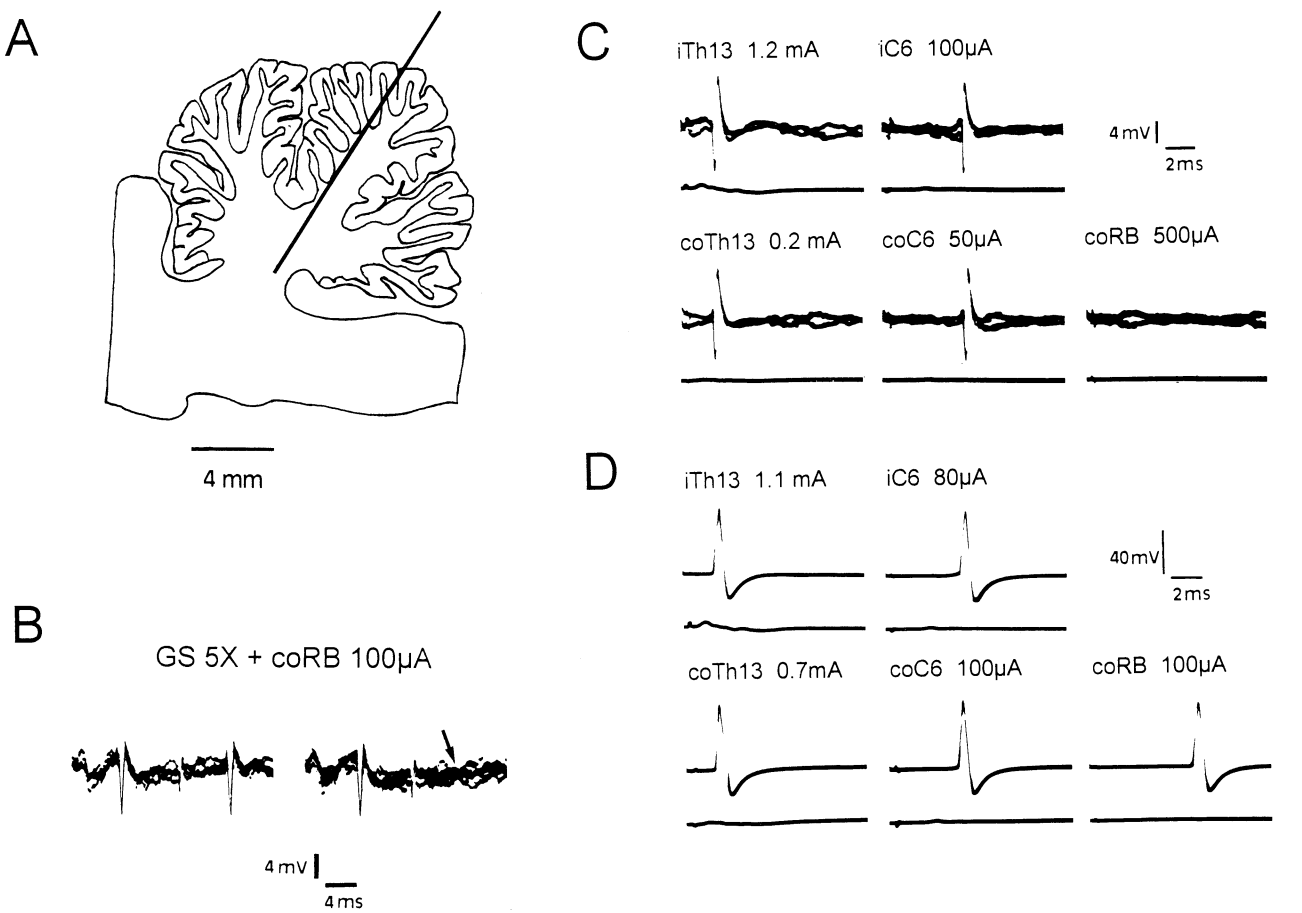

Fig. 1. A, the track of stimulating tungsten electrode insertion in the coRB indicated on the cross-section scheme of the cerebellum. B, records of collision of the antidromic potential evoked after coRB stimulation with synaptic potential resulted from the stimulation of gastrocnemius and soleus nerves (GS 5 X threshold). C, extracellular records from the neurone projecting bilaterally to the C6 segment only. D, intracellular records from the neurone of dual projecting to the C6 segment and to the coRB. In C and D the upper records present extracellular or intracellular antidromic potentials, while the lower records are taken from the surface of the spinal cord.

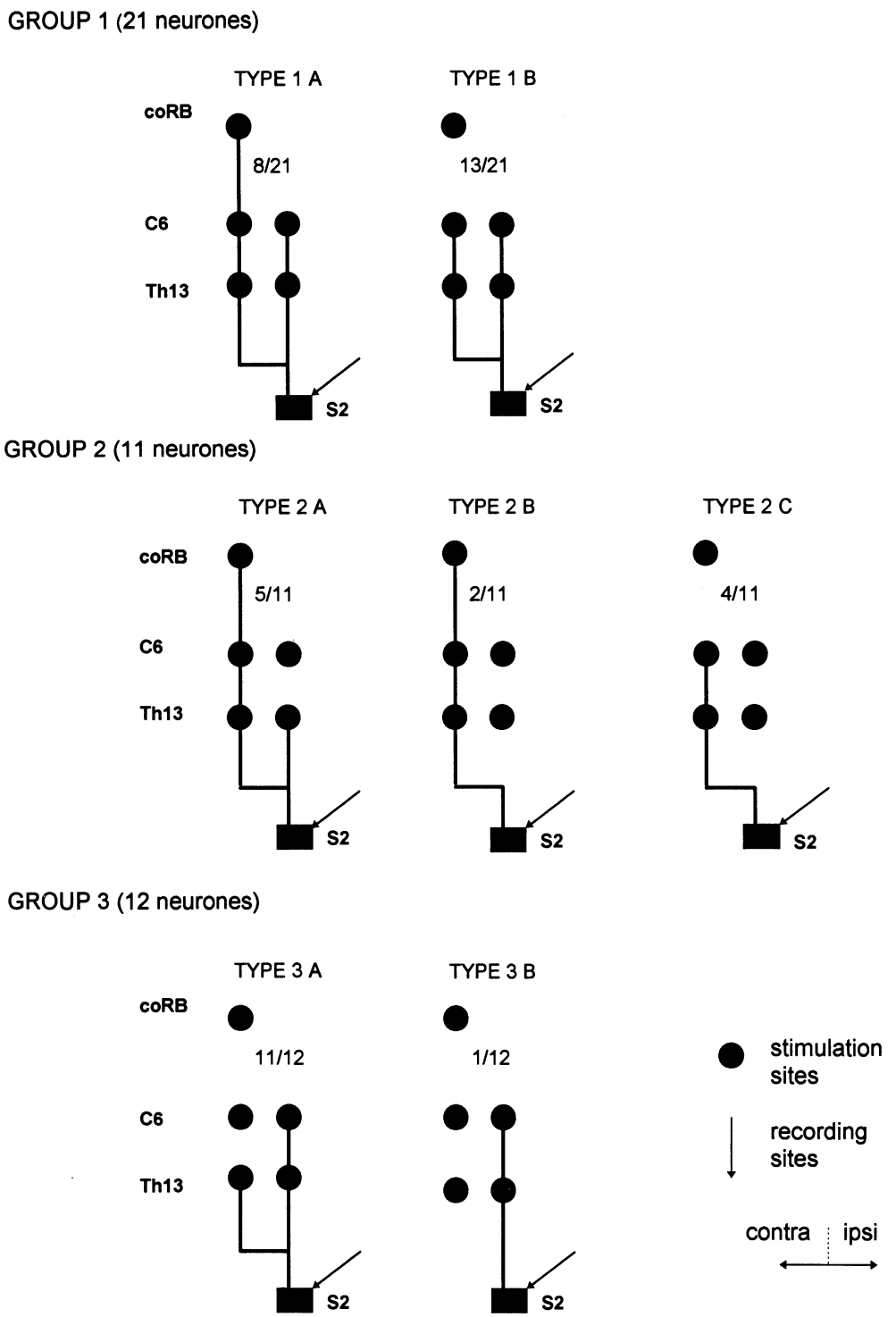

Fig. 2. The scheme illustrating the axonal courses of three groups of investigated neurones: group 1 contains neurones of bilateral projection to the C6 segment (type 1 A, contralateral branches of these neurones reach also the coRB; type 1 B, contralateral branches reach the C6 segment only), group 2 contains neurones of contralateral projection to the C6 segment (type 2 A, contralateral branches of these neurones reach also the coRB and their ipsilateral branches ascend at least to the Th13 segment; type 2 B, axons run exclusively contralaterally and reach the coRB; type 2 C, contralateral branches of these neurones reach only the C6 segment), group 3 contains neurones of ipsilateral projection to the C6 segment (type 3 A, contralateral branches of these neurones ascend at least to the Th13 segment; type 3 B, neurone of exclusive ipsilateral projection to the C6).

although 5 of them ascended also ipsilaterally at least to the thoracic level (Fig. 2 - type 2 A). Seven cells of this group contralaterally ascended to the cerebellum (Fig. 2 - type 2 A, B), while 4 projected to the C6 segment only (Fig. 2 - type 2 C).

Antidromic potentials in 12 neurones (Fig. 2 - group 3) followed ipsilateral stimulation of both Th13 and C6 segments. All but one neurone of this group responded to contralateral stimulation at the Th13 (Fig. 2 - type 3 A). Only one neurone projected exclusively ipsilaterally to the cervical region (Fig. 2 - type 3 B). Cells of this group did not project to the cerebellum.

Summarizing, all of the 44 investigated axons reached the C6 segment bilaterally (21), contralaterally (11) or ipsilaterally (12). However, some of them (15) projected also to the supraspinal level and reached the cerebellum through the coRB.

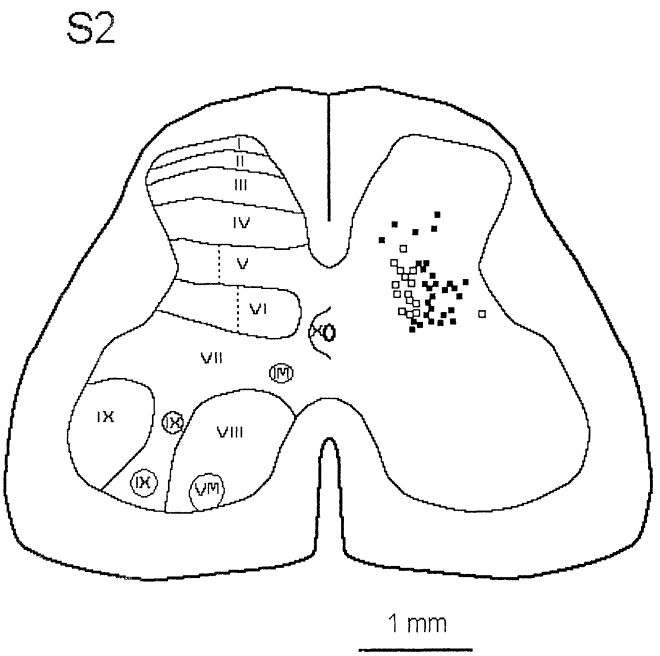

Fig. 3. Distribution of neurones investigated in the present study presented on the outline of the S2 segment. Open squares represented neurones of dual projection to the C6 segment and to the coRB (types 1 A, 2 A and 2 B); filled squares, neurones of bilateral (type 1 B); contralateral (type 2 C) and ipsilateral (types 3 A and 3 B) projections to the C6 segment only.

Distribution of neurones

The location of cells in the grey matter of the second sacral segment was established based on the position of the micropipette tip, i.e. the angle of the micromanipulator, the distance from the midline and depth from the surface of the spinal cord.

Forty-four antidromically activated cells were found 0.88-2.32 mm deep from the dorsal surface of the cord at a distance of 0.1-0.6 mm from the midline with the microelectrode directed 0^{o}-18^{o} medio-laterally and 5^{o}-10^{o} rostro-caudally. The identifited neurones were dis-

TABLE I

Ranges and mean values of axonal conduction velocities (in m/s) calculated separately for 3 distinguished groups of neurones (see text)

Axonal Conduction Velocity (m/s)		Group 1				Group 2						Group 3			
		type 1a		type 1b		type 2a		type 2b		type 2c		type 3a		type 3b	
		ipsi	contra	ipsi	contra	ipsi	contra	ipsi	contra	ipsi	contra	ipsi	contra	ipsi	contra
Calculation	range	48-78	49-78	41-68	42-68	*	63-78	*	57-61	*	51-61	43-73	*	53	*
Between	mean	60.6	62.1	54.0	54.1	*	71.8	*	58.7	*	54.9	57.4	*	*	*
S2 - C6	(±)SD	10.3	9.2	9.3	8.8	*	7.6	*	2.8	*	4.5	8.7	*	*	*
	n	8	8	13	13	*	5	*	2	*	4	11	*	1	*
Calculation	range	*	46-63	*	*	*	58-68	54-58	*	*	*	*	*	*	*
Between	mean	*	52.6	*	*	*	63.6	55.6	*	*	*	*	*	*	*
S2 - coRB	(±)SD	*	6.02	*	*	*	4.4	3.3	*	*	*	*	*	*	*
	n	*	8	*	*	*	5	2	*	*	*	*	*	*	*

SD, standard deviation; n, number of neurones; ipsi, ipsilateral branch; contra, contralateral branch.

tributed mainly in the central part of the dorsal horn of the S2 segment. It was determined that they covered laminae IV(5), V(19) and VI(20) (Rexed 1954). Cell bodies of 15 neurones of dual cervical and cerebellar projections (excluding one neurone) formed a distinctly separate group located more medially, in laminae V and VI. Twenty-nine cells with cervical projection only were dispersed in the whole investigated region, though with a tendency to more lateral location (Fig. 3).

Axonal conduction velocities

Conduction velocities of the studied axons were calculated based on the latencies of antidromic action potentials and corresponding distances between stimulation and recording sites. They were measured separately for each neurone. Table I presents ranges and mean values within the 3 groups of neurones described.

Values of conduction velocities were also measured separately on three distances: between the S2 and Th13 segments, between the Th13 and C6 segments and between the C6 and coRB. A decrease in conduction velocity was seen in most of the investigated neurones. In 17 out of 33 axons ascending ipsilaterally and in 10 out of 32 axons ascending contralaterally a decrease of 20-60% was found when comparing proximal (S2-Th13) and distal (Th13-C6) fragments of axonal branches in the spinal cord. No changes, or changes of less than 20% were found in the remaining 16 ipsilateral axonal branches and 22 contralateral axonal branches.

A significant decrease of conduction was also noted in 12 out of 15 contralateral branches reaching the cerebellum. The slowing of conduction velocities when comparing distances between the S2 and C6 segments (proximal) and between the C6 and coRB (distal) ranged from 20 to 80%. Table II summarizes the above data pertaining to the number of axons and the extent of the conduction velocity decrease.

DISCUSSION

Striking similarities were found between pathways ascending to supraspinal structures and long proprospinal tracts originating in the S2 segment regarding the localization of neurones and their axonal courses in lateral funiculi. Previous investigations (see Introduction) have demonstrated that there are long ascending tracts as well as long propriospinal pathways originating from neurones of Rexeds laminae IV-VI. Moreover, most of their axons run along the spinal cord in the lateral or dorsal parts of lateral funiculi. Dual projections of neurones of the S2 segment have recently been demonstrated in electrophysiological experiments in the cat. Axonal branches of cells of laminae VI-VII projected both to the

TABLE II

The number of axonal branches with of without decrease of conduction velocity when compared distal to proximal parts of axons. Data are presented separately for each of distinguished types of neurones (see text)

Decrease of axonal Conduction velocity		Group 1				Group 2				Group 3					
		type 1a		type 1b		type 2a		type 2b		type 2c		type 3a		type 3b	
		ipsi	contra	ipsi	contra	ipsi	contra	ipsi	contra	ipsi	contra	ipsi	contra	ipsi	contra
Calculation	no decrease	2	4	4	2	*	3	*	0	*	0	5	*	0	*
Between	<20%	2	1	2	6	*	2	*	2	*	2	1	*	0	*
S2 - Th13	20 - 40%	4	2	6	4	*	0	*	0	*	1	5	*	1	*
And	40 - 60%	0	1	1	1	*	0	*	0	*	1	0	*	0	*
Th13 - C6															
Calculation	no decrease	*	0	*	*	*	1	*	0	*	*	*	*	*	*
Between	<20%	*	1	*	*	*	0	*	1	*	*	*	*	*	*
S2 - Th13	20 - 40%	*	3	*	*	*	1	*	1	*	*	*	*	*	*
And	40 - 60%	*	0	*	*	*	2	*	0	*	*	*	*	*	*
C6 - coRB	60 - 80%	*	4	*	*	*	1	*	0	*	*	*	*	*	*

cerebellum and the thalamus (Huber et al. 1994) while axons of laminae VII-VIII neurones have been found to reach both the cerebellum and the cervical segments of the spinal cord (Krutki et al. 1997a).

The results of experiments presented here have clearly proved that axons of lamina IV-VI neurones of the S2 segment also have dual propriospinal as well as cerebellar projections and several types of cells have been distinguished based on different pattern of axonal collaterals (Fig. 2). Fifteen out of 44 cells (types 1 A, 2 A and 2 B) form a distinctly separate group located in the medial part of laminae V-VI of the S2. Values of conduction velocities of the described cells have been a little lower than spino-cerebellar neurones of the S1 segment located in laminae VII and IX and neurones of dual projection located in laminae VII-VIII of the S2 segment which conducted impulses within the range of 61-100 m/s and 48-96 m/s, respectively (Grottel et al. 1991, Krutki et al. 1997a). The significant decrease of conduction velocity observed along investigated axons between the Th13-C6 and C6-coRB fragments in most of the neurones indicates the possibility of axonal collaterals projecting to other than cerebellum supraspinal centres in the brainstem.

The remaining 29 studied cells (types 1B, 2 C, 3 A and 3B) occupy the whole investigated region of laminae IV-VI of the S2 segment and their axons ascend bilaterally, contralaterally or ipsilaterally in lateral funiculi exclusively to the level of the cervical spinal cord. Their axonal conduction velocities have been similar to those described in the previous paper by Mrówczyński (1997) who reported values from 38 to 69 m/s, and different from propriospinal afferent axons presented by Miller et al. (1973) who reported values of 33-57 m/s. Generally, the described projections appeared to be very similar to propriospinal tracts originating in laminae IV-VI neurones located in the lumbar spinal cord (English et al. 1985) and its sacral segments (Krutki et al. 1997, Mrówczyński 1997) that terminated in the grey matter of the cervical level. However, it cannot be excluded that some neurones give off additional collaterals to other spinal segments which is suggested by the observation of the slowing of conduction in distal (Th13-C6) parts of axons. One must notice that this feature was present in the above-mentioned neurones of dual projection as well. It is likely that these propriospinal connections enable the sending of sensory information to motor centers in the cervical and probably also the thoracic spinal cord.

One may suppose that the studied neurones can convey similar information as cells located in laminae IV-V of the lumbo-sacral enlargement (especially segments L5-L6) which have been classified as spino-cerebellar, spino-thalamic and spino-cervical neurones. They have been found to receive mainly monosynaptic influences from group II muscle and skin afferents from hindlimbs (Aoyama et al. 1988, Riddel et al. 1994). Our results cannot confirm that principal input (which has not been investigated) but they suggest that lamina IV-VI neurones of S2 segment send integrated sensory information to many spinal and supraspinal centres by collaterals. It is also possible that these neurones receive descending information from higher spinal segments (Krutki 1997) as well as from supraspinal centres: the motor cortex (Coulter et al. 1976, Hanaway and Smith 1979, Cheema et al. 1984), the red nucleus (Kostyuk and Pilyavsky 1969), the vestibular nuclei (Baldissera and Weight 1969, Akaike 1973) or the reticular formation (Takakusaki et al. 1989). Thus, described neurones participate in integration and transmision of information during movement coordination.

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