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Divergence of lamina VII and VIII neurones of S1 and S2 segments of the cat's spinal cord to the cerebellum and the reticular formation

Piotr Krutki, Kazimierz Grottel and **Włodzimierz Mrówczyński**

Department of Neurobiology, University School of Physical Education, 10 Droga Dębińska St., 61-555 Poznań, Poland

Abstract. Cerebellar and reticular projections of neurones located in sacral segments of the spinal cord were electrophysiologically investigated in α-chloralose anaesthetized cats. Antidromic action potentials were recorded following stimulation of the contralateral restiform body (coRB), contralateral gigantocellular nucleus (coGRN) as well as ipsi- and contralateral lateral funiculus of the 13th thoracic segment (iTh13 and coTh13). Eighty seven neurones were found in the medial lamina VII and lamina VIII of the gray matter of S1 and S2 segments. Their axons ascended in lateral funiculi on the contralateral side and in 46 cases also on the ipsilateral side of the spinal cord. A projection to coRB was found in 20 neurones, to coGRN in 10 and dual projections to both coRB and coGRN in 20 neurones. Axons of the remaining 37 cells were found to ascend to the level of Th13 only. Conduction velocities of neurones investigated were comprised in the range 35-83 m/s and no significant differences were found between particular groups. However, an evident decrease in conduction was observed in most neurones when comparing proximal to distal parts of their axons, suggesting the possibility of more extensive divergence than indicated in this study. The pattern of projections revealed that the information from the periphery is conveyed in parallel to various supraspinal and possibly also spinal centres.

Key words: spinal cord, ascending projection, reticular formation, cerebellum

INTRODUCTION

Numerous studies have been undertaken in cats to investigate spinal neurones that give rise to ascending tracts. Sacral segments of the spinal cord have been paid less attention. However, it has been established both anatomically and electrophysiologically that neurones located in S1 or S2 segments send axons reaching the cerebellum (Snyder et al. 1978, Matsushita et al. 1979, Grant 1982), the thalamus (Carstens and Trevino 1978, Huber et al. 1994), the hypothalamus (Burstein et al. 1996), the reticular formation (Fields et al. 1975, Maunz et al. 1978, Huber et al. 1998), the olivary complex (Armstrong and Schild 1979, Molinari 1984) or various mesencephalic nuclei (Wiberg and Blomquist 1983, Vanderhorst et al. 1996).

Previous experiments performed in our laboratory have been focused mainly on electrophysiological examination of neurones in the S2 segment. It has been revealed that these spinocerebellar, spinothalamic and spinoreticular projections partly overlap. They are distributed mostly in the ventral horn and medial intermediate gray. The axonal course in the white matter as well as axonal conduction velocities of these three groups of fibres have been similar (Krutki et al. 1998, Huber et al. 1999). Moreover, dual projections to the thalamus and the cerebellum have been shown in some of these fibres (Huber et al. 1994). Our observations have led to the suggestion that a divergence to various supraspinal centres can be in fact more frequent than it has been reported so far.

In this study we examined neurones of S1 and S2 segments of the feline spinal cord distributed in laminae VII and VIII to determine their projections to the cerebellum and the reticular formation. According to Grant and Xu (1988) the majority of spinocerebellar axons originating from sacral segments enter the cerebellum through the inferior cerebellar peduncle. Antidromic activation of axons or their terminals in the contralateral inferior cerebellar peduncle and in the contralateral gigantocellular reticular nucleus was made to answer whether there exist neurones of dual projections to both the above structures and whether they form anatomically distinct groups. The locations of neurones, the course of axons in the spinal cord and axonal conduction velocities were investigated in detail.

METHODS

Surgical procedure and animal care

Experiments were performed on 7 adult cats of either sex, weighing 2,500-3,400 g. Principles of animal experiments and Polish Law on the Protection of Animals were respected. For the initial surgery (dissection of the femoral artery and vein, tracheotomy) cats were anaesthetized with ketamine (25-40 mg i.m.) and during the experiment α-chloralose was given (in several doses supplemented as required, up to 50 mg/kg, i.v.). The depth of anaesthesia was controlled by monitoring of withdrawal and corneal reflexes during the operation or diameter of pupils and blood pressure during recordings. Animals were placed in the stereotaxic frame, immobilized by gallamine triethiodide (3 mg/kg/h, i.v.) and artificially ventilated. To reduce respiratory movements bilateral pneumothorax was made in all cases. Bicarbonate solution (100 mM $NaHCO_3$ with 5% glucose) was continously infused (1-2 ml/kg/h) intravenously. The bladder was catheterized to control the volume of urine. Body temperature, systolic blood pressure and end-tidal CO_2 were continously monitored and kept within physiological limits (36–38°C, 90-120 mmHg and 2–4%, respectively).

Hind limb nerves (sural, common peroneal and branches to the gastrocnemius muscle) were transected, dissected free and mounted on bipolar silver wire electrodes for stimulation. To expose required levels of the spinal cord, laminectomies were performed at the levels of Th12-Th13 and L7-S2 segments. The dura was left intact at the thoracic level but was cut at the level of sacral segments, and the pia was opened only in small regions to allow introduction of recording micropipettes into the spinal cord. A craniotomy over the cerebellar cortex was made for insertion of stimulating electrodes. All exposed areas of the spinal cord and the cerebellum as well as dissected nerves were covered with warm paraffin oil (36-38°C).

Stimulation and recording

Varnished tungsten needle stimulating microelectrodes (with tips about 5 m in diameter, exposed for 10-20 μm) were inserted into the inferior cerebellar peduncle (restiform body, coRB) and into the rostral part of the gigantocellular reticular nucleus (coGRN), contralaterally to the recording site, according to Horsley-

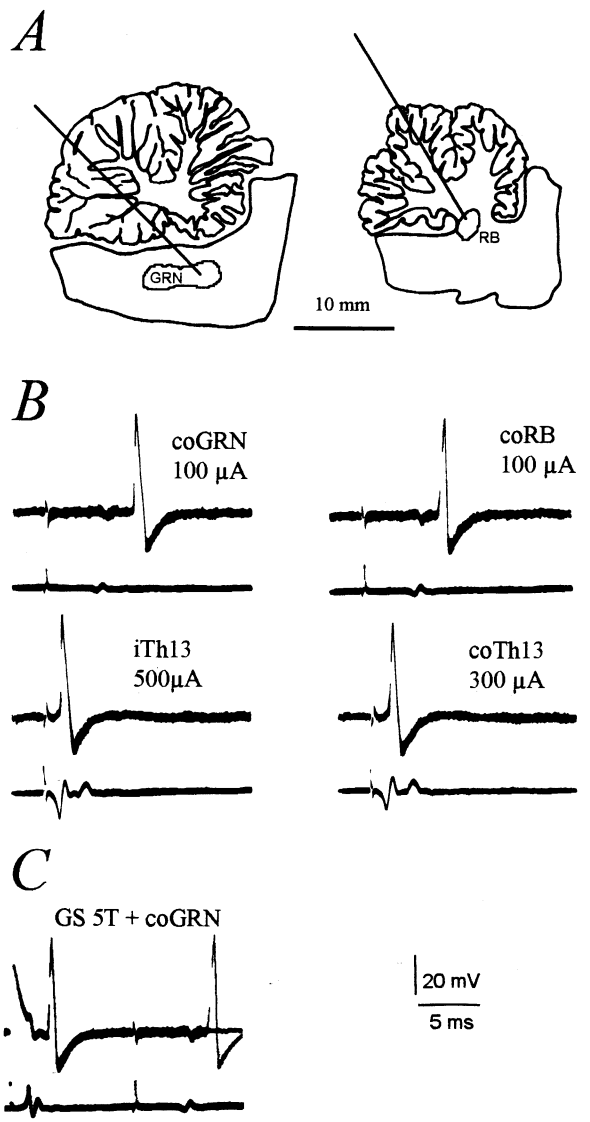

Fig. 1. A, two saggital sections of the brain stem and the cerebellum from one cat with tracks of stimulating electrodes reaching the gigantocellular reticular nucleus (GRN) and the restiform body (RB), respectively. B, records of antidromic action potentials (upper traces) obtained from one S2 neurone projecting both to the cerebellum and the reticular formation, with an axon ascending bilaterally in the spinal cord. Lower traces are records taken from the surface of the cord. C, collision between orthodromic action potential evoked by stimulation of the nerve branch to the gastrocnemius muscle (stimulation strength: 5 times threshold for the most sensitive nerve fibres) and the antidromic spike obtained from the stimulation of the coRB. The critical interval is equal to double antidromic latency plus the refractory period. Abbreviations: coRB, contralateral restiform body; coGRN, contralateral gigantocellular reticular nucleus; iTh13, coTh13, ipsialteral, contralateral 13th thoracic segemnt; GS, nerve to the gastrocnemius-soleus muscle.

-Clarke's coordinates (Berman 1968): L, 5.6; P, 8.0 to 8.5; H, -3.5 to -4.0 and L, 1.2; P, 3.0 to 5.0; H, –6.0 to –8.0, respectively (Fig. 1A). In order to antidromically activate axons ascending in the spinal cord bipolar silver ball electrodes (tip diameters about 0.5 mm, separated by 2-3 mm) were bilaterally placed in parallel to be in contact with the lateral funiculi at the level of the Th13 segment.

Rectangular, negative current pulses of 40-200 μA or 100-500 μA, and 0.2 ms duration were applied at a rate of 3-5 Hz with tungsten or surface electrodes, respectively. To ascertain that microelectrodes were correctly placed, positions of their tips were verified histologically following small electrolytic lesions performed after each experiment.

Nerve branches were stimulated during collision tests by single current pulses of 0.1 ms in duration at a frequency 3-5 Hz, with an intensity expressed in multiples of threshold for the most sensitive nerve fibres in the given nerve.

Extracellular or intracellular recordings of antidromic action potentials from neurones in sacral segments (S1 or S2) were performed with glass micropipettes (tips broken to 1.5–2.5 μm in diameter), filled with 2M potassium citrate solution. Antidromic volleys after stimulation of axons as well as volleys from peripheral afferents were also recorded with monopolar silver ball electrode in contact with the cord dorsum.

Data analysis

Photographs of 3-5 superimposed single sweeps from the oscilloscope screen were analysed. The recognition of antidromicity of a recorded potential was based on the following criteria: "all or none" appearance, constant latency and amplitude, the ability to follow high frequency of stimulation (200 Hz) and collision with orthodromic, nerve-evoked potential (Fuller and Schlag 1976, Lipski 1981). Because not all the neurones responded to the peripheral stimulation, collision tests were performed only in a part of them (45 of the total 87). In the remaining cases all other criteria were respected. An example of the collision test is given in Fig. 1C.

Axonal conduction velocities were calculated from antidromic latencies and distances between stimulating and recording sites. In order to compare mean values of conduction velocities between specified groups of neurones or between proximal and distal parts of their axons Student's *t*-test was used.

RESULTS

Location of neurones, axonal course and projections

Eighty-seven neurones were antidromically activated in the S1 and S2 spinal gray matter following stimulation of the contralateral Th13 segment. In 50 of them (57%) antidromic action potentials were evoked after stimulation of the contralateral restiform body and/or the gigantocellular reticular nucleus. Projections to coRB were found in 20 neurones (23%), to coGRN in 10 (11%) and both to coRB and coGRN in the remaining 20 cases (23%). Examples of records from a neurone with dual supraspinal projections are given in Fig. 1B.

Axons of all investigated cells ascended in lateral funiculi on the contralateral side. However, in 46 cases (43%) axonal branches in ipsilateral lateral funiculi were also present. This occured in 8 out of 20 neurones projecting to the cerebellum but not to GRN, 7 out of 10 neurones projecting to GRN but not to the cerebellum, 11 out of 20 cells projecting both to the cerebellum and the reticular formation as well as 20 out of 37 neurones with axons ascending at least to the thoracic level. Proportions between particular neuronal groups regarding their projections and axonal course are presented in Fig. 2A.

The distribution of recording sites was established on the basis of the micropipette tip positions in the gray matter. All neurones were found to be located at depths between 2.32 and 3.97 mm from the cord surface. The micropipette was inserted 0-0.8 mm from the midline with the micromanipulator directed 4-12° mediolaterally, which corresponded to Rexed's lamina VIII as well as medial parts of lamina VII (Rexed 1954). Cells of various supraspinal projections (i.e., to coRB, coGRN or both) are presented on the outline of the sacral spinal cord in Fig. 2B. They were intermingled with each other and did not form separate groups. However, most neurones projecting to the coGRN only were distributed more dorsally while those of dual supraspinal projections to coRB and coGRN tended to be located deeper, in lamina VIII only.

Latencies of antidromic potentials and axonal conduction velocities

Latencies of antidromic action potentials recorded from 50 neurones with branches ascending beyond the spinal cord were in the range 3.6-7.4 ms (mean ± SD:

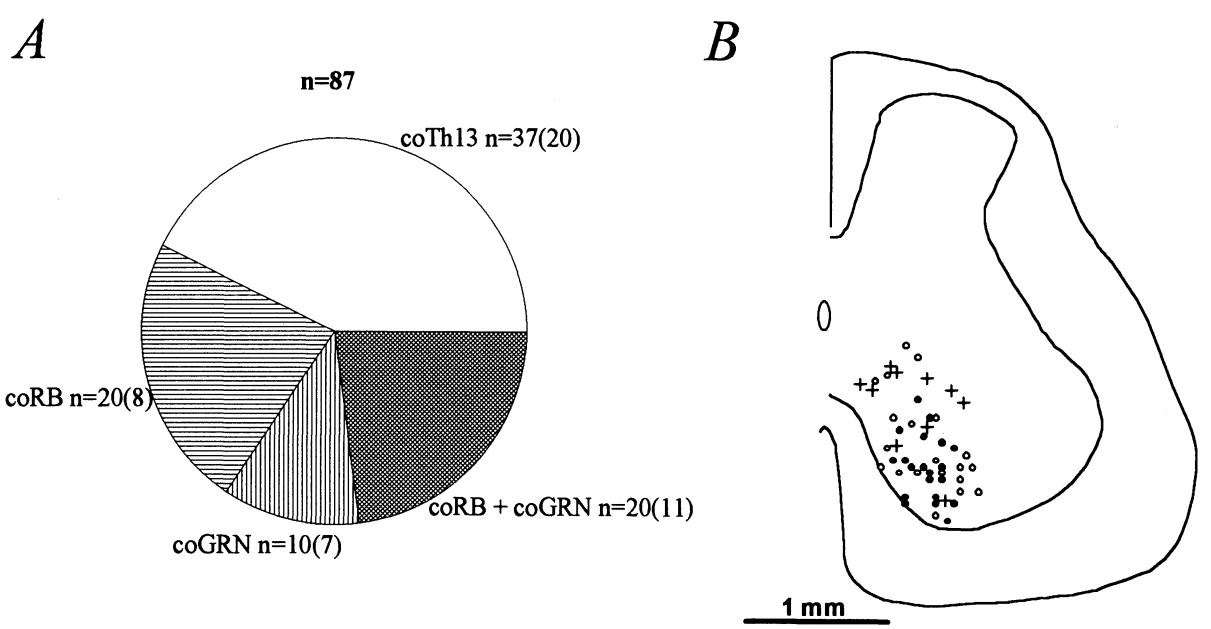

Fig. 2. A, the relative contribution of various types of neurones with respect to their projections and axonal course in the spinal cord in the total sample of 87 neurones investigated. Numbers given in parentheses relate to neurones bilaterally ascending in the spinal cord at the Th13 level. B, the transverse plane of the sacral spinal cord with locations of 50 neurones of cerebellar and/or reticular projections. Crosses represent neurones projecting to coGRN, open circles, to coRB, while filled circles, to both coRB and coGRN.

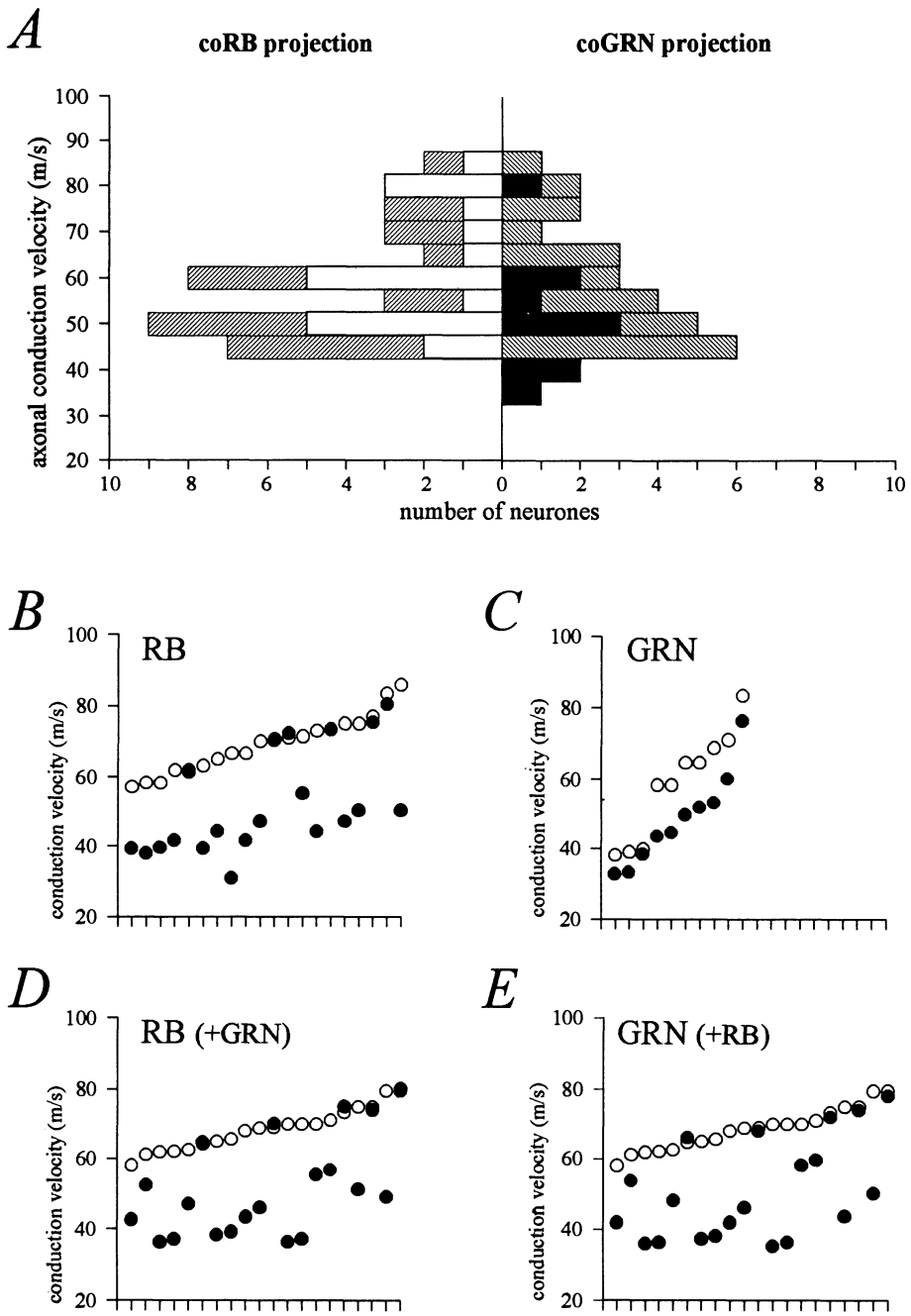

Fig. 3. A, histograms of axonal conduction velocities of the investigated neurones. Open bars represent values for cells of the cerebellar projection (left side); filled bars, for cells of the reticular projection (right side), while hatched bars represent values for neurones of dual projections, measured separately for branches to coRB (left) and coGRN (right). B – E, conduction velocities between sacral and thoracic segments (open circles) compared to those between thoracic segments and coRB or coGRN (filled circles) for particular neurones (presented in succession on the ordinate). Diagrams B and C show those values for cells of exclusive cerebellar or reticular projection, respectively. Diagrams D and E compare values for the same neurones of dual projections, calculated in distal sections of axons separately for branches reaching coRB and coGRN, respectively. In cases where the same values of conduction velocities where measured for distal as well as proximal parts of axons filled symbols cover open symbols.

5.94 ± 1.19 ms, $n = 40$), when measured from coRB or 4.1-9.6 ms (6.54 ± 1.45 ms, $n = 30$), when measured from coGRN. However, because of differences in the size of the animals used and in the respective distances between stimulation and recording sites, axonal conduction velocities were more suitable than latencies for comparison of particular groups of neurones.

Histograms in Fig. 3A show a distribution of axonal conduction velocities of the above-mentioned cells. Values calculated for individual neurones projecting to the cerebellum were 44-83 m/s (mean: 59.23 ± 12.9 m/s, $n = 20$), for neurones projecting to the reticular formation 35-77 m/s (50.3 ± 12.7 m/s, $n = 10$), while for those of dual projections to coRB and coGRN 42-83 m/s (56.1 ± 12.6 m/s, $n = 20$) and 42-82 m/s (55.7 ± 13.0 m/s, $n = 20$) for cerebellar and reticular collaterals, respectively. Conduction velocities of neurones projecting to coGRN seemed to be comprised in lower ranges when compared to neurones reaching the cerebellum. However, these differences were not significant ($P>0.05$, Student's t-test).

Measurement of conduction velocities between sacral and thoracic segments of the spinal cord enabled us to evaluate also these cells where a projection to Th13 but not to RB or GRN was found, as well as ipsilateral branches that were revealed in some cases. Conduction velocities for neurones with axons ascending to supraspinal structures were between 39-83 m/s (mean: 66.8 ± 9.8 m/s, $n = 50$) and 38-86 m/s (66.6 ± 12.8 m/s, $n = 26$) for contralateral and ipsilateral branches, respectively. For neurones with axons ascending to at least the thoracic level conduction velocities were 57-75 m/s (65.7 ± 5.8, $n = 37$) and 39-76 m/s (63.6 ± 10.0, $n = 20$) for contralateral and ipsilateral branches, respectively. No significant differences ($P>0.05$) were found between conduction velocities of these groups.

One should notice, however, that conduction velocities measured between Th13 and sacral segments were higher when compared to those measured between coRB and Th13 or coGRN and Th13. Conduction velocities calculated for proximal (S1/2 – Th13) and distal (Th13 – coRB/coGRN) parts of axons are shown in Fig. 3 B-E. In 14 out of 20 neurones projecting to coRB, in 6 out of 10 neurones projecting to coGRN and in 14 out of 20 neurones of dual projections to coRB and coGRN (in both collaterals), conduction velocity was lower by over 10 m/s and amounted up to 36 m/s, 20 m/s and 35 m/s, respectively.

DISCUSSION

In electrophysiological investigations of neurones to determine their projections to various spinal or brain structures, the adequate positioning of the stimulating electrode as well as the appropriate value of the stimulating current are of the highest importance. In the present study we excluded from the sample one animal with improperly inserted tungsten electrodes, as shown by the results of electrolytic lesions that indicated the locations of stimulating electrodes tips. As described by Ranck (1975) and Bagshaw and Evans (1976) for metal monopolar microelectrodes, only axons within areas of radius smaller than 0.5 mm are expected to be excited with a stimulus strength of 100 μA. In our study the threshold of current pulses when coRB or coGRN were stimulated only occasionally exceeded the above values and amounted up to 200 μA. Only neurones activated from co RB or coGRN with such current strengths were attributed to spinocerebellar or spinoreticular tracts.

Cells of origin of spinocerebellar tracts in sacral segments of the cat spinal cord have been previously found either in the dorsal horn, the intermediate gray or in the ventral horn (Matsushita et al. 1979, Grant et al. 1982). Cell bodies of spinoreticular neurones have been dispersed in the whole gray matter but with the predominant location in laminae VII and VIII (Fields et al. 1975, Maunz et al. 1978). Results presented in this paper confirm the above data and indicate that both types of neurones occupy the same region in the gray matter, i.e., the medial lamina VII and the lamina VIII. Moreover, it has been shown that some of the cells give off collaterals projecting both to the cerebellum and to the reticular formation. Projections to various spinal or supraspinal centres have been previously described for spinoreticular and spinothalamic neurones (Kevetter and Willis 1983, Foreman et al. 1984), spinocerebellar and spinothalamic neurones (Huber et al. 1994), spinothalamic and spinohypothalamic neurones (Katter et al. 1996a,b) or spinocerebellar and propriospinal neurones (Krutki et al. 1998). It seems likely that collateral branching which allows transmission of the same information to more than one centre is a common feature of a significant part of various types of ascending tract neurones.

As it has been known from earlier studies, axons of spinocerebellar as well as spinoreticular neurones from sacral levels of the cord run mainly on the contralateral side (Maunz et al. 1978, Matsushita et al. 1979). This is in agreement with our results. However, in about half of

the investigated cells (26 out of 50, cf. Results) bilateral course of axons at the level of Th13 has been revealed. Such a high percentage has not been reported before. Maunz et al. (1978) reported bilateral projection for about 20% of spinoreticular neurones in the lumbosacral enlargement while Foreman et al. (1984) for 27% of spinoreticular cells in the thoracic cord. Unilateral course of spinocerebellar axons was mentioned in most papers, though some anatomical investigations with neuronal tracers and parallelly performed spinal lesions suggested a possibility of bilateral projections (Matsushita et al. 1979, Grant et al. 1982). In the latest electrophysiological study performed in our laboratory (Krutki et al. 1998) more than half (13 out of 24) of neurones classified as spinocerebellar in the S2 segment have been found to ascend in the spinal cord bilaterally.

The question if ipsilateral branches of some neurones investigated in our study reach RB or GRN on the ipsilateral side remains to be elucidated. For technical reasons it has been impossible to include two additional stimulating electrodes in experiments presented here. Moreover, previous studies in cats have provided no data about bilateral supraspinal projections of sacral neurones. Thus, we must conclude that more experimental research is needed to solve this problem.

Axonal conduction velocities measured in this study (35-83 m/s) are in agrement with previous electrophysiological research on sacral neurones projecting to the cerebellum (Huber et al. 1994, Krutki et al. 1998) or to the reticular formation (Fields et al. 1975) though in some papers also a little higher values are given either for spinocerebellar (61-100 m/s, Grottel et al. 1991) or spinoreticular (16-96 m/s, Maunz et al. 1978, 27-100 m/s, Huber et al. 1999) neurones of sacral origin. It must be emphasized that no significant differences have been observed between conduction velocities for neurones projecting to coRB, coGRN or both.

In 37 neurones supraspinal projections have not been established. However, one should notice that their location as well as axonal course and conduction velocities are not significantly different from those projecting to the coRB or coGRN. They may be long ascending propriospinal neurones to the cervical enlargement. Such neurones with axons running ipsilaterally, contralaterally or bilaterally in the lateral funiculus and conducting with a velocity 41-96 m/s have been found in laminae VII and VIII of the gray matter (Krutki et al. 1997). On the other hand, we cannot exclude that some of these neurones may project to other centres in the brainstem or the thalamus that was not investigated in this study. The existence of such projections from sacral spinal cord neurones was described in several anatomical as well as electrophysiological papers (cf. Introduction).

In most neurones projecting to coRB or/and coGRN an evident decrease in conduction velocity (up to 36 m/s, cf. Results) has been observed in distal parts (above Th13) of axons in comparison to their proximal (S1/2-Th13) parts. Such a feature has been previously reported for other types of cells: spinocervical and dorsal horn spinocerebellar neurones (Riddell et al. 1994) as well as long propriospinal neurones – both descending (Krutki 1997) and ascending (Krutki et al. 1997, 1998). This observation suggests that pattern of divergence of the investigated neurones may be more complex by giving off additional collateral branches at various levels of the spinal cord.

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