Bilateral projection of neurones of the C6 segment to S1 and S2 segments of the spinal cord in the cat

Piotr Krutki

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

Abstract. Sacral projections of neurones located in the C6 segment of the spinal cord were electrophysiologically investigated in α-chloralose anaesthetized cats. The cell bodies were found mainly in lamina VIII and in the ventromedial part of lamina VII of the C6 segment. At the thoracic level their axons descended in lateral funiculi, mostly on both sides and only exceptionally contra- or ipsilaterally. However, bilateral projection to sacral segments was less frequent (25 neurones). It is concluded that axons terminate at different levels on both sides of the spinal cord and only part of them project bilaterally to S1/S2 segments. Conduction velocities calculated for all the axons varied from 38 to 80 m/s and were significantly slower for their distal parts. Therefore it is suggested that descending axons send collaterals at various spinal levels. The presented data indicate the importance of these neurones for interlimb coordination.

INTRODUCTION

It is generally assumed that the essential elements in the system generating complex patterns of muscle activity - underlying spinal reflexes and locomotion - are propriospinal neurones (Sherrington 1906, Lundberg 1979, Grillner 1981, Berkowitz and Stein 1994b, c). These descending many segments and interconnecting cervical and lumbosacral enlargements deserve special attention because of their contribution to coordination of movements of forelimbs and hindlimbs (Jankowska et al. 1974, English 1980, Bem et al. 1995).

The existence of long descending propriospinal pathways originating from the cervical level was first reported by Sherrington and Laslett (1903) who applied the method of anterograde degeneration with Marchi staining to demonstrate the existence of long descending fibres in lateral as well as ventral columns of the spinal cord. The same method combined with the Nauta technique was adapted by Barilari and Kuypers (1969) to prove that both descending and ascending long propriospinal tracts terminate bilaterally in the spinal grey matter, mainly in lamina VIII and the medial part of lamina VII (Rexed 1954).

Experiments with horseradish peroxidase transport confirmed the existence of descending, bilaterally projecting, propriospinal pathways interconnecting spinal enlargements in reptiles (Kusuma and Donkelaar 1980, Berkowitz and Stein 1994a) and in mammals (Matsushita et al. 1979, Skinner et al. 1979, Yezierski et al. 1980). Usually attention was paid to neurones with axonal terminations in lumbar segments, while the sacral part of the cord was less explored. However, it has been shown that 60% of fibres in the white matter of the S2 segment in the cat are propriospinal (Chung and Coggeshall 1988).

The reflex activity of the limbs was investigated following stimulation of nerves (Lloyd 1942, Schomburg et al. 1978) or the cervical spinal cord (Iwahara et al. 1991) and these studies brought electrophysiological evidence of interconnections between centres governing movements of the limbs, also in man (Sarica and Ertekin 1985). In order to find peripheral as well as supraspinal input on neurones of those centres, electrical potentials were recorded from motoneurones of the cervical enlargement (Illert et al. 1977, Illert and Tanaka 1978, Alstenmark et al. 1984a) and from C3-C4 propriospinal neurones projecting to motoneurones of C6-Th1 segments, controlling the forelimb in the cat (Illert et al.

1978, 1981, Alstenmark et al. 1984b, Alstenmark et al. 1986). Similar techniques were applied to investigate neurones of C3-C5 (Alstenmark et al. 1987a, b) or C5-Th1 segments (Skinner et al. 1979), which give rise to long pathways descending to thoracic or lumbar segments of the cord. Kostyuk et al. (1971) and Jankowska et al. (1974, 1983) found direct, monosynaptic effects of long descending propriospinal neurones evoked in interneurones and motoneurones controlling hindlimb muscles.

The aim of this study was to demonstrate direct projections of neurones of the C6 segment to the first and second sacral segments of the cat's spinal cord. Location of cell bodies, course of axons in the spinal cord and axonal conduction velocities are presented and the possible function of these neurones is discussed.

METHODS

Experiments were conducted on 12 adult cats weighing 1,700-3,700 g. Anaesthesia induced by ketamine (25-40 mg/kg, i.m.) for preliminary surgical procedures was maintained using several doses of α-chloralose (up to 50 mg/kg, i.v.) (Jankowska et al. 1995) throughout the rest of the experiment. Depth of anaesthesia was monitored by controlling withdrawal and corneal reflexes during the operation and diameter of pupils and blood pressure during recordings. The animals were immobilized with gallamine triethiodide (about 3 mg/kg/h) and artificially ventilated. Bilateral pneumothorax was made in all cases to reduce respiratory movements. Temperature and systolic blood pressure were controlled and kept between 36-38°C and 90-120 mmHg, respectively. Continuous intravenous infusion of bicarbonate solution (100 mM $NaHCO_3$ with 5% glucose, 1-2 ml/kg/h) was done during both preparation and recording, the bladder being catheterized.

Nerves of the forelimb: ulnar (Uln), radial (Rad) and median (Med), were transected, dissected free and prepared for stimulation with tunnel electrodes mounted under the skin. The spinal cord was exposed by laminectomies at three levels: L7-S2, Th12-Th13 and C6-C7 segments. The dura was opened in small areas at the levels of cervical and sacral segments while left intact at the thoracic level. Only small holes in the pia were made in places for introduction of recording and stimulating electrodes. All the exposed areas of the spinal cord were covered with warm (37 ± 1°C) paraffin oil.

In order to antidromically stimulate axons of investigated neurones, two bipolar silver ball-tipped electrodes

(with tips about 0.5 mm diameter, separated by 3 mm) were placed at the level of Th13 segment, in parallel, on both sides of dorsolateral funiculi (dlf) and two varnished tungsten electrodes (tip diameter 3-5 μm) were inserted into the spinal grey of S1/S2 segments bilaterally, perpendicular to the surface, 1.1-1.3 mm lateral from the midline at a depth of 2.3-2.7 mm. Single pulses of 0.2 ms duration, with current magnitude of 0.1-1.2 mA through the surface electrodes and of 35-200 μA through the tungsten electrodes, were applied at a rate of 3-5 Hz. The position of an electrode tip in the spinal grey matter of S1/S2 segments was verified after each experiment by electrolytic lesion.

Nerve branches were stimulated with single pulses of 0.1 ms duration at frequency 3-5 Hz, with intensity expressed in multiples of threshold for the most excitable fibres in a nerve (Jack 1978).

Antidromic volleys after stimulation at Th13 or S1/S2 level as well as volleys from peripheral afferents were recorded with a monopolar silver ball electrode placed on the dorsal surface of the C6 segment. Extracellular and intracellular recordings from neurones of C6 segment were made using glass micropipettes with tip diameters of 1.5-2.0 μm, filled with 2M potassium citrate solution. Sites of recordings (locations of neurones) were determined in each case from angular position of a micropipette, distance from the midline and depth from the surface of the cord.

The recognition of antidromic potential was based on criteria described previously by Fuller and Schlag (1976) and Lipski (1981). They included "all or nothing" appearance of an action potential with constant latency and amplitude, sharp threshold, the ability to follow high frequency of stimulation (>150 Hz) and collision with orthodromically evoked potential.

The records were analysed from the photographs of 2-5 superimposed sweeps from the oscilloscope screen. In order to compare antidromic latencies and axonal conduction velocities for groups of neurones, Student's t-test was used.
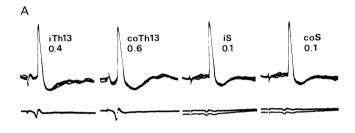
RESULTS
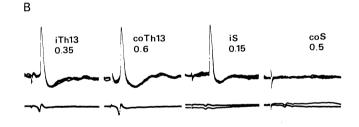
Unilateral and bilateral projection to S1/S2 segments

The sample included 42 neurones. Twenty-five could be antidromically activated from both ipsi- and contralateral spinal grey of S1/S2 segment. In 8 cases anti-

dromic responses were obtained after contralateral only and in 9 cases after exclusively ipsilateral S1/S2 stimulation. However, in most cases (37) antidromic action potentials were recorded after stimulation of both ipsi- and contralateral dlf at Th13 level. Four neurones were antidromically invaded only by contralateral and one only by ipsilateral stimulation.

Figure 1 shows intracellular records from 3 different neurones of bilateral (A), ipsilateral (B) or contralateral (C) projection to S1/S2 segments. Note that both neurones with unilateral sacral projection presented in Fig. 1 B and C were activated antidromically from ipsilateral as well as contralateral Th13.

The minimal current intensities required for stimulation of fibres at Th13 level (0.1-1.2 mA) allow us to as-
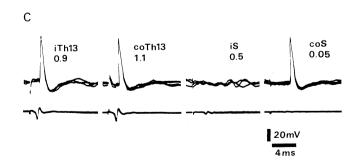

Fig. 1. Intracellular records of antidromic action potentials (upper traces) from three different neurones of the C6 segment projecting to sacral segments bilaterally (A), ipsilaterally (B) or contralaterally (C) after stimulation in 4 places, as indicated. Intensities of stimuli are given above the records in mA. Lower traces are records from the surface of the spinal cord.
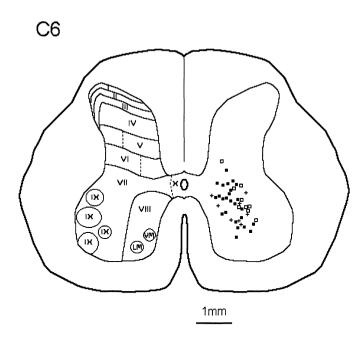
C6

1mm

Fig. 2. Distribution of investigated neurones within the spinal grey of the C6 segment. Filled squares represent neurones of bilateral; open squares, of ipsilateral; crosses, of contralateral sacral projection.

certain that all the investigated axons run within the lateral funiculus and most of them in its dorsal part. The threshold for stimulation of axon terminals in S1/S2 spinal grey ranged from 35 to 100 μA, but in exceptional cases was raised up to 200 μA. The stimulus strength of 100 μA is able to excite the largest and fastest fibres within an area of radius 0.5 mm (Ranck 1975, Bagshaw and Evans 1976). Therefore, regarding approximate axonal conduction velocities of investigated neurones and location of stimulating tungsten electrodes, it could be expected that only axons on the side of stimulation were excited.

Location of cell bodies in C6 segment

Distribution of neurones (established based on a place, angle and depth of micropipette introduction into the spinal cord) is illustrated in Fig. 2. Cell bodies were found in depths from 3.13 to 5.01 mm from the surface of the spinal cord with microelectrode directed 4-8° mediolaterally. They were located mainly (40 out of 42) in Rexed's lamina VIII and medial and ventral parts of lamina VII. Two neurones were present in the medial part of lamina VI.
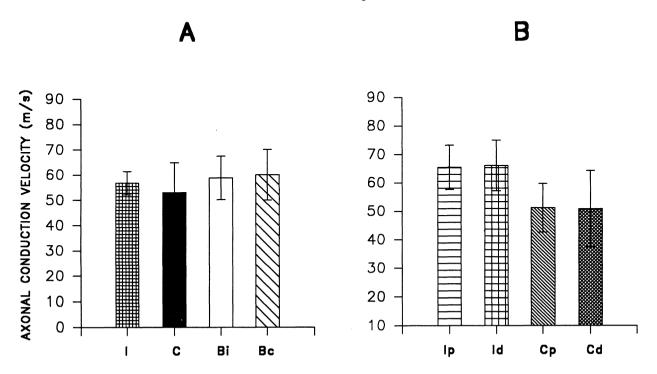
A

B

Fig. 3. A, comparison of mean values (± SD) of axonal conduction velocities for particular groups of neurones projecting to S1/S2 segments ipsilaterally (I), contralaterally (C) or bilaterally (Bi, ipsilateral branch; Bc, contralateral branch). B, mean conduction velocities (± SD) for proximal (C6 - Th13) and distal (Th13 - S1/S2) parts of axons. Ip, Id, values for ipsilateral branches (proximal and distal parts, respectively); Cp, Cd, values for contralateral branches (proximal and distal parts, respectively).

The distribution of bilaterally and unilaterally project-ing neurones shows discrete differences. Cells with bi-lateral sacral projections are dispersed in the whole marked region. Ipsilaterally projecting neurones seem to be located more dorsally and laterally - mainly in lamina VII, while those with contralateral projections were found more ventrally and medially - mainly in lamina VIII.

Axonal conduction velocities

No significant statistical differences ($P>0.05$) were found between axonal conduction velocities calculated after stimulation at the sacral level when comparing groups of neurones of ipsilateral, contralateral and bilat-eral projections to S1/S2 segments (Fig. 3A). Values ranged from 50 to 63 m/s (57 ± 5: mean $\pm$ SD, $n = 9$) for neurones projecting to S1/S2 ipsilaterally, 38-73 m/s (53 ± 12, $n = 8$) for cells projecting contralaterally, 41-74 m/s (59 ± 9, $n = 25$) and 40-80 m/s (60 ± 10, $n = 25$) for neur-ones with bilateral sacral projection, for ipsilateral and contralateral branches, respectively.

Despite certain dispersion of values for various neur-ones, conduction velocities counted in one bilaterally projecting neurone after stimulation of its ipsilateral or contralateral branch were similar. In 20 out of 25 cases they were identical or differed by less than 10%. Com-parison of conduction velocities for ipsilateral and con-tralateral axon collaterals of one neurone confirms the earlier noticed fact that there are no significant differen-ces between these two branches.

Figure 3B presents conduction velocities calculated separately for distances from C6 to Th13 and from Th13 to S1/S2. The mean values in a sector from the cell body to Th13 level were 66 ± 8 m/s ($n = 34$) for ipsilateral and 67 ± 9 m/s ($n = 33$) for contralateral branches. Conduc-tion velocities calculated in a sector from Th13 to S1/S2 were 51 ± 9 m/s ($n = 34$) and 51 ± 13 m/s ($n = 33$), re-spectively. These data demonstrate a statistically signi-ficant ($P<0.05$) decrease in conduction velocities when comparing distal to proximal parts of descending axons.

DISCUSSION

Unilateral and bilateral projection to sacral segments

A possibility of existence of crossed descending pro-priospinal pathways was at first denied (Sherrington and Laslett 1903), but both ipsilateral and contralateral course of axons of nerve cells interconnecting cervical and lumbosacral enlargements was later suggested in electrophysiological (Lloyd 1942) as well as neuroana-tomical research (Barilari and Kuypers 1969, Matsushita et al. 1979, Skinner et al. 1979). Nevertheless, because of methods used, those experiments didn't answer the question whether axons descending on both sides of the spinal cord are branches of the same or separate neur-ones. The results described in this paper have shown that most of the investigated neurones of C6 segment have axons dividing into branches descending bilaterally and only a few run exclusively ipsi- or contralaterally. How-ever, the site of axonal division has not been determined.

The analysis presented in Results has shown that axons of almost all the neurones run bilaterally at the Th13 level but their termination in the S1/S2 segments is bilateral as well as ipsilateral or contralateral only. It is suggested that those with axons descending bilaterally at the thoracic level and antidromically excited only from one side of the sacral spinal cord give terminal col-laterals at different spinal levels - in S1 or S2 segment on one side, whereas between S1/S2 and Th13 on the other.

Course of fibres within lateral funiculi

Previous studies showed various locations of axons of propriospinal neurones. Berkowitz and Stein (1994a) proved that they were dispersed through the whole white matter of the spinal cord in reptiles. However, in mammals axons seem to be distributed more regularly. Sherrington and Laslett (1903) demonstrated that in dog they run mainly in the ventral as well as lateral funiculus. On the other hand, Barilari and Kuypers (1969) suggested that propriospinal axons run almost exclusively in medial parts of ventral funiculi and to a lesser extent in dorsal funiculi. Also, the experiments of English (1980) pointed to the latter location. In contrast, results of studies on isolated spinal segments in rats indicate a dif-fused distribution of both ascending and descending pro-priospinal fibres in all funiculi of the spinal cord (Chung and Coggeshall 1983, Chung et al. 1987).

Axons of nerve cells presented in this study have de-scended bilaterally in lateral funiculi, mostly in their dor-sal parts (dlf). Such a location, though not ever coinciding with data described above, is in good agree-ment with results of other electrophysiological experi-ments that proved that long ascending (Gernandt and

Shinamura 1961) as well as long descending propriospinal pathways (Jankowska et al. 1974, Yamaguchi 1986, Bem et al. 1995) run also within the dorsolateral funiculi.

Considering differences between data from other studies it seems likely that the presented neurones are only a part of cells projecting from C6 segment to S1/S2 segments. It cannot be excluded that there exist neurones sending their branches in ventral or dorsal funiculi.

Location of neurones in the sixth cervical segment

Results of the presented study demonstrate that most of investigated neurones have been encountered in lamina VIII and ventromedial part of lamina VII of the spinal grey of C6 segment. The distribution is in agreement with previous neuroanatomical studies on neurones of cervical segments with long axons descending to lumbar and sacral segments (Barilari and Kuypers 1969, Matsushita et al. 1979, Skinner et al. 1979, Yezierski et al. 1980). It is worth noticing that such a location of propriospinal neurones (laminae VII and VIII) is characteristic also for neurones of long ascending axons (Barilari and Kuypers 1969, Molenaar and Kuypers 1978) as well as for short propriospinal neurones (both ascending and descending) connecting neighbouring spinal segments (Rustioni et al. 1971, Molenaar et al. 1974, Molenaar 1978, Grant et al. 1980, Hiramatsu 1983).

This distribution of cell bodies of investigated neurones projecting to sacral segments bilaterally and unilaterally doesn't seem to be accidental. Matsushita et al. (1979) suggested that neurones of crossed projections to the lumbosacral enlargement are located more ventrally and medially in spinal grey matter of cervical segments whereas those of uncrossed projections are situated more dorsally and laterally. The presented results confirm these observations but only as concerns neurones with exclusively ipsilateral or contralateral projections. The cells with axons descending to sacral segments bilaterally have been found throughout the whole area occupied by the above groups. The significance of such a distribution is still unknown. However, it is likely that it is associated with different synaptic input on particular groups of neurones from periphery or supraspinal centres.

Axonal conduction velocities

Considerable differences between conduction velocities of investigated axons have been observed (the mini-

mal: 38 m/s, the maximal: 80 m/s). This implies certain differences in the size of nerve cells and thickness of descending axons. On the other hand, regarding similar values of axonal conduction velocities, two branches of the same neurone don't seem to be essentially different in size.

Conduction velocities measured in this study are similar to those acquired previously for neurones with cell bodies in the cervical enlargement (C5-Th1) descending to lumbar segments of cat spinal cord (59 ± 22 m/s, Skinner et al. 1979). In a few studies higher values were obtained for propriospinal neurones in lateral funiculi (100 m/s, Jankowska et al. 1974; 101 m/s, Alstenmark et al. 1981). However, in one case the location of neurones was not investigated and conduction velocities were measured between Th3 and Th11 only, and in the other the results concerned C3-C4 propriospinal neurones and measurements were made between C7 and Th9 segments. In all, our results confirm previous observations that neurones descending many segments conduct faster than short propriospinal neurones connecting neighbouring spinal segments for which conduction velocities were 36.4-46.1 m/s (Kostyuk et al. 1971) and 44 m/s (Alstenmark et al. 1981).

Comparison of axonal conduction velocities in rostral and caudal parts (C6-Th13 and Th13-S1/S2, respectively) have shown differences. Both ipsi- and contralateral branches have conducted significantly faster in their proximal sector. The slowing of conductance along the axon is a feature commonly observed in branching spinal afferents (Fu and Schomburg 1974). This suggests that investigated neurones can give collaterals to various spinal segments and thereby diverge more extensively than into two descending branches only. The fact of unilateral projection to sacral segments despite bilateral course at the thoracic level in some cases supports the above hypothesis.

Function of descending projections from C6 to S1/S2 segments

The main function of neurones presented in this paper seems to be coordination of movements of fore- and hindlimbs. This has been shown in several studies on reflexes evoked in hindlimbs after stimulation of cervical spinal cord in decerebrate cat (Yamaguchi 1986, Iwahara et al. 1991) as well as in studies on motor coordination after spinal lesions (Bem et al. 1995). Results of these experiments have emphasized the essential role of fibres in

dorsolateral funiculi. To support the hypothesis that spinal centres controlling movements of forelimbs and hindlimbs cooperate with each other, the existence of sacral and lumbar propriospinal neurones ascending to cervical segments has been demonstrated both anatomically (Barilari and Kuypers 1969) and electrophysiologically (Gernandt and Shinamura 1961, Miller et al. 1973). Another group of experiments has brought in turn the evidence that at least part of long descending propriospinal neurones have direct, monosynaptic connections with motoneurones or interneurones in spinal reflex pathways (Jankowska et al. 1974, 1983). The extensive convergence of influences from supraspinal centres, as vestibular nuclei (Hongo et al. 1975), cerebral cortex, red nucleus, reticular formation (Alstenmark et al. 1987a,b) has also been demonstrated in propriospinal neurones. Moreover, distribution of investigated cells in the spinal grey - in laminae VII and VIII mainly - seems to be perfect for transferring information from forelimb afferents to centres controlling hindlimb muscles.

The name "propriospinal" referring to investigated neurones has been avoided since based on the presented data it has been impossible to verify such a statement. To question whether they actually are propriospinal seems to be justified for there is evidence that some neurones located in cervical segments with axons descending along spinal cord give collaterals also to supraspinal structures. It has been electrophysiologically demonstrated that neurones of C3-C4 segments with direct influence on motoneurones of forelimb muscles in the cat give ascending branches to the lateral reticular nucleus (Illert and Lundberg 1978, Alstenmark et al. 1981). Also, anatomical studies in rats by Verburgh and Kuypers (1987) show that numerous cells of C3-C8 segments send branches descending to lumbar and sacral segments as well as ascending above the spinal level.

The possibility of giving off collaterals to supraspinal structures as well as to different spinal segments suggests that the information forwarded by investigated neurones reaches more than one centre and thereby may coordinate movements not only of forelimbs and hindlimbs but neck and trunk as well. The prevailing bilateral projection to S1/S2 segments points to complex and many-sided mechanisms of cooperation of the above-mentioned centres. It is necessary to stress that the presented results relate only to a fragment of the whole system of neurones connecting anatomically and functionally particular segments of the spinal cord.

REFERENCES

Alstenmark B., Johannisson T., Lundberg A. (1986) The inhibitory feedback pathway from the forelimb to C3-C4 propriospinal neurones investigated with natural stimulation. Neurosci. Res. 3: 451-456.

Alstenmark B., Lindström S., Lundberg A., Sybirska E. (1981) Integration in descending motor pathways controlling the forelimb in the cat. 8. Ascending projection to the lateral reticular nucleus from C3-C4 propriospinal neurones also projecting to forelimb motoneurones. Exp. Brain Res. 42: 282-298.

Alstenmark B., Lundberg A., Pinter M., Sasaki S. (1987a) Long C3-C5 propriospinal neurones in the cat. Brain Res. 404: 382-388.

Alstenmark B., Lundberg A., Pinter M., Sasaki S. (1987b) Subpopulations and functions of long C3-C5 propriospinal neurones. Brain Res. 404: 395-400.

Alstenmark B., Lundberg A., Sasaki S. (1984a) Integration in descending motor pathways controlling the forelimb in the cat. 10. Inhibitory pathways to forelimb motoneurones via C3-C4 propriospinal neurones. Exp. Brain Res. 56: 279 - 292.

Alstenmark B., Lundberg A., Sasaki S. (1984b) Integration in descending motor pathways controlling the forelimb in the cat. 11. Inhibitory pathways from higher motor centres and forelimb afferents to C3-C4 propriospinal neurones. Exp. Brain Res. 56: 293-307.

Bagshaw E.V., Evans M.H. (1976) Measurement of current spread from microelectrodes when stimulating within the nervous system. Exp. Brain Res. 25:391-400

Barilari M.G., Kuypers H.G.J.M. (1969) Propriospinal fibers interconnecting the spinal enlargements in the cat. Brain Res. 14: 321-330.

Bem T., Górska T., Majczyński H., Zmysłowski W. (1995) Different patterns of fore-hindlimb coordination during overground locomotion in cats with ventral and lateral spinal lesions. Exp. Brain res. 104:70-80.

Berkowitz A., Stein P.S.G. (1994a) Descending propriospinal axons in the hindlimb enlargement of the red - eared turtle: cells of origin and funicular courses. J. Comp. Neurol. 346: 321-336.

Berkowitz A., Stein P.S.G. (1994b) Activity of descending propriospinal axons in the turtle hindlimb enlargement dur-

ing two forms of fictive scratching: broad tuning to regions of the body surface. J. Neurosci. 14: 5089-5104.

Berkowitz A., Stein P.S.G. (1994c) Activity of descending propriospinal axons in the turtle hindlimb enlargement during two forms of fictive scratching: phase analyses. J. Neurosci. 14: 5105-5119.

Chung K., Coggeshall R.E. (1983) Propriospinal fibres in the rat. J. Comp. Neurol. 217: 47-53.

Chung K., Coggeshall R.E. (1988) Propriospinal fibres in the white matter of the cat sacral spinal cord. J. Comp. Neurol. 269: 612-617.

Chung K., Langford L.A., Coggeshall R.E. (1987) Primary afferent and propriospinal fibres in the rat dorsal and dorsolateral funiculi. J. Comp. Neurol. 263: 68-75.

English A.W. (1980) Interlimb coordination during stepping in the cat: effects of dorsal column section. J. Neurophysiol. 44: 270-279

Fu T.C., Schomburg E.D. (1974) Electrophysiological investigation of the projection of secondary muscle spindle afferents in the cat spinal cord. Acta Physiol. Scand. 91: 314-329.

Fuller J.H, Schlag J.D. (1976) Determination of antidromic excitation by the collision test: problems of interpretation. Brain Res. 112: 283-298.

Gernandt B.E., Shinamura M. (1961) Mechanism of interlimb reflexes in cat. J. Neurophysiol. 24: 665-677.

Grant G., Illert M., Tanaka R. (1980) Integration in descending motor pathways controlling the forelimb in the cat. 6. Anatomical evidence consistent with the existence of C3-C4 propriospinal neurones projecting to forelimb motor nuclei. Exp. Brain Res. 38: 87-93.

Grillner S. (1981) Control of locomotion in bipeds, tetrapods, and fish. In: Handbook of physiology. The nervous system II (Ed. V. Brooks). Am. Physiol. Soc., Bethesda, MD, p. 1179-1236.

Hiramatsu K. (1983) Spinal afferents to lamina IX of the cervical enlargement in the rat studied by the retrograde transport of horseradish peroxidase. Brain Res. 292: 375-377.

Hongo T., Kudo N., Tanaka R. (1975) The vestibulospinal tract: Crossed and uncrossed effects on hindlimb motoneurones in the cat. Exp. Brain Res. 24: 37-55.

Illert M., Jankowska E., Lundberg A., Odutola A. (1981) Integration in descending motor pathways controlling the forelimb in the cat. 7. Effects from the reticular formation on C3-C4 propriospinal neurones. Exp. Brain Res. 42: 269-281.

Illert M., Lundberg A. (1978) Collateral connections to the lateral reticular nucleus from cervical propriospinal neurones projecting to forelimb motoneurones in the cat. Neurosci. Lett. 7: 167-172.

Illert M., Lundberg A., Padel Y., Tanaka R. (1978) Integration in descending motor pathways controlling the forelimb in the cat. 5. Properties of and monosynaptic excitatory convergence on C3 - C4 propriospinal neurones. Exp. Brain Res. 33: 101-130.

Illert M., Lundberg A., Tanaka R. (1977) Integration in descending motor pathways controlling the forelimb in the cat. 3. Convergence on propriospinal neurones transmitting disynaptic excitation from the corticospinal tract and other descending tracts. Exp. Brain Res. 29: 323-346.

Illert M., Tanaka R. (1978) Integration in descending motor pathways controlling the forelimb in the cat. 4. Corticospinal inhibition of forelimb motoneurones mediated by short propriospinal neurones. Exp. Brain Res. 31: 131-141.

Iwahara T., Atsuta Y., Garcia-Rill E., Skinner R. D. (1991) Spinal cord stimulation-induced locomotion in the adult cat. Brain Res. Bull. 28: 99-105.

Jack J.J.B. (1978) Some methods for selective activation of muscle afferent fibres. In: Studies in neurophysiology (Ed. R. Porter). Cambridge University Press, Cambridge, p. 156-176.

Jankowska E., Krutki P., Szabo-Läckberg Z., Hammar I. (1995) Effects of serotonin on dorsal horn dorsal spinocerebellar tract neurones. Neuroscience 67: 489-495.

Jankowska E., Lundberg A., Roberts W.J., Stuart D. (1974) A long proriospinal system with direct effect on motoneurones and on interneurones in the cat lumbosacral cord. Exp. Brain Res. 21: 169-194.

Jankowska E., Lundberg A., Stuart D. (1983) Propriospinal control of interneurons in spinal reflex pathways from tendon organs in the cat. Brain Res. 261: 317-320.

Kostyuk P.G., Vasilenko D.A., Lang E. (1971) Propriospinal pathways in the dorsolateral funiculus and their effects on lumbosacral motoneuronal pools. Brain Res. 28: 233-249.

Kusuma A., Donkelaar, H.J. (1980) Propriospinal fibers interconnecting the spinal enlargements in some quadrupedal reptiles. J. Comp. Neurol. 193: 871-891.

Lipski J. (1981) Antidromic activation of neurones as an analytic tool in the study of the central nervous system. J. Neurosci. Methods 4: 1-32.

Lloyd D.P.C. (1942) Mediation of descending long spinal reflex activity. J. Neurophysiol. 5: 435-458.

Lundberg A. (1979) Integration in a propriospinal motor centre controlling the forelimb in the cat. In: Integration in the nervous system. A symposium in honor of David P. C. Lloyd and Rafael Lorente de Nó. (Eds. H. Asanuma and V. J. Wilson). Igaku - Shoin, Tokyo, p. 47-65.

Matsushita M., Ikeda M., Hosoya Y. (1979) The location of spinal neurons with long descending axons (long descending propriospinal tract neurons) in the cat: a study with the horseradish peroxidase technique. J. Comp. Neurol. 184: 63-79.

Miller S., Reitsma D.J., Van Der Meché F.G.A. (1973) Functional organization of long ascending propriospinal pathways linking lumbo-sacral and cervical segments in the cat. Brain Res. 62: 169-188.

Molenaar I. (1978) The distribution of propriospinal neurones projecting to different motoneuronal cell groups in the cat's brachial cord. Brain Res. 158: 203-206.

Molenaar I., Kuypers H.G.J.M. (1978) Cells of origin of propriospinal fibres and of fibres ascending to supraspinal levels. A HRP study in cat and rhesus monkey. Brain Res. 152: 429-450.

Molenaar I., Rustioni A., Kuypers H.G.J.M. (1974) The location of cells of origin of the fibres in the ventral and the lateral funiculus of the cat's lumbo-sacral cord. Brain Res. 78: 239-254.

Ranck Jr., J.B. (1975) Which elements are excited in electrical stimulation of mammalian central nervous system: a review. Brain Res. 98: 417-440

Rexed B. (1954) A cytoarchitectonic atlas of the spinal cord in the cat. J. Comp. Neurol. 100: 297-351.

Rustioni A., Kuypers H.G.J.M., Holstege G. (1971) Propriospinal projections from the ventral and lateral funiculi to the motoneurones in the lumbosacral cord of the cat. Brain Res. 34: 255-275.

Sarica Y., Ertekin C. (1985) Descending lumbosacral cord potentials (DLCP) evoked by stimulation of the median nerve. Brain Res. 325: 299-301.

Sherrington C.S. (1906) Observations on the scratch - reflex in the spinal dog. J. Physiol. 34: 1-50.

Sherrington C.S., Laslett E.E. (1903) Observations on some spinal reflexes and the interconnection of spinal segments. J. Physiol. 29: 58-96.

Schomburg E.D., Meinck H.M., Hausten J., Roesler J. (1978) Fuctional organization of the spinal reflex pathways from forelimb afferents to hindlimb motoneurones in the cat. Brain Res. 139: 21-33.

Skinner R.D., Coulter J.D., Adams R.J., Remmel R.S. (1979) Cells of origin of long descending propriospinal fibers connecting the spinal enlargements in cat and monkey determined by horseradish peroxidase and electrophysiological techniques. J. Comp. Neurol. 188: 443-454.

Verburgh C.A., Kuypers H.G.J.M. (1987) Branching neurones in the cervical spinal cord: a retrograde fluorescent double-labeling study in the rat. Exp. Brain Res. 68: 565-578.

Yamaguchi T. (1986) Descending pathways eliciting forelimb stepping in the lateral funiculus: experimental studies with stimulation and lesion of the cervical cord in decerebrate cats. Brain Res. 379: 125-136.

Yezierski R.P., Culberson J.L., Brown P.B. (1980) Cells of origin of propriospinal connections to cat lumbosacral gray as determined with horseradish peroxidase. Exp. Neurol. 69: 493-512.