FUNCTIONAL ROLE OF PROPRIOSPINAL NEURONES IN THE CONTROL OF FORELIMB MOVEMENTS

A behavioural and electrophysiological study

BY

BROR ALSTERMARK

GÖTEBORG 1983

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V. Alstermark, B. and Sasaki, S. 1983. Electromyographic activity in fast and slow elbow extensors during a visually guided forelimb movement in cats. Brain Res., 259, 155-158.

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ABSTRACT

ALSTERMARK, B. 1983. Functional role of propriospinal neurones in the control of forelimb movements. A behavioural and electrophysiological study. 1-32. Department of Physiology, University of Göteborg, Box 33031, S-400 33 Göteborg, Sweden.

Propriospinal neurones (PNs) in the C3-C4 segments, which mediate disynaptic excitation from higher motor centres to forelimb motoneurones, have been analysed in behavioural and electrophysiological experiments.

The effect of spinal cord lesions interrupting the input to the C3-C4 PNs and/or the forelimb segments was investigated on a forelimb movement. The results show that a command for target reaching is mediated by the C3-C4 PNs but a command for food-taking by interneurones in the forelimb segments.

Electrical stimulation in the region of the lateral reticular nucleus (LRN) gave antidromic activation of C3-C4 PNs which showed that they have an ascending collateral to the LRN. It is postulated that the cerebellum is informed about the activity in the C3-C4 PNs. Stimulation in the LRN evoked a monosynaptic EPSP in forelimb motoneurones which is assumed to be mediated by the bifurcating axons of the C3-C4 PNs. A comparison of the LRN EPSP amplitude with the homonymous group I EPSP amplitude, input resistance and afterhyperpolarization duration suggested correlation with motor unit type in the order S > FR > FF. Analysis of the time course of the LRN EPSP indicated that it is mediated by PNs with different axonal conduction velocities. Fast motoneurones receive projection predominantly from fast PNs, while slow motoneurones receive input from fast and slow PNs.

In most motoneurones the amplitude of the disynaptic pyramidal (Pyr) EPSP was smaller than the LRN EPSP amplitude. There was a negative correlation between the ratio of these amplitudes (Pyr EPSP : LRN EPSP) and the Pyr segmental latency. It is suggested that this relation reflects the excitability level in the PNs.

Intracellular recording from C3-C4 PNs revealed disynaptic IPSPs evoked from higher motor centres and from forelimb afferents. Disynaptic pyramidal IPSPs were mediated mainly via local spinal inhibitory interneurones. Two different spinal inhibitory systems were disclosed. One system received convergence from cortico-, rubro-, tecto- and reticulospinal fibres and might give feed-forward inhibition. The other system which was strongly activated by cutaneous and/or muscle afferents may provide feed-back inhibition of the C3-C4 PNs.

A differential electromyographic (EMG) activity was recorded in the fast lateral (LaT) and slow medial (MeT) heads of triceps brachii during target reaching. MeT was tonically active during standing but became gradually less active during the extensor thrust preceding limb lifting. The converse pattern was found in LaT. During the protraction, LaT became strongly active while MeT was inactive or only weakly active. It is suggested that these differences in EMG reflect a differential control of fast and slow motor units.

Key words: Forelimb movement - Spinal cord lesions - C3-C4 propriospinal neurones - Motoneurones - LRN - Inhibition - EMG - Fast and slow muscles.

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CONTENTS

INTRODUCTION

Modern investigations of the neuronal organization of descending pathways began with Lloyd's study of pyramidal effects in the cat spinal cord (Lloyd 1941). He used the technique of conditioning monosynaptic test reflexes (Renshaw 1940) and showed that temporal facilitation was required to evoke pyramidal excitation in motoneurones suggesting that intercalated neurones mediated the effect. The same principal approach was used by Lundberg and Voorhoeve (1962) who recorded intracellularly from motoneurones and found facilitation from the sensorimotor cortex of excitatory and inhibitory segmental reflexes. It was shown that the interaction between corticospinal volleys and impulses from hindlimb afferents occurred in the interneurones mediating the reflexes to motoneurones. This was confirmed when Lundberg et al. (1962) recorded directly from interneurones and observed convergence from cortex and hindlimb afferents. However, it was difficult to assess the synaptic linkage from the corticospinal tract, because the temporal dispersion made measurements of the segmental latency uncertain. This was a major reason for Illert et al. (1976) to investigate cortico-motoneuronal effects in the forelimb segments, where the corticospinal volley is still rather synchronized. They observed a distinct EPSP with a segmental latency indicating a disynaptic linkage (Illert et al. 1976) and proceeded to analyse the location of the intercalated neurone (Illert et al. 1977). By making acute spinal cord transections of the cortico- and rubrospinal tracts at different levels, they could show that the disynaptic pyramidal and rubral EPSPs were relayed via propriospinal neurones (PNs) located in the third and fourth cervical segments (C3-C4 PNs) (Illert et al. 1977). The existence of such short PNs was verified by retrograde labelling of cell bodies located in the C3-C4 segments after small injections of horseradish peroxidase into the forelimb motor nuclei (Grant et al. 1980). The disynaptic pyramidal EPSP in forelimb motoneurones was then used as a test for studying convergence onto the C3-C4 PNs. With this indirect method Illert et al. (1977, 1981) demonstrated monosynaptic excitatory convergence onto the C3-C4 PNs from cortico, rubro-, tecto- and reticulospinal fibres and from low threshold cutaneous and group I muscle afferents. Pyramidal stimulation evoked not only excitation but also inhibition in forelimb motoneurones (Illert et al. 1976). Illert and Tanaka (1978) could show that at least part of this inhibition was trisynaptically mediated by C3-C4 PNs and the Ia inhibitory interneurones.

So far, the C3-C4 PNs were characterized indirectly by recording

from motoneurones. The analysis was continued by recording directly from candidate neurones in the C3-C4 segments. They were identified as PNs by antidromic stimulation of their axons in the ventral part of the lateral funicle in the forelimb segments (Illert et al. 1978). Monosynaptic excitation was found in the C3-C4 PNs from each of the systems giving facilitation of the disynaptic pyramidal EPSPs in motoneurones (Illert et al. 1978, 1981).

The broad convergence from several supraspinal centres and the periphery was interesting, and one aim of the present thesis was to use this propriospinal system as a model for investigating the role of pre-motoneuronal integration in motor control. Another important feature of the C3-C4 PNs is that they have an ascending axon collateral to the lateral reticular nucleus (LRN) (Illert and Lundberg 1978), which is a major mossy fibre input to the cerebellum (Corvaja et al. 1977, Hrycyshyn and Flumerfelt 1981). The ascending projection from the C3-C4 PNs to the LRN has now been systematically analysed and also used as a tool for investigating the propriospinal projection to forelimb motoneurones in more detail.

RESULTS

A. Functional role of the C3-C4 PNs (Paper I)

The C3-C4 PNs are effectively activated by impulses in the corticospinal and rubrospinal tracts (Illert et al. 1977, 1978). In order to study if a descending command is mediated via the C3-C4 PNs, a movement was used which is known to depend on the pyramidal (Górska and Sybirska 1980) and rubrospinal (Sybirska and Górska 1980) tracts. Cats were trained to make a single, swift forelimb movement to retrieve food after insertion of the paw into a narrow tube placed either horizontally at shoulder level or vertically on the floor. The movement consists of two major components: i) "the target-reaching movement"; limb lifting, directing the forepaw to the tube opening and inserting it into the tube, and ii) "the food-taking movement"; grasping a small morsel of food with the claws inside the tube, retracting the limb, supinating the forepaw and bringing the food to the mouth.

The cell bodies of the C3-C4 PNs are located outside the forelimb segments (C6-Th1) and their axons descend in the ventral part of the lateral funicle (VLF; Illert et al. 1977, 1978), whereas the cortico- and

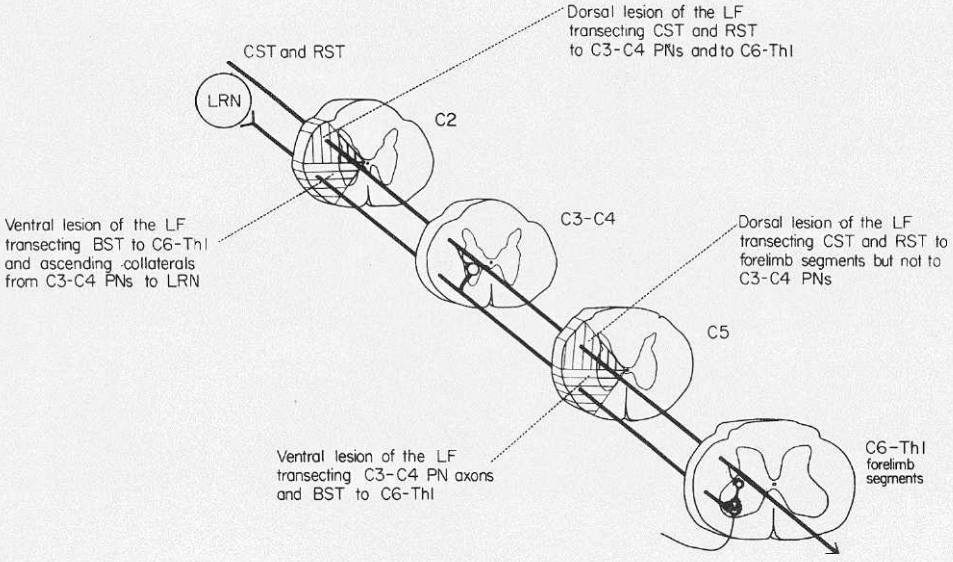

Fig. 1. Schematic drawing of the cervical cord showing the different lesions and the trajectories of the relevant fibre tracts. Abbreviations: corticospinal tract - CST; rubrospinal tracts - RST; bulbospinal tracts - BST; propriospinal neurone - PN; lateral reticular nucleus - LRN; lateral funicle - LF.

rubrospinal tracts descend in the dorsal part of the lateral funicle (DLF; Nyberg-Hansen 1966). It is thus possible to make differential spinal cord lesions, so that a command in the cortico- and rubrospinal tracts can be transmitted either via the C3-C4 PNs after a C5/C6 DLF transection or by the segmental interneuronal network after a C5/C6 VLF transection, which interrupts the axons of the C3-C4 PNs (Fig. 1). The cortico- and rubrospinal tracts could also be transected just rostral to the C3-C4 PNs (Fig. 1) interrupting the input both to the C3-C4 PNs and the segmental interneurones. After the latter lesion, the target-reaching and the food-taking movement were severely impaired indicating that the major pathways relaying these motor commands had been interrupted.

1. The target-reaching movement

Figure 2 A illustrates the movement after a C5/C6 DLF transection. The cat initiated limb lifting in a normal manner by a rapid accelerative movement. Thereafter, the speed declined during protraction, and finally the forepaw was smoothly inserted into the tube. Comparison with the normal

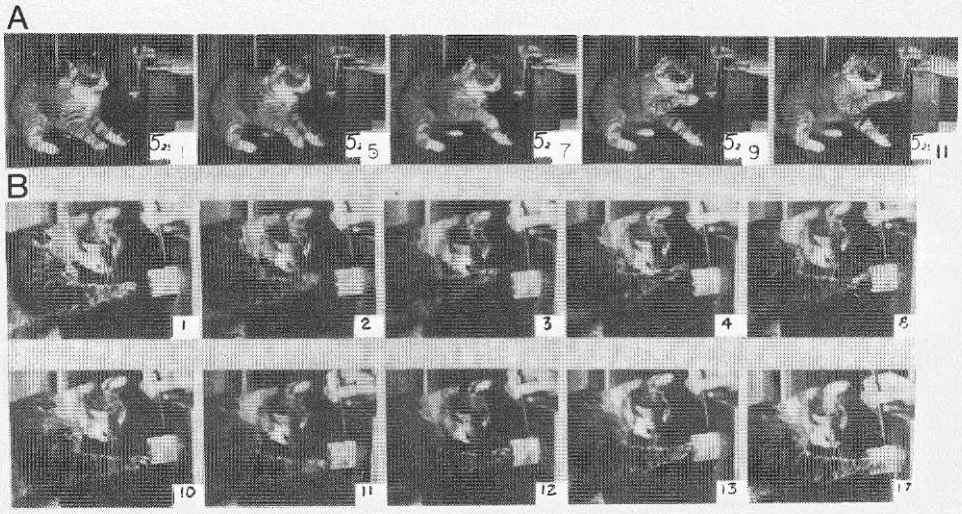

Fig. 2. Target-reaching movement. A, a cat with a C5/C6 DLF transection 8 days postoperatively. Moving film was always taken at 32 frames/s; frame number is indicated in each picture. Observe the precision in the reaching movement; the accurate timing of the wrist extension enabling the forepaw to be inserted in one swift movement. B shows target-reaching in a cat with a C5/C6 VLF lesion one month postoperatively. Limb lifting was initiated in a seemingly normal manner (not illustrated). Note the error in the trajectory of the reaching movement in frame 2, giving an overshoot. Corrective movement resulted in an undershoot (frame 10) before insertion (12-17).

cat revealed no defect in the target-reaching movement (see Fig. 1 in Paper I). However, after the C5/C6 VLF transection a clear deficit in aiming was discovered as shown in Fig. 2 B. The lifting movement started in a normal way (not illustrated), but before insertion of the forepaw into the tube, a quick upward deviation occurred followed by an undershoot. These movements appeared in any direction around the tube opening and were described as ataxia. It was not limited to this particular test situation but also occurred when the animal made a forelimb protraction to take a piece of food placed on a table without any spatial restrictions.

2. The food-taking movement

After a C5/C6 DLF transection the food-taking movement was lacking (early postoperative phase). The cats were unable to grasp the food but could use the claws passively, hooking and pressing the forepaw against the inside of the tube. Note in Fig. 3 A that the food drops from the tube.

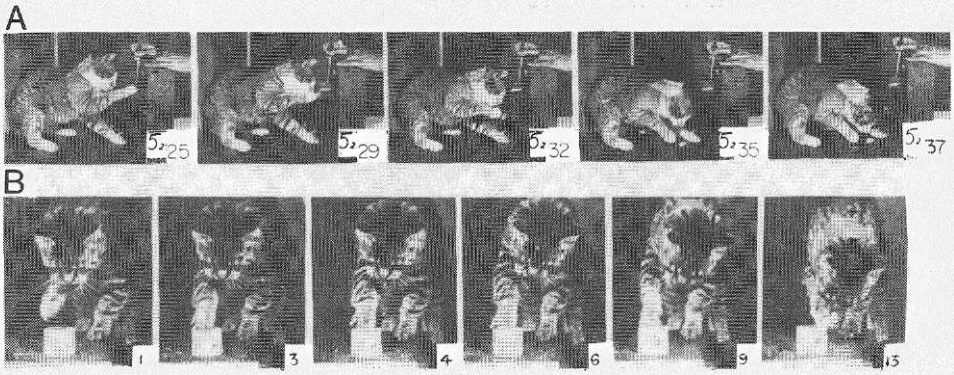

Fig. 3. Food-taking movement. A, same cat as in Fig. 2 A with a C5/C6 DLF lesion. Note the virtually complete loss of toe grasping and paw supination resulting in an inability of holding the morsel which dropped (frame 32) to the floor. B, same cat as in Fig. 2 B with a C5/C6 VLF transection. The morsel was grasped with toe flexion and brought to the mouth with the paw supinated. To maintain the position during grasping, the cats used their fifth toe to stabilize the paw (6).

Even when the food was hooked to the claws, the cats were unable to bring it to the mouth with the wrist in a supinated position. In contrast, the cats with a C5/C6 VLF transection could actively grasp and hold the food with the claws while bringing it to the mouth as shown in Fig. 3 B. Note also that the cat abducts the fifth toe and grips around the upper edge of the tube. This was observed in all the cats with a C5/C6 VLF transection but never in the normal animals. It is possible that this "new" strategy developed to prevent ataxia and to stabilize the paw during grasping.

Lesions were also made in the VLF at the C2/C3 level (Fig. 1) in order to determine if other ascending and descending fibres contribute to the deficit after the C5/C6 transection (cf. Discussion for the ascending collateral to the LRN from the C3-C4 PNs). No deficit at all was observed either in the target-reaching or in the food-taking movements.

B. Double projection of the C3-C4 PNs (Paper II)

1. Ascending projection to the LRN

The C3-C4 PNs have an ascending axon collateral to the LRN (Illert and Lundberg 1978 and Paper II). This projection was analysed by systematic tracking in and around the LRN searching for low threshold points and antidromic latency shifts as indicators of termination. Figure 4 A shows extracellular records of a PN activated at low threshold from two tracks both in and outside the LRN as indicated in Fig. 4 B. Note the latency increase from depth 3.5 to 4 mm (track b) and the stepwise change in latency with increasing stimulus intensity. The longitudinal extent of termination within the LRN is given for another PN in Fig. 4 C,D. It was activated at low threshold within the LRN at 2 mm caudal to obex, at obex and 1 mm rostral to obex, but not at 2 mm rostral to obex which is just rostral to the LRN.

The results showed that the stem axons of the C3-C4 PNs enter the LRN from a dorsomedial position in the caudal part of the nucleus and then terminate at several discrete levels within the entire nucleus.

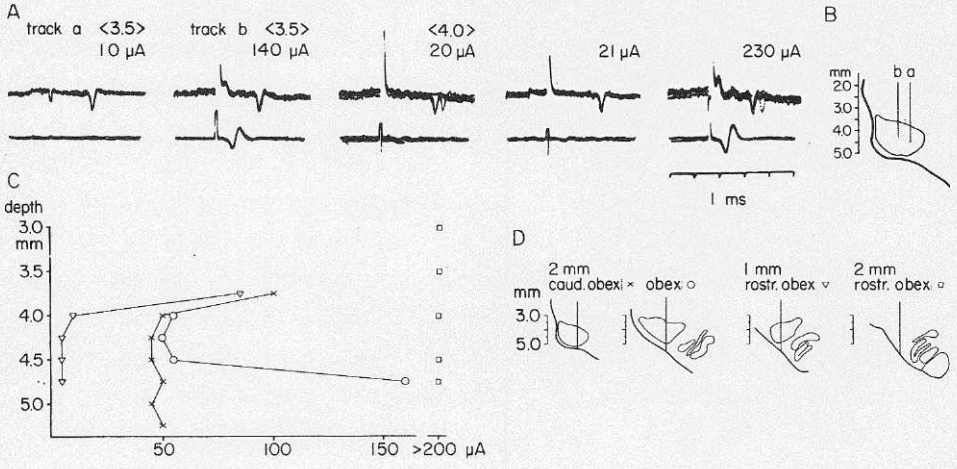

Fig. 4. Threshold mapping for antidromic activation of C3-C4 PNs from regions in and around the LRN. A,B, recordings from one PN during stimulation just dorsal to and within the LRN. Note at depth 4.0 mm in track b the stepwise change in latency with increasing stimulus strength. C and D are from another PN which could be activated at different levels in the LRN at low threshold but not from a position just rostral to the LRN.

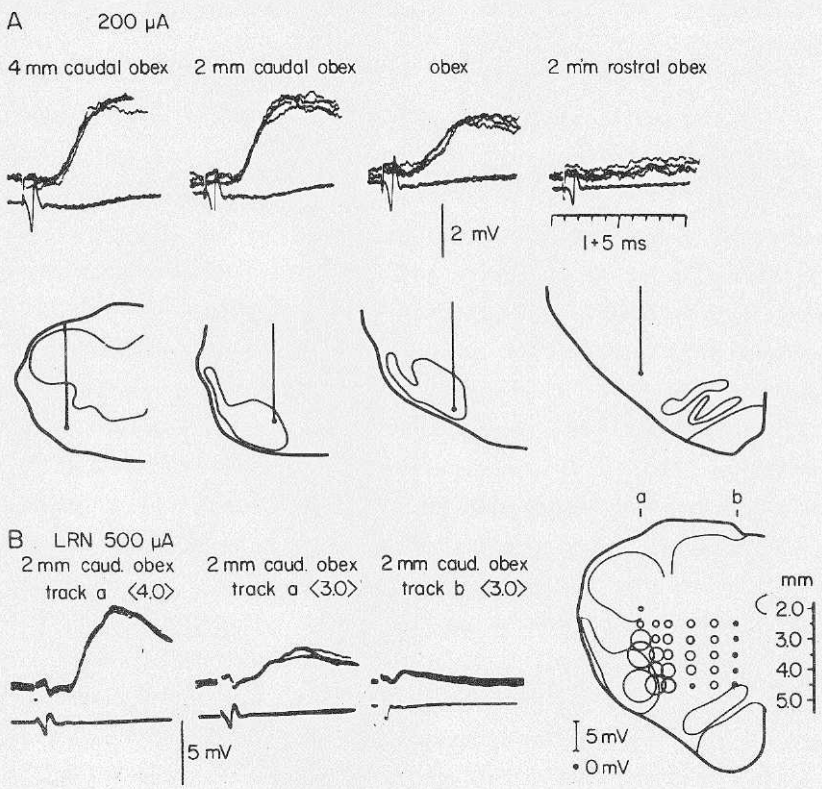

Fig. 5. Mapping of the monosynaptic LRN EPSP in forelimb motoneurones. A and B illustrate that the largest LRN EPSP could be evoked from the LRN but not dorsal, medial or rostral to it.

2. Effects in motoneurones by direct activation of the C3-C4 PNs in the LRN

Electrical stimulation in the LRN evokes a monosynaptic EPSP in forelimb motoneurones which presumably is mediated via the bifurcating axons of the C3-C4 PNs (Illert and Lundberg 1978, Papers II and III). Results of systematic tracking in and around the LRN are illustrated in Fig. 5. In one motoneurone (A), longitudinally spaced tracks showed that the largest EPSP was evoked from the caudal part of the LRN and that it gradually diminished rostrally and was virtually gone in a position just rostral to the nucleus. A transverse track (B) in the caudal part of the LRN revealed a dramatic decrease in size medially and dorsally. In track b, Fig. 5 B, a small monosynaptic EPSP was elicited, which has a short latency and duration. It is presumably mediated by fast reticulospinal fibres (Peterson et al. 1979).

C. Comparison of the projection from the C3-C4 PNs to fast and slow motoneurones (Paper III)

Tne next step in the analysis used the provisional assumption that the LRN EPSP is mediated exclusively via C3-C4 PNs and thus provides an indicator of the excitatory projection from C3-C4 PNs to forelimb motoneurones. Direct stimulation of the C3-C4 PNs has the advantage that a comparison of both quantitative and qualitative measurements can be made. In the case of synaptic activation of the C3-C4 PNs by pyramidal volleys, the synaptically evoked EPSPs in forelimb motoneurones are dependent on the excitability level in the intercalated neurones (see Section C:3). Experiments (Paper III) showed that it is possible to evoke a maximal or >90 % maximal LRN EPSP from a single stimulus position and that the LRN EPSP is not contaminated (due to stimulus escape) by another smaller monosynaptic EPSP from a medial system (Peterson et al. 1979).

1. Correlation of the LRN EPSP amplitude with motor unit type

Three types of motor units with different mechanical and histochemical properties have been distinguished (for review see Burke 1981): the fast and easily fatiguable (FF), the fast and fatigue resistant (FR) and the slow type (S). In motoneurones the amplitude of the homonymous group I EPSP, the input resistance and afterhyperpolarization (AHP) is positively correlated with motor unit type in the order S > FR > FF (cf. Burke 1981). In order to investigate the LRN EPSP in relation to motor unit type, a comparison was made with these parameters.

Three different motoneurones innervating the shoulder muscle infraspinatus are illustrated in Fig. 6 A-C, D-F and G-I. There appeared to be a correlation between the LRN EPSP and the homonymous group I EPSP. Both were largest in motoneurones with long AHP duration (A-C). These relationships are firmly established in the diagrams (Fig. 6 J-L) where the LRN EPSP amplitude is plotted versus the homonymous group I EPSP amplitude, the AHP duration and the input resistance, respectively. A clear positive correlation was found between the LRN EPSP amplitude and each of these parameters.

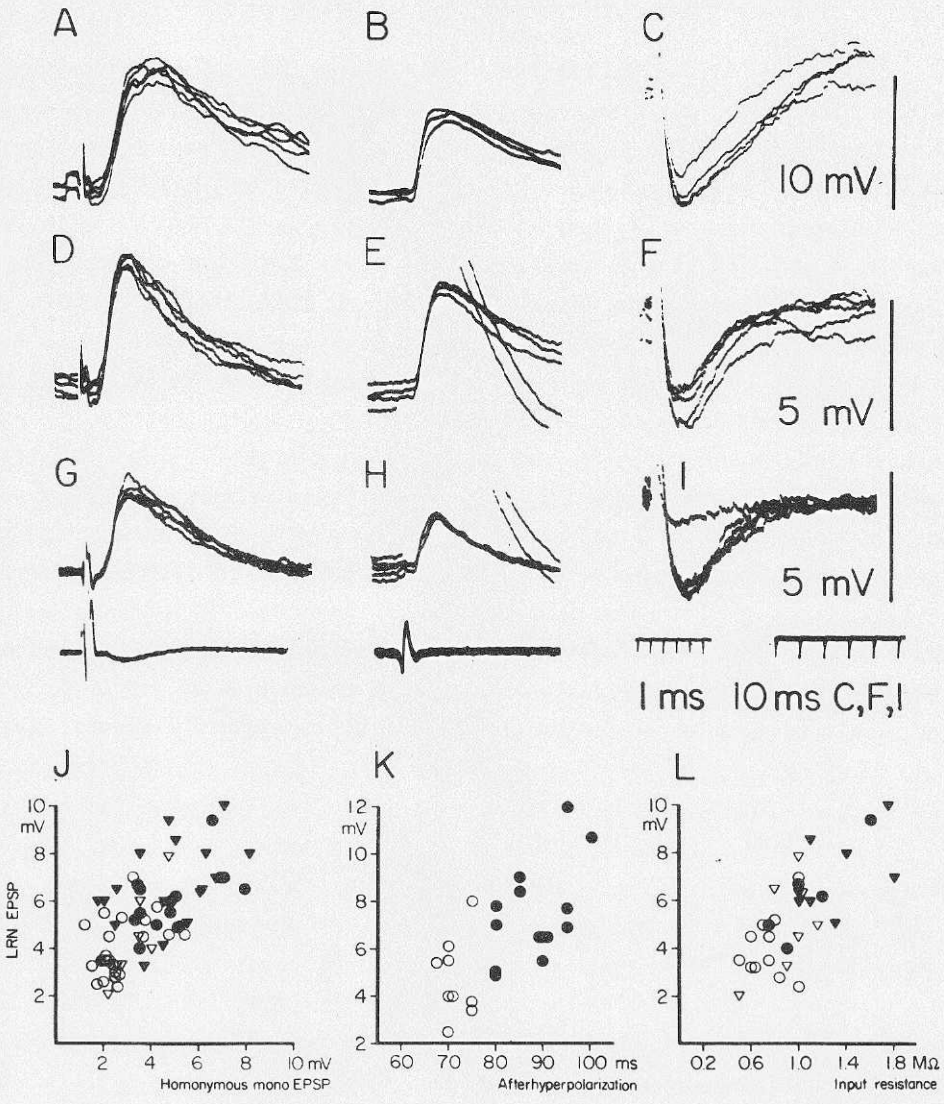

Fig. 6. Comparison of the LRN EPSP amplitude with motor unit type. Three different motoneurones (A-C, D-F and G-I) are shown for comparison of the LRN EPSP (A-G), homonymous group I EPSP (B-H) and AHP duration (C-I). A positive correlation for these parameters was obtained (I,K) and also for the input resistance (L). Filled symbols indicate slow motoneurones and open symbols fast motoneurones.

2. Comparison of the LRN EPSP time course; subgroups of PNs

Figure 7 A and B show the growth of the LRN EPSP with increasing stimulus intensity in a fast and a slow motoneurone, respectively. At weak stimulus intensity (20 µA) both EPSPs have about the same time-to-peak (Fig. 7 C), but with strong stimulus intensity (200, 500 µA) the EPSP in the slow motoneurone (B) had a longer overall duration. In the bottom records in Fig. 7 B several small humps can be seen in the rising phase. They might be mediated by fibres with different conduction velocities, as suggested from the results in Paper II (cf. Illert et al. 1978), where a wide range of conduction velocities was found for the double projecting C3-C4 PNs. It was shown that the relatively longer EPSP duration in slow versus fast motoneurones is not caused by additional di- or polysynaptic EPSPs or by the presence of IPSPs undercutting the EPSP in fast motoneurones. A possible contribution of different membrane time constants in fast and slow motoneurones cannot be ruled out (Burke 1968) but would certainly not explain the prolongation of the LRN EPSP with increasing stimulus strength (Fig. 7 C). An analysis of unitary LRN EPSPs suggested that there is no differential soma-dendritic termination of fibres to fast and slow motoneurones. In conjunction, the results strongly suggest that

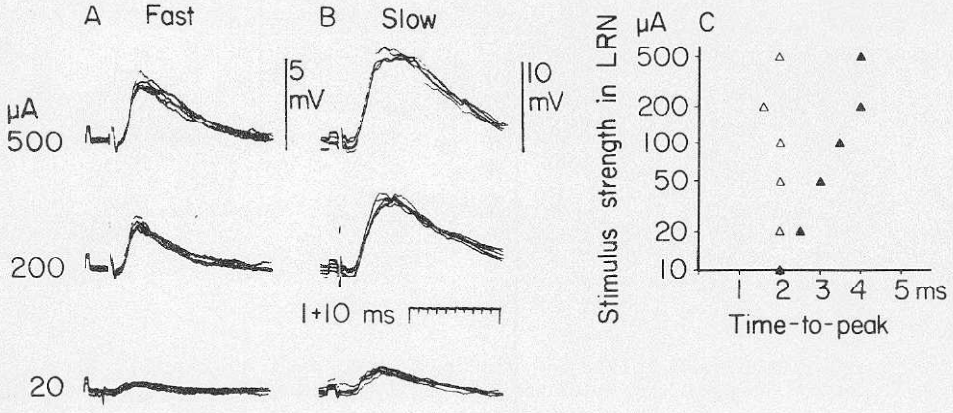

Fig. 7. Time course of the LRN EPSP in fast and slow motoneurones. Comparison between the fast (A) and slow (B) motoneurone revealed a considerably longer duration of the LRN EPSP in the latter at high stimulus strength (500 µA) but less so at weak intensity (20 µA). C shows measurements of time-to-peak for the slow (filled triangles) and fast (open triangles) motoneurone. Note the logarithmic ordinate.

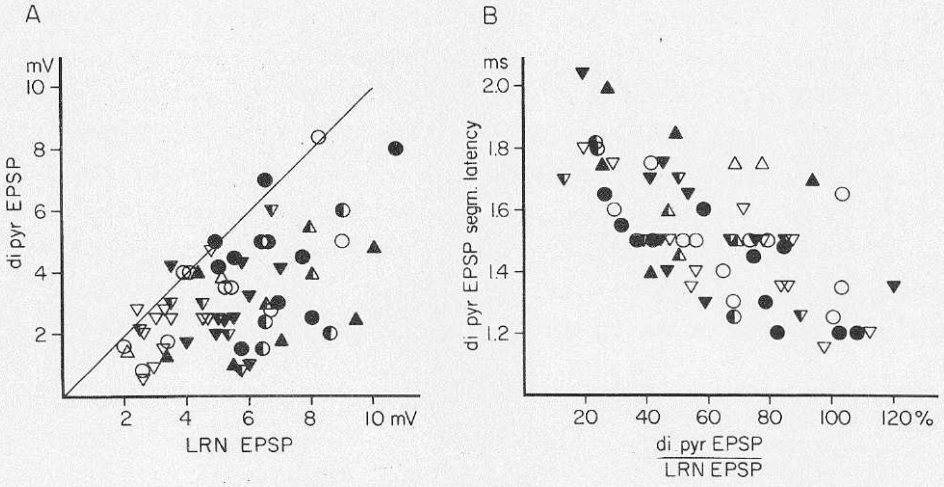

Fig. 8. Comparison of the disynaptic pyramidal EPSP and the LRN EPSP amplitudes in A. Their amplitude ratio is plotted versus the segmental latency of the disynaptic pyramidal EPSP showing a clear negative correlation. Filled and open symbols indicate slow and fast motoneurones, respectively. Half-filled symbols are used for unclassified motoneurones.

the LRN EPSP is composed of many small EPSPs mediated by PNs with different conduction velocities (Paper II). With weak stimulation the largest fibres are predominantly activated, while more slowly conducting fibres are activated with increasing strength thus giving the longer LRN EPSP duration in slow motoneurones.

It is postulated that fast PNs project both to fast and slow motoneurones, while slow PNs project predominantly to slow motoneurones.

3. Comparison of the disynaptic pyramidal EPSP and the LRN EPSP

Since C3-C4 PNs which project both to the LRN and to the forelimb segments are effectively activated by pyramidal volleys, it was suggested that these cells mediate disynaptic pyramidal EPSPs in forelimb motoneurones (Illert and Lundberg 1978). Thus, if all the C3-C4 PNs were activated by corticospinal volleys, the monosynaptic LRN and disynaptic pyramidal EPSPs would be expected to have the same amplitude. A direct comparison of the disynaptic pyramidal EPSP and the LRN EPSP is shown in Fig. 8 A. The same size was observed only in a few cases, while in the majority of cells the pyramidal EPSP was smaller than the LRN EPSP. The

amplitude of the disynaptic pyramidal EPSP is dependent on the excitability level in the C3-C4 PNs. Thus, the cases with a ratio of the disynaptic pyramdial EPSP : LRN EPSP less than 100 % might be explained by a reduced excitability level in the C3-C4 PNs. If so, it might be expected that also the time to firing in the C3-C4 PNs would be longer. The relationship between the segmental latency for the disynaptic pyramidal EPSP was therefore plotted versus the amplitude ratio disynaptic pyramidal EPSP : LRN EPSP as illustrated in Fig. 8 B. A clear negative correlation was obtained both for fast and slow motoneurones. It was proposed that low excitability might be due to inhibition.

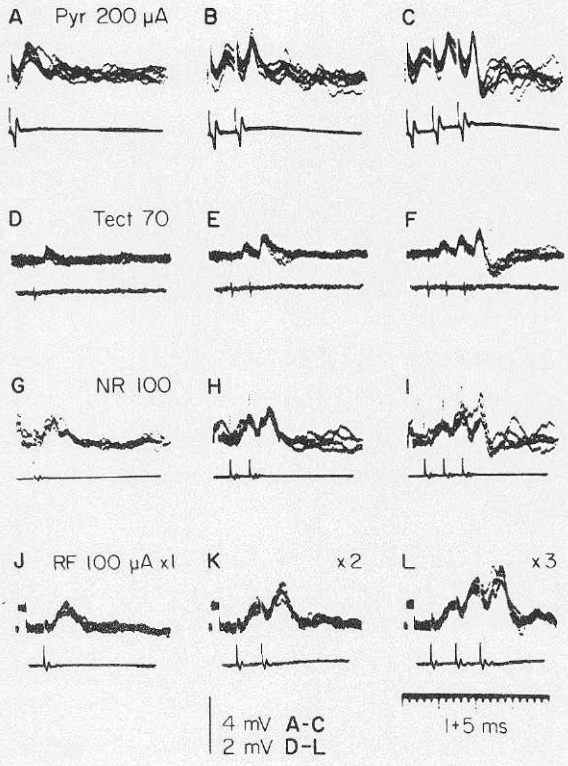

Fig. 9. Disynaptic inhibition from higher centres evoked in PNs. Note the marked temporal facilitation with increasing number of volleys. Abbreviations: pyramid - Pyr; tectum - Tect; nucleus ruber - NR and reticular formation - RF.

D. Inhibitory control of C3-C4 PNs from descending pathways and forelimb afferents (Paper IV)

In a previous study (Illert et al. 1978) intracellular recordings from C3-C4 PNs revealed that they receive monosynaptic excitation from the cortico-, rubro-, tecto- and reticulospinal tracts and from low threshold muscle and cutaneous forelimb afferents. It was also found that these systems could inhibit the C3-C4 PNs (Illert et al. 1975, Lundberg 1979). The different inhibitory pathways controlling the C3-C4 PNs have now been analysed systematically.

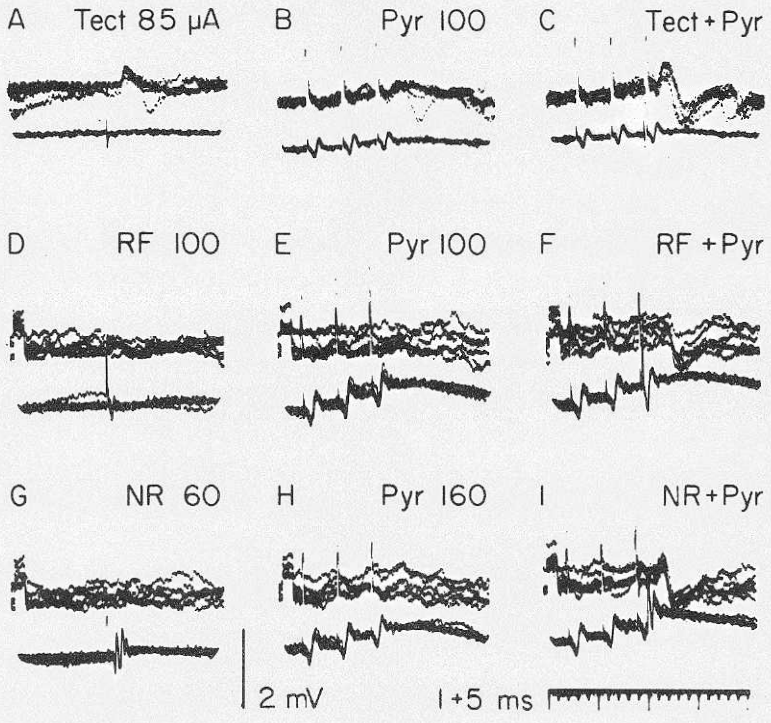

Fig. 10. Convergence from descending tracts onto the inhibitory interneurones mediating the disynaptic inhibition in C3-C4 PNs. The testing pyramidal stimulation (B,E,H) and the respective conditioning stimuli (A,D,G) gave virtually no inhibition, while combining the two (C,F,I) revealed a marked inhibition.

1. Inhibition from descending pathways

Figure 9 shows examples of disynaptic IPSPs in different C3-C4 PNs evoked from the corticospinal (A-C), tectospinal (D-F), rubrospinal (G-I) and reticulospinal (J-L) tracts. Note that a train of stimuli was required to evoke the disynaptic IPSP. Usually, the third volley was the effective one. A monosynaptic EPSP was evoked by each stimulus confirming the earlier work by Illert et al. (1978).

After a corticospinal transection at C2, stimulation of the pyramid only occasionally evoked disynaptic IPSPs in the C3-C4 PNs. These IPSPs had much smaller amplitudes than those obtained before the lesion. The findings suggest the existence of two inhibitory cortico-propriospinal pathways; one via medullary reticulospinal neurones (Illert et al. 1981) and another via spinal inhibitory interneurones. Because of the pronounced decrease in IPSP amplitude after the C2 transection, it is suggested that the inhibitory pathway via spinal inhibitory interneurones is quantitatively much more effective. Since the latencies of the pyramidal IPSPs are so brief, it is postulated that the spinal inhibitory interneurones are not located in the forelimb segments but rather locally in the C3-C4 segments.

The possibility that the descending systems converge onto the same inhibitory interneurones was also investigated (Fig. 10). Pyramidal stimulation was used as a test (B,E,H) and adjusted in strength to give no or a very small disynaptic IPSP in the PNs. A pronounced spatial facilitation was elicited from the tectospinal (A,C), reticulospinal (D,F) and rubrospinal (G,I) fibres. It was therefore postulated that the inhibitory systems with descending convergence give feed-forward inhibition of the C3-C4 PNs.

2. Inhibition from forelimb afferents

The disynaptic IPSPs evoked from cutaneous afferents were often evoked by a single stimulus (Fig. 11 A-C) and did not change with repetitive stimulation. By contrast, disynaptic IPSPs produced by muscle afferents often required a train of stimuli (Fig. 11 D-F) and showed marked temporal facilitation.

Convergence on the inhibitory interneurones was demonstrated for muscle (Tri) and cutaneous afferents (SR) (Fig. 11 G-I) and between a mixed nerve (median; Med) and the pyramid (Fig. 11 J-L). However, it was a consistent finding that facilitation from the nerves of the disynaptic IPSP evoked from tectum and nucleus ruber was only very weak or lacking. For

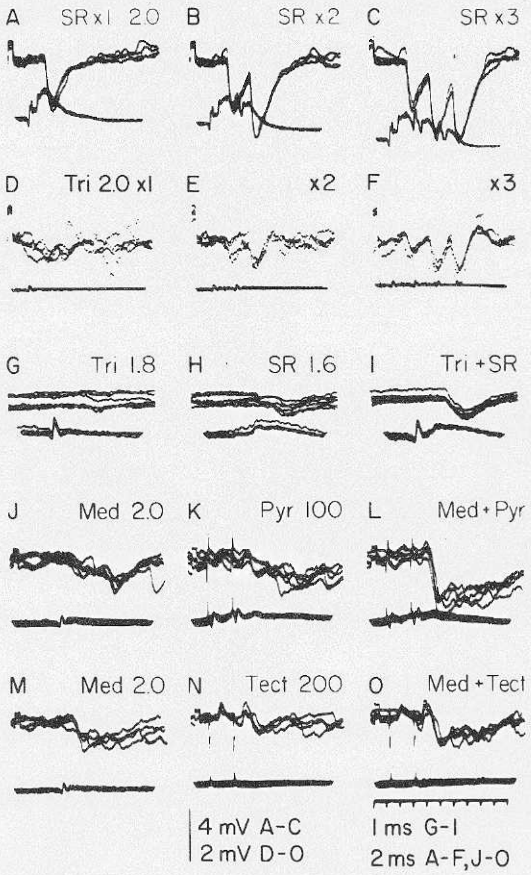

Fig. 11. A-F, disynaptic inhibition from forelimb afferents evoked in PNs. In A-C is illustrated a strong linkage from a cutaneous nerve (superficial radial - SR) which gave almost no temporal facilitation, while in D-F stimulation of a muscle nerve (triceps - Tri) revealed a clear temporal facilitation. Convergence between SR and Tri is presented in G-I and between the mixed nerve (median - Med) and the pyramid in J-L. However, no clear facilitation was obtained of the tectal IPSP from Med (M-O) which was recorded from the same PN as in J-L. See text.

comparison, the effect from the mixed nerve (Med) was tested both for the disynaptic IPSP evoked from the pyramid (Fig. 11 J-L) and tectum (Fig. 11 M-O) in the same PN. Because of the convergence pattern, it was postulated that the disynaptic inhibition from forelimb afferents is mediated by a special system of inhibitory interneurones and provides feed-back inhibition of the C3-C4 PNs. However, even though these inhibitory interneurones are strongly activated by impulses from forelimb afferents, they are also under some descending control from corticospinal fibres.

E. EMG activity in fast and slow elbow extensors during target reaching (Paper V)

It was shown by Illert et al. (1976) and also in Paper II that fast triceps motoneurones receive predominantly pyramidal excitation, while slow triceps motoneurones receive mainly mixed excitation-inhibition or dominating inhibition. It was therefore of interest to study if differences exist in the activation pattern between the fast lateral head (LaT) and the slow medial head (MeT) of triceps (Collatos et al. 1977).

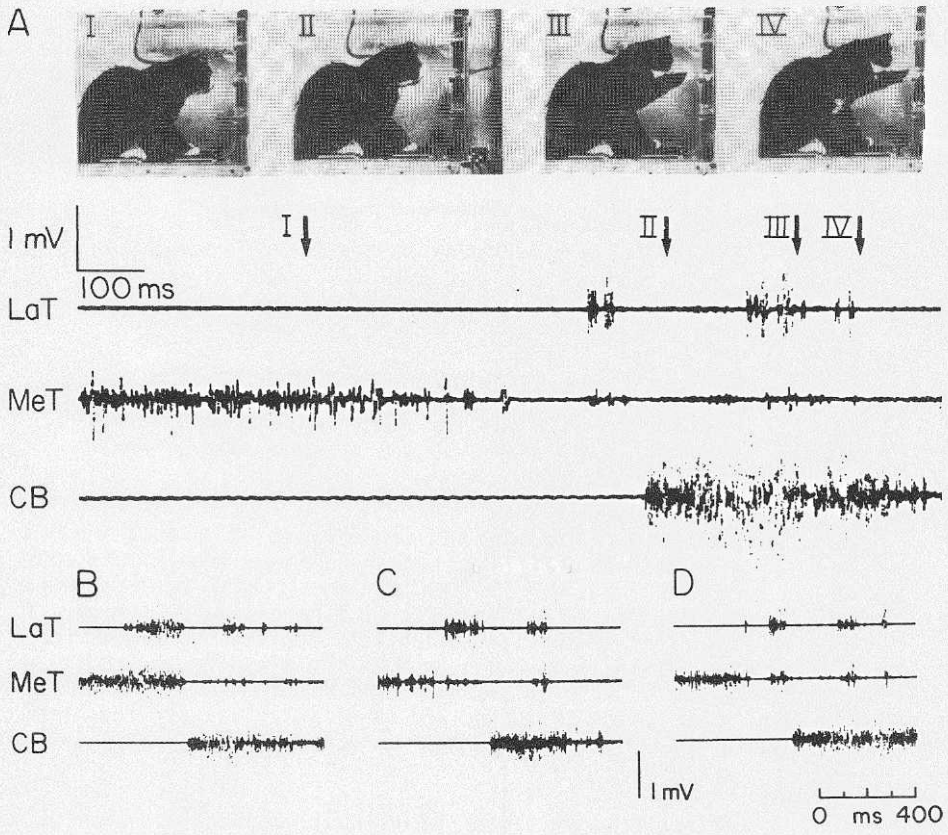

Fig. 12. EMG activity recorded from elbow extensors (LaT and MeT) and an elbow flexor (CB) during target-reaching. The usual differential activity pattern in LaT and MeT is shown in A. Labelled arrows refer to the pictures above. Less common patterns of EMG activity are illustrated in B-D. See text.

The most frequently observed pattern of EMG activity is shown in Fig. 12 A. During quiet standing MeT was tonically active while LaT was completely inactive. Just before limb lifting, the activity in MeT decreased, while an intense burst of activity appeared in LaT. The activity in LaT stopped abruptly upon activation of the elbow flexor cleidobrachialis (CB) but recurred when the limb had reached the tube level and started to protract toward the tube opening. Almost no activity was observed in MeT during the entire target-reaching movement. However, while the pattern for the fast LaT seemed to be fixed, several variations were observed for the slow MeT as illustrated in Fig. 12 B-D. In B, the activity in MeT did not cease prior to lifting but was instead present in parallel with LaT. Figure 12 C shows a second period of activity in MeT during the protractive phase and in D, a parallel activity in MeT and LaT just before lifting and during protraction. It is not known whether these less common patterns in MeT represent activity in slow motor units or in some of the few fast motor units. In some cases the cat failed to insert the forepaw in one swift movement but made several protracting movements outside the tube opening. Repeated sequences of activity then occurred both in LaT and MeT which appeared to be time-locked to each new protraction of the forepaw toward the tube (Alstermark and Sasaki, unpublished observations).

GENERAL DISCUSSION

1. Functional aspects of neuronal organization

The C3-C4 PNs are characterized by extensive projection from descending tracts (cortico-, rubro-, tecto-, and reticulospinal) and from low threshold cutaneous and muscle afferents from the forelimb (Illert et al. 1978). However, they do not seem to receive projection from vestibulospinal fibres or from neck afferents (Alstermark, Lundberg and Sasaki, unpublished observations). It was postulated earlier that convergence from supraspinal motor centres and forelimb afferents at a pre-motoneuronal level is advantageous, since it allows for an idependent control without interferring with other pathways acting on the motoneurones (Illert et al. 1977). This idea originates from Sherrington (1906) who discussed the internuncial pathway also as a common pathway and only used the term "final common pathway" for motoneurones in the sense that it represented the "highest degree of communism".

The major point of the investigation in Paper I was to study if a descending command for a voluntary movement can be relayed in the C3-C4 segments. The most relevant lesions are those made in the DLF at the C2/C3 and the C5/C6 levels. The food-taking movement was absent after both lesions, while target reaching was severely impaired after the former lesion but executed normally after the latter lesion. The results suggest that a descending command for target reaching can be mediated by the C3-C4 PNs. This is the first interneuronal system in the spinal cord to which a command-mediating function has been linked. Accordingly, the C3-C4 PNs provide an interesting model for correlation of neuronal organization and function. One of the interesting features of the C3-C4 PNs is the broad convergence from descending tracts and forelimb afferents. It was proposed that some of the convergent systems may function to "up-date" the descending command at a pre-motoneuronal level (Illert et al. 1977). It is now desirable to test this hypothesis in behavioural experiments. For example, cats have been trained to execute target reaching to one of several tubes. During an ongoing movement they can use a visual cue to make a rapid change of the trajectory to another tube (Alstermark, Gorska, Johannisson and Lundberg, unpublished). This test may be used to investigate the role of tectospinal control of the C3-C4 PNs.

The food-taking movement disappeared after a complete transection of the cortico- and rubrospinal tracts at C5/C6 which shows that this movement is not primarily governed by C3-C4 PNs but by interneuronal

systems in the forelimb segments. Even after a complete transection of the cortico- and rubrospinal tracts at C5/C6, some recovery of the food-taking movement occurred 4-6 weeks postoperatively. It is likely that the main control of the food-taking movement is exerted by corticospinal fibres, but rubrospinal and to some extent reticulospinal fibres may also contribute. A much earlier and more complete recovery appeared in one cat in which a substantial part (60 %) of the rubrospinal fibres was spared. This finding has been confirmed in several other cats with incomplete rubrospinal lesions (Alstermark, Górska, Johannisson and Lundberg, unpublished). It was striking that the onset of recovery for both grasping and supination started at the same time and that both components appeared together in one sequence indicating a common control, which was ascribed to reticulospinal fibres.

Górska and Sybirska (1980) found that the food-taking movement was absent not only after a pyramidal transection at the level of the trapezoid body but also after a lesion in the red nucleus (Sybirska and Górska 1980). Since the same tests and training procedures were used both in their studies and in Paper I, it is puzzling why in the former case neither the rubro- nor the corticospinal tract could compensate for the loss of the other, while in the latter study a marked recovery was found even with a partly lesioned rubrospinal tract.

The target-reaching movement was always preceded or accompanied by an orienting head movement. However, the C3-C4 PNs do not influence neck motoneurones, which are instead strongly controlled by medullary reticulospinal neurones (Alstermark et al. 1983). Thus, the different components of the overall movement appear to be controlled by different neuronal circuitries: head orientation via reticulospinal neurones, target reaching via C3-C4 PNs and food-taking via segmental interneurones. How, then, does the central nervous system coordinate the movement? One possibility could be that the same corticofugal fibres control these functionally different circuits by collateral action. Illert et al. (1977) showed that collaterals to C3-C4 PNs are given off from cortico- and rubrospinal fibres projecting down to the forelimb segments. Furthermore, it seems likely that the corticoreticular fibres, activating the reticulospinal neurones to neck motoneurones, are also collaterals from corticospinal fibres (Alstermark et al. 1983). However, such a simple model with a common command signal is unsatisfactory, since it does not easily allow for the sequential movement pattern with a high degree of independence of the three components.

2. Comparison with other propriospinal systems

From a functional point of view, it is of interest to compare different propriospinal systems. Short PNs located in the L3-L6 segments projecting to lower lumbar segments have been identified (Vasilenko et al. 1972). Possibly, some of them receive monosynaptic cortico- and rubrospinal excitation, but in most, a temporal facilitation was found indicating that intercalated neurones mediate the effect. Kozhanov and Shapovalov (1977) recorded from L3-L4 descending PNs and found monosynaptic excitation from vestibulo- and reticulospinal fibres but not from corticospinal fibres. Presumably, the lumbar PNs are not functionally equivalent to the C3-C4 PNs. However, Kozhanov and Shapovalov (1977) also recorded from short PNs in L3-L4 segments in monkeys and found there monosynaptic corticospinal excitation. This connexion might have evolved to subserve an increased motor repertoire in the hindlimbs.

Recent experiments have confirmed the existence of long PNs in the C3-C4 segments (Illert et al. 1978, Alstermark, Lundberg, Pinter and Sasaki, unpublished). They are located in laminae VII-VIII and project ipsilaterally or contralaterally (after cervical crossing) down to lumbar segments. In addition to monosynaptic excitation from cortico-, rubro-, tecto- and reticulospinal inputs, which they have in common with the short C3-C4 PNs, they are also monosynaptically excited from the medial and lateral vestibular nuclei. It is tentatively proposed that the long C3-C4 PNs may produce postural adjustments in the hindlimbs during a target-reaching movement by a parallel command from the motor centres governing the short C3-C4 PNs.

Other PNs, also under supraspinal control (Skinner and Remmel 1980), take origin in the forelimb segments, and some have monosynaptic and disynaptic connexions with hindlimb motoneurones (Jankowska et al. 1974, 1983). It was also shown that long forelimb PNs are effectively activated by forelimb afferents (Schomburg et al. 1978), a feature not found in the C3-C4 PNs (Illert et al. 1978). Similarly, long ascending PNs from lumbar segments activated by hindlimb afferents evoke effects in forelimb motoneurones (Miller et al. 1973). These long descending and ascending PNs from the limb segments are considered to regulate interlimb co-ordination during rhythmic activity as was first described by Sherrington and Laslett (1903) in the scratch reflex.

3. The information to the LRN from the C3-C4 PNs

The LRN receives via the ascending axon collateral from the C3-C4 PNs an "efferent copy" of the activity which reaches the motoneurones. Illert and Lundberg (1978) proposed that this feed-back information may allow the cerebellum to produce fast corrections of the activity in the C3-C4 PNs (Illert et al. 1977). It is not known how this ascending information is processed in LRN or the cerebellum, but it is noteworthy that a C2/C3 VLF transection interrupting the ascending collateral to the LRN gave no deficit in target reaching (Paper I). A negative finding like this is not conclusive, and a detailed analysis might be required to detect minor changes in the movement. However, one possibility could be that the ascending information is needed primarily during learning and that highly trained animals can perform without cerebellar feed-back corrections.

It is of interest to compare ascending connexions from different spinal motor centres to the cerebellum. Figure 13 A shows how the last-order interneurone via a short collateral may influence an ascending neurone projecting directly to the cerebellum. Such connexion has been

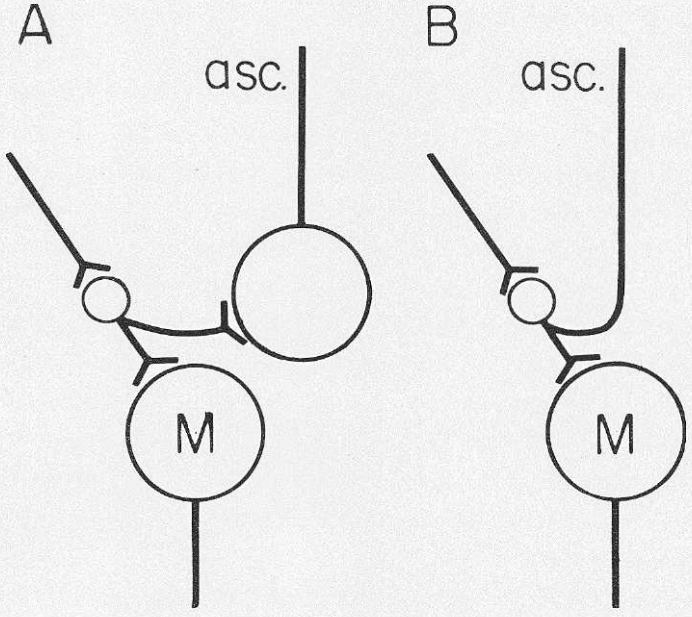

Fig. 13. Two modes of connexions which allow ascending pathways to convey information about intrinsic spinal activity, in the case illustrated from last-order interneurones projecting directly to motoneurones (M).

proven for the Ia inhibitory interneurones to the ventral spinocerebellar tract neurones (VSCT; Gustafsson and Lindström 1973). A detailed investigation of input patterns to VSCT neurones have suggested a highly complex organization, indicating the existence of a multitude of VSCT neurones receiving input from many different interneuronal systems also projecting to motoneurones (Lundberg and Weight 1971). The alternative in B is represented by the C3-C4 PNs with a long ascending collateral to the LRN which in turn projects to the cerebellum. It can be argued whether or not these two examples (A,B) in fact represent principally different ways for conveying ascending information, since in case B the ascending collaterals from the C3-C4 PNs also contact a relay neurone which projects directly to the cerebellum. The relevant comparison might instead be between the LRN and VSCT neurones. It cannot be excluded that integration in the LRN is as complex as in the VSCT. In fact, it has been pointed out that the bVFRT-LRN neurones have several properties in common with the VSCT system (Clendenin et al. 1974). A functional similarity is also indicated by the rhythmic activity observed both in VSCT and bVFRT-LRN neurones during fictitious scratching (Arshavsky et al. 1978a,b).

4. Possible mechanisms for ataxia

After the C5/C6 VLF transection, the cats could lift and protract the limb but could not guide the forepaw accurately to the target. Instead, ataxic movements appeared before the animal succeeded to insert the forepaw into the tube. Since no ataxia was observed after a C2/C3 VLF transection, it was suggested that the ataxic movements were caused by the interruption of the C3-C4 PN axons. However, it would be desirable to repeat the experiments with more restricted C5/C6 VLF lesions. With time, the ataxia decreased both in amplitude and frequency of occurrence but could easily be made to reappear by changing the target position. No complete recovery during the entire postoperative period (5.5-9 months) was found. The ataxia did not resemble the type observed by Gilman et al. (1976) after cerebellar ablation or deafferentation which had a higher frequency and occurred during the whole movement.

The mechanism for the ataxia is unknown but two possibilities will be considered. In Paper III it was found that the projection of C3-C4 PNs was correlated with motor unit type and suggested that two special subgroups of PNs project to slow motoneurones. It was also proposed that these subgroups might be of particular importance in controlling precise positioning during aiming. If so, the explanation for the ataxia after the

C5/C6 VLF lesion might be faulty recruitment of motor unit types during aiming. For example, when only small adjustments in force are needed, some large tension, fast units might be erroneously activated causing ataxic movements.

In the discussion of Paper I it was proposed that after the C5/C6 VLF transection, the C3-C4 PNs might be protected from degeneration because of the intact ascending collateral to LRN (Brodal 1981 and Paper I). As a consequence, the cerebellum still receives feed-back information about the activity in the C3-C4 PNs even if they do not influence the forelimb motoneurones. One possibility could be that this mismatch in afferent-efferent information might lead the cerebellum to produce erroneous corrections which appear as ataxia. This hypothesis is testable since transection of the ascending collaterals would remove the false feed-back information.

5. Feed-forward inhibition

In Paper IV it was shown that each of the descending systems giving monosynaptic excitation in C3-C4 PNs (Illert et al. 1975, 1978) also evoke disynaptic inhibition. Spatial facilitation of the disynaptic IPSP in C3-C4 PNs showed similar convergence from descending fibres onto the inhibitory interneurones as for the C3-C4 PNs. Because of this parallelism in the control, it seems likely that the inhibitory line can provide feed-forward inhibition of PNs not required in a certain movement or part of a movement. Such feed-forward inhibition may not be restricted to different sets of PNs projecting to various motoneurone combinations (discussed in Paper IV) but could also be related to the control of the groups of PNs (Paper III) which project differentially to fast and slow motoneurones. In respect to the latter possibility, it is interesting that a differential activation was observed in fast and slow elbow extensor muscles during target reaching (Paper V). The fast LaT was usually completely inactive during the preceding stance but became briskly activated just before limb lifting and a second time during protraction. Conversely, the slow MeT was tonically active during standing but inactive just prior to limb lifting.

6. Feed-back inhibition

Only about half of the C3-C4 PNs receive monosynaptic excitatory input from primary forelimb afferents (Illert et al. 1978). This excitation is weak in comparison with the descending excitation. In contrast, all of the C3-C4 PNs receive a strong disynaptic inhibition from different nerves (Paper IV) which was often evoked by a single stimulus showing strong linkage to the inhibitory interneurones. These inhibitory interneurones appear to be governed mainly by forelimb afferents but are also controlled from the corticospinal tract. It is suggested that they may give feed-back inhibition of the C3-C4 PNs during a movement. Since the inhibitory interneurones are activated by primary afferents in the dorsal column, it is possible to test their contribution during the target-reaching movement. Experiments in progress (Alstermark, Górska, Johannisson and Lundberg) have shown a dramatic deficit after a combined transection of the DLF and the dorsal column at C5/C6. Instead of performing one swift target-reaching movement (observed after the C5/C6 DLF lesion alone; Paper I) into the tube, the cat persistently overshot the tube opening.

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