

PATTERN OF MONOSYNAPTIC Ia CONNECTIONS IN THE CAT FORELIMB

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SUMMARY

1. In anaesthetized cats intracellular records were obtained from antidromically identified motoneurons. The motor nuclei to the elbow extensor and flexor muscles and to the muscles innervated by the deep radial, ulnar and median nerves were investigated. The maximum Ia EPSPs from electrical stimulation of various peripheral nerves were measured. The characteristic convergence and projection patterns to each motor nucleus were established from pooled data.

2. The total aggregates of the Ia EPSPs between the different motor nuclei ranged from 3.5 to 11.7 mV. The smallest aggregates were found in the nuclei to the digit muscles. The ratio of the heteronymous *versus* homonymous EPSP amplitudes varied between 3.9 and 0.5. A general rule which would govern the distribution of the EPSP aggregates, such as a proximo-distal gradient, was not observed.

3. The Ia connections followed a complex but highly organized pattern. Bidirectional and unidirectional pathways were present. In many cases the convergence pattern of a motor nucleus included muscles acting at different joints. The connections of one nucleus were not necessarily restricted to one side of the limb, but could cross the radio-ulnar plane.

4. Muscles with similar actions onto the same joint were interconnected with bidirectional, rather balanced Ia pathways. Such relations were also present between close functional synergists and then often extended across several joints. The relations between the anatomical extensors of wrist and digits were graded according to the neighbourhood of these muscles. It is suggested that this reflects the graded mechanical synergism in the wrist action of these muscles.

5. A large number of unidirectional or strongly skewed bidirectional Ia pathways project from proximal to distal muscles. It is suggested that they may serve a readjustment of distal joints during changes in the position of proximal ones (e.g. stabilization of the position of the radio-ulnar plane during elbow extension in case of the unidirectional projections onto supinator and abductor pollicis longus motoneurons).

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6. The motor nuclei to some multifunctional muscles display a negative correlation between different heteronymous Ia inputs: motoneurons with a large input from one muscle show a significant tendency to receive a smaller input from another muscle and vice versa. This organization leads to subpopulations of neurones with different convergence patterns within the same motor nucleus.

7. Motor nuclei with bidirectional Ia relations between each other displayed similar convergence and projection patterns. They were combined into 'Ia synergistic groups'. One motor nucleus may belong to several groups. The groups are discussed in relation to co-activation patterns of forelimb muscles in motor behaviour. It is suggested that many of the muscular synergies which are necessary for the differentiated use of the cat forelimb are matched by corresponding patterns of Ia connections.

INTRODUCTION

Primary muscle spindle afferents (Ia afferents) have monosynaptic connections with the α -motoneurons of the receptor-bearing muscle (homonymous projection) and with motor nuclei innervating mechanical or functional synergists (heteronymous projection). These pathways transmit length signals from the peripheral receptor apparatus to the central nervous system, thereby supplying balanced and co-ordinated excitation to distinct groups of motoneurons. Besides their contribution to reflex adjustments of limb position, they may support execution of central motor commands, since the transmitted length signal is, via the γ -motoneurons, controlled from the brain (reviewed by Hulliger, 1984).

Organization of the Ia pathways has been extensively investigated in the hindlimb of cat (Lloyd, 1946*a, b*; Eccles, Eccles & Lundberg, 1957; Eccles & Lundberg, 1958) and monkey (Hongo, Lundberg, Phillips & Thompson, 1984). Strong Ia connections are present between muscles acting in the same direction on a common joint (Lloyd, 1946*a, b*). Muscles working together at different joints as either physiological flexors or extensors may also be Ia interconnected (Eccles *et al.* 1957; Eccles & Lundberg, 1958). These findings have led to the hypothesis that the Ia connections of the cat hindlimb have developed to assist locomotion (Eccles & Lundberg, 1958; Engberg & Lundberg, 1969; Lundberg, 1969).

Despite several studies on the Ia connections of the cat and monkey forelimb (Clough, Kernell & Phillips, 1968; Eccles *et al.* 1957; Eccles & Lundberg, 1958; Schmidt & Willis 1963; Willis, Tate, Ashworth & Willis, 1966) our knowledge on their organization has remained superficial. This is a drawback since the upper extremity receives increasing interest in current research on motor control. To understand the organization of forelimb movements it is necessary to have complete knowledge of the architecture of the Ia connections. There is the equally important and more general aspect that fore- and hindlimb differ in their mechanical capabilities. Knowledge of the Ia pathways would allow conclusions to what extent different mechanical requirements find a correlate in the Ia system.

In this study a detailed analysis was performed on the pattern of monosynaptic Ia connections in the cat forelimb. Part I will describe the connections between elbow flexors, elbow extensors and muscles supplied by the deep radial nerve (DR); Part II the pathways from the median (M) and ulnar (U) muscles. It will be discussed how

the Ia pattern can support the mechanical capability of the forelimb and assist the control of complex movements at joints with several degrees of freedom. Preliminary results have been published in abstract form (Fritz, Illert & Saggau, 1978*a, b*, 1981; Fritz & Illert, 1981; Fritz, Illert, de la Motte & Reeh, 1984). The complete material has been published in form of two theses (Fritz, 1981; de la Motte, 1988).

METHODS

Two separate series of experiments were performed which will be reported as part I and part II. In the first series (N.F., M.I., P.S.) surgery was performed on twenty-four cats under ether; the animals were subsequently anaesthetized with α -chloralose (40–60 mg kg⁻¹ i.v.). The second series (N.F., M.I., S.d.I.M., P.R.) consisted of twenty-one cats. In nine cats, where the connections between the distally located median and ulnar muscles were analysed, barbiturate anaesthesia (40 mg kg⁻¹ i.p.) was used, since it resulted in more stable conditions during the time-consuming nerve dissections. The remaining twelve cats were used in an investigation of the more proximal muscles; surgery was performed under ether and the animals were subsequently anaesthetized with α -chloralose (40–60 mg kg⁻¹). In both series gallamine triethiodide was given during intracellular recording and the respiration was then artificially maintained. The end-expiratory CO₂ concentration was kept between 3.5 and 5.0 pCO₂. A pneumothorax was performed. The depth of anaesthesia was monitored by the degree of pupillary constriction. Small doses of Nembutal (5 mg kg⁻¹ i.p.) or Thiopental (2.5 mg i.v.) were added when necessary. The arterial blood pressure was monitored and, when necessary, maintained above 80 mmHg by i.v. infusion of a nor-adrenaline-dextran solution. The rectal temperature was kept between 36 and 38 °C.

The nerves listed in Table 1 were dissected in the left forelimb and cut distally. Figure 1 shows origin and insertion of the respective muscles. In part I all indicated nerves were dissected and stimulated in one and the same experiment; in part II, where this was not possible because of the large number of nerves, different combinations of nerves were dissected in the different experiments. The limb was pronated and placed in a metal bath which was filled with liquid and temperature-stabilized (37 °C) paraffin oil. The nerves were mounted on bipolar silver hook electrodes at the lateral side of the limb. The nerves were stimulated with square-wave voltage pulses of 0.1 ms duration. Surface potentials were recorded from the cord dorsum near the dorsal root entry zone to monitor stimulation of the peripheral nerves. Stimulus strength is expressed in multiples of threshold. A laminectomy was performed from C5–Th1. α -Motoneurons were intracellularly recorded with glass microelectrodes (3–6 M Ω resistance; 2 M potassium acetate). The amplified signals were displayed on an oscilloscope and photographed for analysis.

In tracking for the motor nuclei we followed the anatomical data obtained previously (Fritz, Illert & Reeh, 1986; Fritz, Illert & Saggau, 1986). Motoneurons were identified by antidromic invasion from one of the dissected nerves (Brock, Coombs & Eccles, 1953; Fig. 5). The antidromic action potentials occurred in all cases before the onset of the homonymous EPSPs. Neurons were investigated when their action potentials were larger than or equal to 50 mV. These EPSPs evoked from peripheral muscle nerves were classified as monosynaptic when the intraspinal latencies were shorter than 1.2 ms and the thresholds between 1.0 and 1.4 *T*. The maximal heteronymous Ia EPSPs were obtained by grading the stimulus strength. In the case of homonymous connections assessment of the maximal Ia EPSPs was complicated by antidromic invasion from the stimulated nerve. In about half of the neurons the homonymous EPSP was maximal at a stimulus strength subthreshold for antidromic invasion; in the other neurons antidromic invasion was prevented by hyperpolarizing the membrane potential, and the amplitude of the maximal homonymous EPSP was then calculated as described by Eccles *et al.* (1957). Presence of motoneuronal or interneuronal extracellular fields could be a complicating factor in assessing the size of the maximal EPSPs. After withdrawal of the microelectrode from the intracellular position the extracellular signals were routinely recorded and, if necessary, subtracted from the intracellular potential.

The data from the neurons belonging to a common motor nucleus were pooled. The projection from a nerve onto a motoneuron was treated as positive when the EPSP size was equal to or exceeded 0.1 mV. Doubtful cases were treated as not tested. The EPSP amplitudes are presented as mean values with standard deviations (in a given nerve-nucleus combination the amplitudes of

TABLE 1. List of dissected muscle nerves or nerve stems

M. biceps brachii	Bi	†*
M. brachialis	Br	†*
M. triceps brachii	Tri	†*
caput longum	TLo	†*
caput mediale	TM	†*
caput laterale	TLa	†*
M. anconeus	An	†*
N. radialis profundus	DR	†*
M. brachioradialis	BRD	†*
M. extensor carpi radialis longus	ECRL	†*
M. extensor carpi radialis brevis	ECRB	†*
M. extensor carpi radialis longus and brevis	ECR	†*
M. supinator	Sup	†*
M. extensor digitorum communis	EDC	†
M. extensor digitorum lateralis	EDL	†
M. extensor carpi ulnaris	ECU	†*
M. abductor pollicis longus	APL	†*
M. extensor indicis proprius	EIP	†
N. medianus	M	†*
M. pronator teres	PrT	*
M. flexor carpi radialis	FCR	*
M. flexor digitorum profundus	FP	*
caput secundum (supplied by the median nerve)	FP2m	*
caput tertium–quintum	FP3,4,5	*
M. palmaris longus	PL	*
M. pronator quadratus	PQ	*
Intrinsic paw muscles supplied by the median nerve	MHd	*
N. ulnaris	UI	†*
M. flexor carpi ulnaris (humeral head)	FCUh	*
M. flexor carpi ulnaris (ulnar head)	FCUu	*
M. flexor digitorum profundus	FP	*
caput primum	FP1	*
caput secundum (supplied by the ulnar nerve)	FP2u	*
Intrinsic paw muscles supplied by the ulnar nerve	UHd	*

The symbols †,* indicate that the nerve was dissected in part I or part II of the investigation respectively.

the EPSPs recorded in the different cells were added and divided by the number of all cells tested in this combination, i.e. including the cells without an EPSP). A possible dependence within a motor nucleus between EPSPs generated from different nerves was tested with linear regression in combination with a *t* test and with contingency tables combined with the χ -square test (Spiegel, 1972). Negative correlations with significance levels better than 0.1 are described as part of the respective convergence patterns; the others will not be dealt with further.

The Ia connections are described by the following terms which have, explicitly or implicitly, been used previously (Eccles *et al.* 1957; Eccles & Lundberg, 1958; Hongo *et al.* 1984). The term 'Ia relation between muscles' describes the heteronymous Ia connections from the muscles in question to the respective motor nuclei. Such relations may be *unidirectional* (Ia afferents of one muscle project onto motoneurons of another without a corresponding reciprocal projection) or *bidirectional* (mutual connections between Ia afferents and motoneurons of both muscles). Bidirectional relations are termed *balanced* when the frequencies and the mean amplitudes of the EPSPs are rather similar; they are termed *skewed* when one reciprocal projection substantially exceeds the other one.

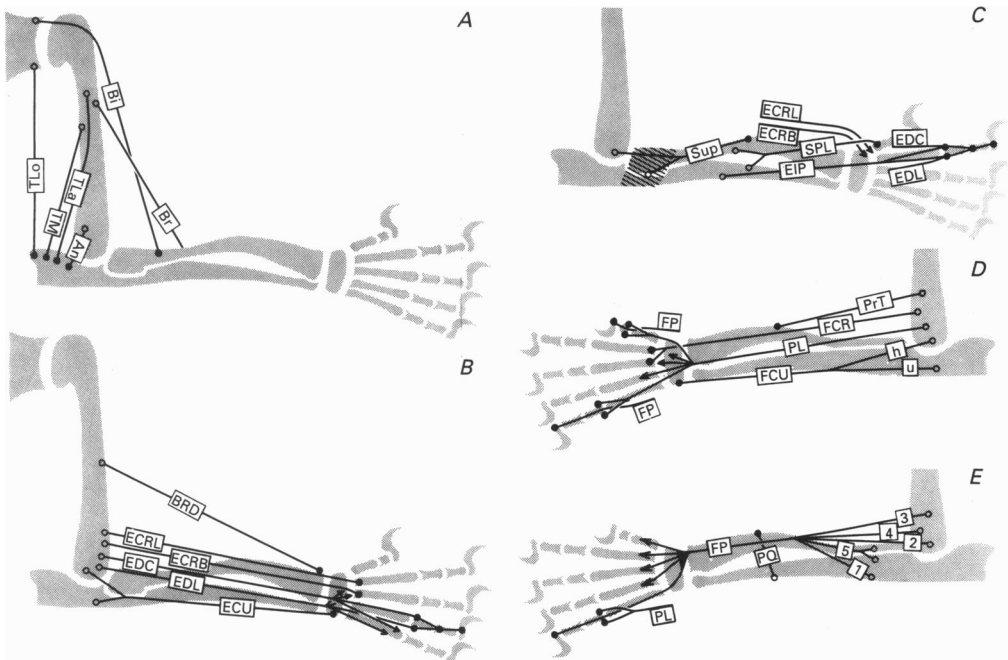


Fig. 1. Origin and insertion of the investigated forelimb muscles. *A* illustrates the elbow muscles. *B* shows the superficial, *C* the deep layer of the muscles located on the lateral side of the forelimb. *D* illustrates the superficial, *E* the deep layer of the palmar forelimb muscles. ○ indicate the origin, ● the insertion of the muscles. Insertion of the EDC/EDL and of the PL/FP muscles is illustrated for one digit only. The hatched area in *C* indicates the ligamentum annulare. Course of the muscles is based on the descriptions by Reighard & Jennings (1934), Crouch (1969) and on our own observations in post-mortem preparations. The abbreviations are listed in Table 1.

RESULTS

Part I: connections between the flexors and extensors of the elbow and the muscles supplied by the deep radial nerve

Data are presented from 354 motoneurons with action potentials larger than or equal to 50 mV; eleven additional BRD and EIP motoneurons are included, although their action potential was below 50 mV. This was done because both nuclei contain rather few neurones (Fritz, Illert & Saggau, 1986) which made a large number of penetrations difficult.

Amount of Ia excitation

Figure 2 compares Ia excitation in the different motor nuclei with respect to the total aggregates of the Ia EPSPs and the homonymous and heteronymous effects. The nuclei have been ranked according to the size of the total aggregates. Anconeus (An) motoneurons have not been included because we recorded from only two cells. The mean values of the total aggregates ranged from 4.4 to 10.4 mV. This is comparable to the values in the cat hindlimb (summarized in Hongo *et al.* 1984),

although the very large aggregates of up to 15 mV recorded in soleus motoneurons are missing. A clear-cut organizing principle does not become evident, but the motor nuclei to muscles acting on the elbow and/or the wrist tend to have larger aggregates than the nuclei to the muscles acting on the digits. The same tendency is seen when the relations between the heteronymous and homonymous EPSPs are calculated.

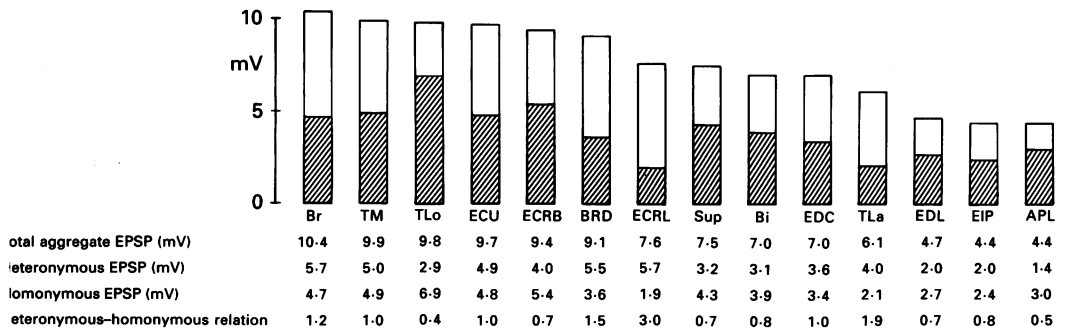


Fig. 2. Aggregate Ia EPSPs in the motor nuclei investigated in part I. To obtain the total aggregate EPSPs the mean values of the heteronymous EPSPs were added (open area) to the maximal homonymous EPSPs (hatched area). The relations between heteronymous and homonymous EPSP are indicated. The motor nuclei are arranged according to the size of the total aggregate EPSP.

Relations below 1.0 are found in the digit muscles, relations above 1.0 in most elbow muscles (note the relation of 0.4 in TLo). It seems meaningful that the Ia effects are small in the motor nuclei to the digit extensors, since a strong Ia control of these muscles would conflict with their use during manipulatory movements (Hongo *et al.* 1984). On the other hand, there are also clear exceptions. They indicate that the distribution of the heteronymous and homonymous EPSP aggregates does not follow a general rule, like a proximo-distal gradient, but that it is the consequence of the specific mechanical action of each individual muscle.

Patterns of Ia connections

The numbers of neurones with monosynaptic EPSPs in the different nerve-nucleus combinations are listed in Table 2. Heteronymous Ia excitation has wide receptive fields in many motor nuclei. The distribution of the pathways is highly organized. It appears that groups of nuclei have similar, if not identical, Ia patterns. A structure of this grouping is proposed in Fig. 6. Nuclei with a similar Ia pattern are mostly interconnected by bidirectional, in many cases balanced, pathways. To simplify the description of the complex relations and to promote a functional interpretation of the respective connections we will not describe each motor nucleus separately, but treat its Ia connections in the context of the respective 'Ia synergistic groups'.

Triceps group. This group consists of the elbow extensors TLo, TM, TLa, An. The group members displayed regular bidirectional connections (Table 2) and the amplitudes of the maximal Ia EPSPs point to balanced relations (Table 3). Eccles *et al.* (1957) reported a strong influence from TLo afferents on motoneurons of the short muscles, but only very little heteronymous Ia excitation from the other elbow

TABLE 2. Monosynaptic Ia excitation in identified forelimb motoneurons to the Tri, Bi, Br and deep radial muscles

Motoneurons	Nerves																
	TLo	TM	TLa	An	Bi	Br	BRD	ECRL	ECRB	EDC	EIP	EDL	ECU	Sup	APL	UI	M
TL0	24 (24)	24 (24)	17 (23)	20 (23)	— (21)	— (21)	— (21)	— (20)	— (20)	— (20)	— (20)	— (20)	— (20)	— (20)	— (20)	— (24)	— (24)
TM	5 (6)	6 (6)	6 (6)	6 (6)	— (5)	— (6)	— (6)	— (6)	— (6)	— (6)	— (4)	— (4)	— (4)	— (6)	— (4)	— (6)	— (6)
TLa	8 (8)	8 (8)	8 (8)	8 (8)	— (7)	— (8)	— (8)	— (8)	— (8)	— (8)	— (6)	— (6)	— (6)	— (8)	— (6)	— (7)	— (7)
An	2 (2)	2 (2)	2 (2)	2 (2)	— (2)	— (2)	— (2)	— (2)	— (2)	— (2)	— (2)	— (2)	— (2)	— (2)	— (2)	— (1)	— (1)
Bi	— (36)	— (34)	— (41)	— (41)	43 (43)	43 (43)	34 (41)	29 (33)	19 (33)	— (33)	— (38)	— (38)	— (38)	— (42)	— (38)	— (26)	6 (34)
Br	— (50)	— (49)	— (51)	— (52)	55 (56)	56 (56)	55 (56)	45 (46)	36 (42)	— (50)	— (48)	— (50)	— (50)	— (52)	— (51)	— (51)	39 (53)
BRD	— (8)	— (7)	— (8)	— (8)	13 (14)	14 (14)	14 (14)	9 (9)	9 (9)	— (13)	— (11)	— (10)	— (10)	— (13)	— (10)	— (11)	11 (13)
ECRL	— (18)	— (17)	— (17)	— (17)	18 (18)	18 (18)	15 (17)	18 (18)	18 (18)	2 (17)	— (15)	— (15)	— (15)	— (15)	— (15)	— (15)	14 (17)
ECRB	— (17)	— (17)	— (17)	— (17)	18 (18)	16 (17)	12 (17)	18 (18)	14 (18)	— (18)	— (17)	— (17)	— (17)	— (17)	— (17)	— (14)	10 (18)
EDC	— (34)	— (34)	— (33)	— (33)	— (34)	— (32)	— (35)	5 (31)	30 (32)	40 (40)	25 (30)	34 (39)	16 (37)	— (39)	— (30)	— (38)	1 (37)
EIP	— (9)	— (9)	— (9)	1 (9)	— (8)	— (9)	— (10)	— (9)	8 (9)	9 (10)	10 (10)	5 (10)	— (10)	— (10)	4 (10)	— (9)	— (9)
EDL	— (18)	— (18)	— (19)	— (19)	— (17)	— (18)	— (19)	— (20)	1 (20)	22 (30)	5 (30)	30 (30)	29 (30)	— (24)	— (29)	2 (27)	2 (27)
ECU	34 (34)	30 (32)	15 (33)	17 (33)	— (36)	— (37)	— (35)	— (25)	— (26)	— (32)	1 (19)	21 (36)	38 (38)	— (32)	— (19)	26 (27)	14 (33)
Sup	8 (24)	7 (21)	12 (27)	17 (25)	22 (28)	6 (26)	1 (27)	7 (22)	11 (22)	— (24)	— (15)	— (23)	— (23)	28 (28)	9 (15)	1 (21)	5 (25)
APL	1 (21)	2 (20)	1 (21)	4 (20)	9 (20)	— (21)	1 (22)	1 (23)	4 (22)	— (23)	11 (23)	2 (23)	— (23)	9 (23)	23 (23)	— (23)	5 (22)

Material from part I. The motor nuclei are listed from top to bottom, the stimulated nerves from left to right. Upper row: number of cells with a monosynaptic Ia EPSP from the tested nerve; —, Ia excitation not found in any cell. Lower row (in parentheses): number of neurones tested.

TABLE 3. Mean amplitude of the Ia EPSPs evoked in elbow extensor (left) and flexor (right) motoneurons

Motoneurons	Nerves			Motoneurons					Nerves				
	TL _o	TM	TL _a	An	Bi	Br	BRD	Bi	Br	BRD	ECRL	ECRB	M
TL _o	6.9 ± 2.4 (18)	1.9 ± 1.2 (24)	0.4 ± 0.4 (23)	0.6 ± 0.5 (22)	Bi	3.9 ± 1.6 (15)	1.7 ± 1.1 (41)	0.3 ± 0.3 (41)	0.3 ± 0.2 (33)	0.2 ± 0.2 (33)	0.1 ± 0.2 (34)		
TM	2.2 ± 1.6 (6)	4.9 ± 1.2 (3)	1.9 ± 0.9 (5)	0.9 ± 0.5 (6)	Br	1.0 ± 0.7 (53)	4.7 ± 1.6 (24)	1.3 ± 0.9 (56)	1.0 ± 0.4 (46)	0.4 ± 0.4 (42)	0.7 ± 0.6 (43)		
TL _a	1.7 ± 1.1 (8)	1.6 ± 1.1 (8)	2.1 ± 0.1 (2)	0.7 ± 0.4 (8)	BRD	0.6 ± 0.3 (13)	2.1 ± 1.2 (13)	3.6 ± 3.3 (2)	0.8 ± 0.6 (8)	0.5 ± 0.3 (9)	0.7 ± 0.5 (11)		

Material from part I. The motor nuclei are listed from top to bottom, the stimulated nerves from left to right. Upper row: mean EPSPs in mV (± s.d.). Lower row (in parentheses): number of cells tested.

TABLE 4. Correlations between different Ia inputs converging onto TL_o, EDC, EDL, ECU and PrT motoneurons

Nucleus	Nerve 1	Nerve 2	<i>k</i>	<i>P_r</i>	<i>P_c</i>	Figure
TL _o 23	TM	TL _a	0.69	0.05	0.025	—
TL _o 22	TM	An	0.44	0.025	n.s.	—
TL _o 22	TL _a	An	0.64	0.005	n.s.	—
EDC 32	EDL	ECRB	-0.28	0.1	0.25	4A
EDC 30	ECRB	ECU	-0.23	0.1	n.s.	—
EDC 38	ECU	EDL	0.54	0.005	0.05	4B
EDL 30	EDC	ECU	-0.17	0.2	n.s.	4C
ECU 27	EDL	UI	-0.45	0.01	0.025	4D
ECU 34	EDL	TL _o	-0.37	0.025	n.s.	4E
ECU 33	EDL	TM	-0.47	0.005	0.025	—
ECU 33	TM	TL _o	0.64	0.05	0.005	—
ECU 25	TL _o	UI	0.51	0.005	0.01	4F
ECU 24	TM	UI	0.28	0.1	n.s.	—
PrT 63	Bi	FCR	-0.28	0.025	0.25	4G
PrT 58	BRD + ECR	FCR	-0.30	0.025	0.25	4H
PrT 64	Br	FCR	-0.40	0.005	0.005	—

The motor nuclei and the number of neurons tested with a defined nerve combination (nerve 1, nerve 2) are listed in the left-hand column (nucleus). *k*, correlation coefficient; *P_r*, significance for the linear regression; *P_c*, significance for the χ -square test; n.s., not significant; the right-hand column gives the figure number in case of illustrations.

extensors in TLo motoneurons. The low value of 0.4 found in our material for the ratio between heteronymous and homonymous Ia excitation (Table 3) supports these findings. It is larger than the one reported by these authors (0.2), which could indicate that neurones with large heteronymous EPSPs are overrepresented in our material. The maximal Ia EPSPs evoked in TLo motoneurons from the different Tri nerves were positively correlated with each other (Table 4). With exception of FCR no Ia excitation was present in the elbow extensor motoneurons from distal forelimb muscles (Table 7; Schmidt & Willis, 1963). All Tri muscles projected unidirectional Ia pathways to the ECU, Sup and APL motor nuclei.

Biceps group. The elbow flexors Bi, Br, BRD and the radial wrist extensors ECRL and ECRB form a common group. Strong bidirectional connections between the group members and convergence onto them from Ia afferents of the median nerve are characteristic features (Tables 2, 3 and 5). The latter projection originates from the PrT muscle (part II, Table 7), which is therefore included in the biceps group (Fig. 7). All group members, but most frequently Bi and ECRB, project unidirectionally onto the Sup and APL nuclei (Table 5). The double-joint Bi maintains skewed relations with some group members: the projections from BRD, ECRL and ECRB are not as frequent and strong as in the reverse direction. These asymmetric relations may be correlated with the action of the Bi on the shoulder joint, similar to the case of the TLo. Brachialis (Br) and BRD, which are close mechanical synergists, have stronger connections with each other than with the other muscles. A similar relation is present in case of the ECRL and ECRB.

Group of wrist and digit extensors. ECRL, ECRB, EDC, EDL and ECU are treated as a common group, although they could also be considered as a system of overlapping Ia synergistic groups. Strong bidirectional connections exist between pairs of muscles only: ECRL and ECRB, ECRB and EDC, EDC and EDL, EDL and ECU; the connections between the more distant muscles are weak (Tables 2 and 5). This pattern follows the anatomical arrangement of the muscles in the limb and combines the anatomical neighbours with each other. The distribution of the bidirectional Ia pathways between these muscles apparently follows a 'neighbouring principle'.

The muscles of this group are wrist extensors; ECRL, ECRB and EDC cause in addition different degrees of adduction, EDL and ECU of abduction. Although EDC and EDL affect the metacarpal and phalangeal joints, the wrist action is regarded as the common group feature. The radio-ulnar position of the muscles in the forearm represents the direction of their wrist action. Thus the neighbouring principle (i.e. bidirectional Ia connections between anatomical neighbours) connects muscles with similar mechanical actions, but disconnects at the same time the radial and ulnar wrist extensors which are antagonists in adduction/abduction movements.

The relations between the wrist and digit extensors are skewed (Tables 2 and 5). Nearly all EDC motoneurons received Ia excitation from ECRB afferents (94%), but only 78% of the ECRB motoneurons were excited from the EDC nerve. This skewedness becomes more obvious when the mean EPSPs are compared (0.7 versus 0.4 mV). A similar asymmetry was observed between EDC and ECU. The projection from ECU afferents onto EDC motoneurons was fairly regular (43%), whereas the reciprocal connection never occurred. The relation between EDL and ECU was also skewed (97 versus 58%; 0.9 versus 0.3 mV). These data suggest that the wrist

TABLE 5. Mean amplitudes of the Ia EPSPs evoked in the long extensors of the wrist and digits and in the Sup and APL motor nuclei

	Nerves																	
	TLo	TM	TLa	An	Bi	Br	BRD	ECRL	ECRB	EDC	EDL	EIP	ECU	Sup	APL	UI	M	
ECRL	(18)	(17)	(17)	(17)	1.0±0.4 (18)	0.9±0.4 (18)	0.4±0.2 (17)	1.9±0.2 (8)	2.7±1.3 (18)	< 0.1 (17)	—	—	—	—	—	—	0.6±0.4 (14)	
ECRB	(17)	(17)	(17)	(17)	0.7±0.5 (18)	0.5±0.3 (16)	0.2±0.1 (17)	1.6±0.8 (17)	5.4±2.5 (14)	0.4±0.4 (18)	—	—	—	—	—	—	0.6±0.8 (15)	
EDC	(34)	(34)	(34)	(33)	—	—	—	< 0.1 (31)	0.7±0.6 (32)	3.4±2.3 (22)	0.9±0.9 (40)	0.6±0.6 (31)	0.2±0.3 (38)	—	—	—	< 0.1 (37)	
EIP	(9)	(9)	(9)	(9)	—	—	—	—	0.3±0.3 (8)	1.1±1.1 (10)	0.4±0.5 (10)	2.4±1.5 (6)	—	—	0.2±0.4 (10)	—	—	
EDL	(18)	(18)	(18)	(19)	—	—	—	—	< 0.1 (20)	0.7±0.8 (30)	2.7±1.1 (16)	< 0.1 (30)	0.9±0.6 (30)	—	—	< 0.1 (29)	< 0.1 (27)	
ECU	(34)	(33)	(34)	(32)	—	—	—	—	—	—	0.3±0.5 (38)	< 0.1 (19)	4.8±1.5 (12)	—	—	1.9±1.3 (27)	0.4±0.6 (33)	
Sup	(24)	(21)	(27)	(25)	0.5±0.6 (28)	0.1±0.2 (26)	< 0.1 (27)	0.2±0.2 (22)	0.1±0.1 (22)	—	(24)	(23)	(15)	(23)	4.3±1.5 (12)	0.3±0.6 (15)	< 0.1 (21)	< 0.1 (25)
APL	(21)	(20)	(21)	(20)	0.1±0.2 (20)	—	< 0.1 (21)	< 0.1 (23)	< 0.1 (22)	—	< 0.1 (23)	0.3±0.4 (23)	—	—	0.1±0.2 (23)	3.0±1.2 (17)	—	0.2±0.5 (22)

Material from part I. The motor nuclei are listed from top to bottom, the stimulated nerves from left to right. Upper row: mean EPSPs in mV (± s.d.); —, Ia excitation was not present in any cell. Lower row (in parentheses): number of cells tested.

extensors have stronger actions on the motoneurons of the digit extensors than in the reverse direction.

A differentiation within the EDC motor nucleus is suggested by correlation tests which were applied on the different projections onto the EDC motoneurons. Figure 3 illustrates this finding with sample records. The four EDC motoneurons were

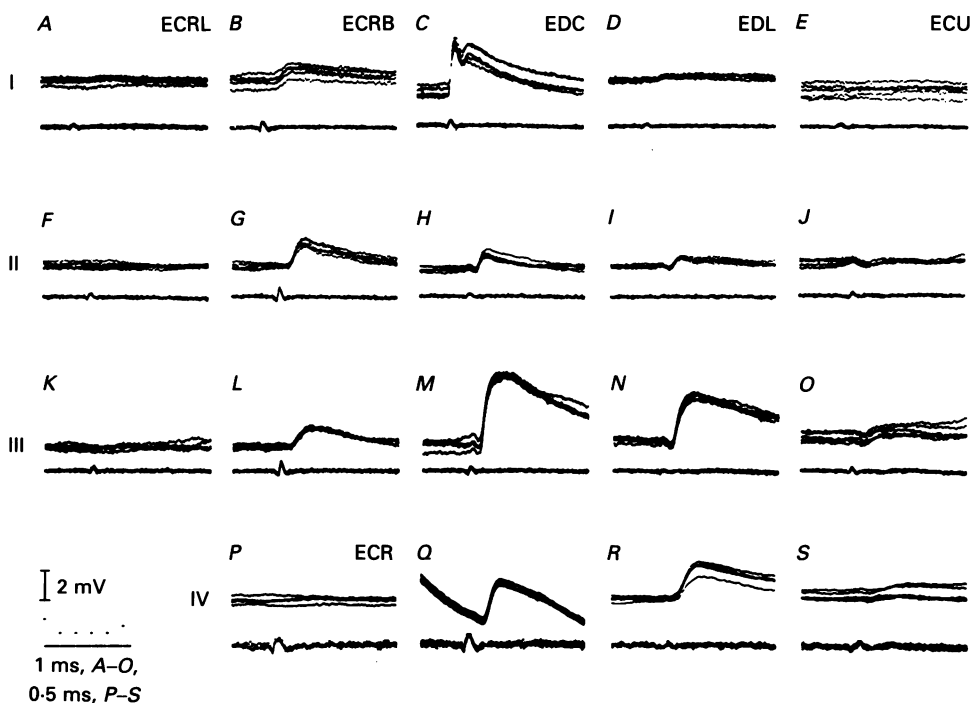


Fig. 3. Intracellular records from four different EDC motoneurons. The motoneurons I-IV are indicated at the left of each row. The stimulated nerves are arranged in their radio-ulnar anatomical order and indicated above the specimen records *A-E*. The upper traces are intracellular records, the lower traces are records from the spinal cord surface at the level of the respective motoneurons. The voltage calibrations apply to the intracellular records. Note that there is an M spike in *C*. In *Q* the EPSP is superimposed on the decay phase of a hyperpolarizing current pulse which was used to prevent antidromic invasion of the motoneurone. All Ia EPSPs are maximal.

predominantly influenced from either the radial (neurone I and II) or the ulnar neighbouring muscles (neurone III and IV). Linear regression statistics (Table 4) suggested that the sizes of the EPSPs generated in EDC motoneurons by the radial neighbour ECRB were negatively correlated with the sizes of the EPSPs generated by the ulnar neighbour EDL (Fig. 4A). Correlation of the EPSPs generated from the ECRB with those generated from the more distant ECU was also weakly negative (not illustrated), whereas correlation between the EPSPs from the two ulnar neighbours EDL and ECU was positive (Fig. 4B). A similar situation was observed in EDL motoneurons: a weak negative correlation between the projections from the

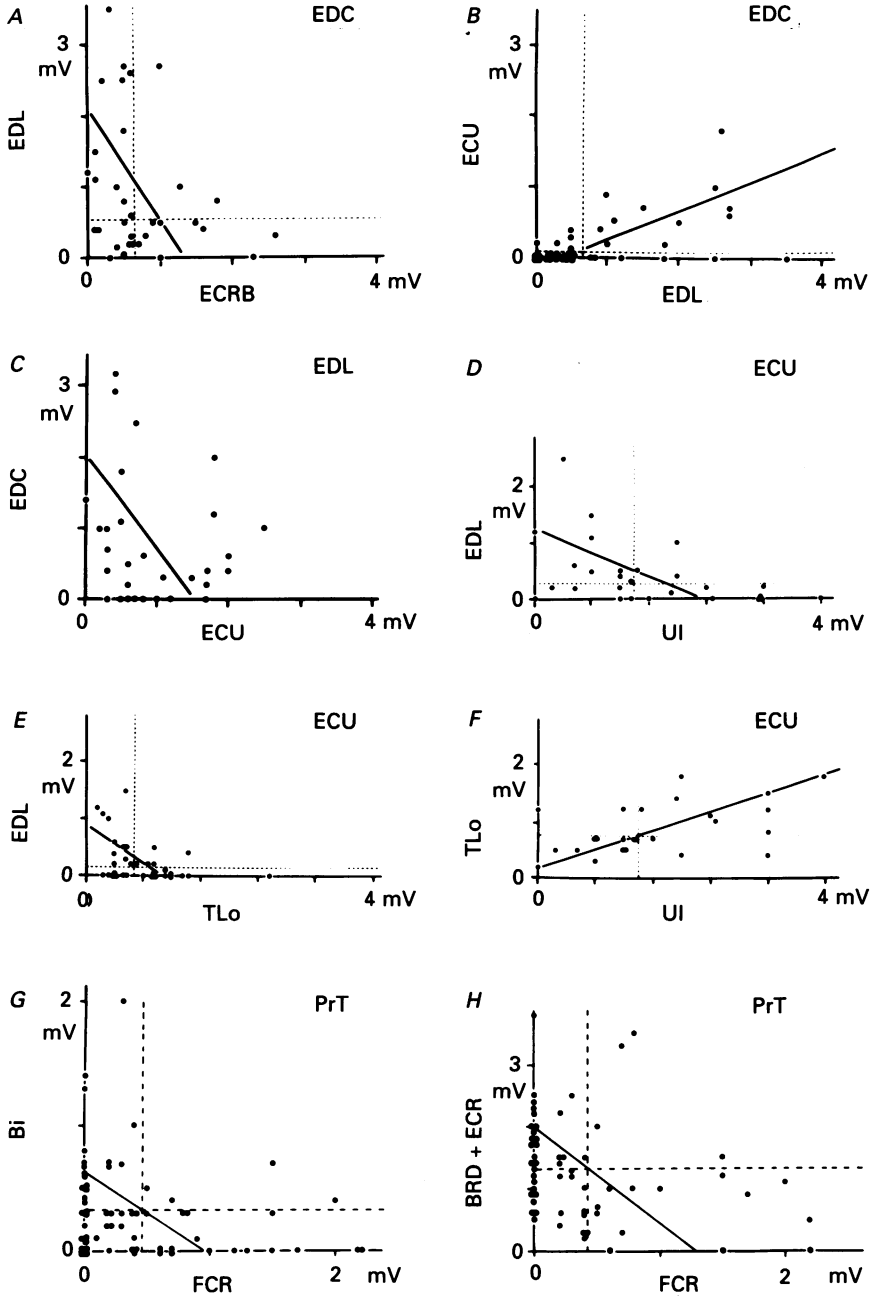


Fig. 4. Interdependence of the Ia inputs converging onto EDC (*A* and *B*), EDL (*C*), ECU (*D*–*F*) and PrT (*G* and *H*) motoneurons. Each point represents one motoneurone; the coordinates give the size of the maximal Ia EPSPs evoked in that neurone from the respective Ia systems. The dashed lines in *A*, *B* and *D*–*H* give the border lines for the use of contingency tables. The number of cells, the correlation coefficients and the significance values for the linear regression and the χ -square test are listed in Table 3.

radial EDC and the ulnar ECU (Fig. 4C). In addition to these negative correlations these muscles have the further common feature that they belong to several Ia synergistic groups: ECRL and ECRB to the biceps group, EDC and EDL to the group of the extensors of the four ulnar digits; ECU forms a separate group.

Extensors of the four ulnar digits. Ia convergence onto the EIP motoneurons is similar to that received by the EDC and EDL (Tables 2 and 5), but it does not fit the neighbouring principle at the elbow joint. Therefore EIP, EDC and EDL are combined into a separate group. The muscles have bidirectional but skewed relations with each other. The connection between EIP and EDC is slightly skewed, that between EIP and EDL strongly skewed (mean EPSP from EDL in EIP 0.4 mV, from EIP in EDL below 0.1 mV; the corresponding projection frequencies were 50 *versus* 17%). The Ia relations with the muscles outside the group are similar. Differences exist in the connections with the ECU, ECRB and APL: only EIP but not the other two nuclei has Ia relations with the APL.

The three muscles act as extensors of the digits. The EIP inserts regularly at the first and second digit. The EDC inserts at the radial side of the index, which may be reflected by the strong bidirectional connections between the two muscles. The skewedness in the EDL-EIP relation may be a genuine effect or mirror the lack of an EDL insertion on the index in some cats (Reighard & Jennings, 1934).

Extensor carpi ulnaris. The ECU is treated separately since strong Ia projections from the elbow extensors and from the median and the ulnar nerves separate this muscle from the group of the wrist and digit extensors (Tables 2 and 5). The convergence from TLo afferents was present in all ECU motoneurons. The EPSPs generated from TLo were larger than those from the other elbow extensors. Convergence from median and ulnar nerves occurred with high frequencies (M: 42%, U1: 95%). The responsible afferents mainly arise from the FCU, FCR and PQ (see part II, Tables 7 and 8). Based on the size of the summed Ia EPSPs, excitation of the ECU muscle predominantly originates from physiological extensors (sum of EPSPs generated by TLo, TM, TLa, An, median and ulnar nerves: 4.3 *versus* 0.3 mV from EDL). The bidirectional relation between ECU and EDL does not fit such an extensor pattern. The statistical analysis (Table 4) showed that the EPSPs from EDL were negatively correlated with the EPSPs generated from TLo, TM and ulnar afferents (Fig. 4D and E). The correlation was positive between the EPSPs from the TLo, TM and ulnar nerves (for TLo-U1 combination see Fig. 4F). This suggests that Ia activation of the ECU muscle is achieved from two different functional groups, and that the single motoneurons are under the strong influence of either the one or the other source. This double function is reflected by the EMG pattern of the ECU during food-taking movements and locomotion (English, 1978; Hoffmann, Illert & Wiedemann, 1985, 1986).

Supinator group. Supinator (Sup) and APL were grouped together since both nuclei have several features in common (Tables 2 and 5). Most characteristic is the coincident unidirectional projection onto the same cell from Ia afferents of the triceps and of the biceps group. In the convergence received from the triceps group, An dominated over the others; in that from the biceps group, Bi and ECRB dominated. The frequent projections from the median nerve mainly originate from the FCR (see part II, Table 7). Sup and APL project to a limited number of motor

nuclei only: Sup to APL, APL to EIP and FCR (part II). This narrow projection field is interesting in view of the broad Ia receptive field of both nuclei. The qualitative similarity in the convergence received by them is striking, but there are quantitative differences. Thus the APL received less heteronymous Ia convergence than did the Sup; two APL motoneurons were devoid of any heteronymous Ia excitation which was not observed in the Sup nucleus.

TABLE 6. Ia convergence onto Sup motoneurons

Unit	AP	HEP	TLo	TM	TLa	An	Bi	Br	ECRL	ECRB	APL	Ul	M
1	70	+					0.7	—				+	0.5
2	75	+					0.1	—					—
3	75	+	—	0.3	0.3	0.3	0.2	—	—	—			—
4	65	+	—	0.3	1.0	0.4	0.3	0.2	—	—			—
5	60	+	—	0.3	0.8	0.3	0.3	—	—	—			—
6	63	+	—	—	0.5	0.3	0.3	—	—	0.4			—
7	87	+	—				0.6	0.6					0.3
8	80	+	—		0.1		1.2		0.5	—			—
9	78	+	0.8	—	—	—	1.1	—					+
10	55	+	0.5	0.2	0.3	0.5	0.2	—					—
11	85	4.5			0.4	0.3	—	—	—	—			—
12	75	+			0.4	0.5	1.7	0.4	—	0.5			—
13	52	1.5	0.1	—	—	—	0.2	—	0.6	0.3	0.7		—
14	60	3.0	0.1	—	0.1	0.1	0.3	0.5	0.2	—	0.5		—
15	60	6.5	—	0.5	0.2	0.3	—	—	—	—	0.2		—
16	56	7.0	0.2	0.4	—	0.2	—	—	—	—	—		—
17	75	3.8	—	0.1	0.2	0.5	—	—	0.3	0.2	—		—
18	62	+	—	—	—	0.3	0.2	—	—	0.3	—		—
19	65	4.4	0.3	—	—	0.3	0.4	—	—	—	—		0.5
20	60	+	0.3	—	—	0.4	0.4	—	—	—	0.3		0.7
21	85	6.0	—	—	—	0.2	0.7	—	—	0.4	0.5		—
22	72	4.0	—	—	—	—	0.2	—	0.4	0.3	0.9		—
23	50	4.0	—	—	—	0.6	1.1	—	—	—	2.2		—
24	70	4.0	0.4	—	—	0.5	2.0	0.7	—	0.3	1.8		—
25	70	3.5	—	—	—	—	2.2	0.5	0.3	0.4	1.0		—
26	67	+	—	—	—	—	—	—	—	0.4	—		—
27	65	+	—	—	—	—	—	—	0.3	0.2	—		—
28	70	+	—	—	0.6	—	1.2	—	—	—	—		—

Material from part I. The neurones are listed from top to bottom. The amplitude of the antidromic action potential (AP), the size of the maximal homonymous Ia EPSP (HEP) and the amplitude of the Ia EPSPs evoked from the different nerves is given in mV. +, size of the Ia EPSP could not be established; —, no Ia convergence; no entry, combination was not tested.

Table 5 lists the mean EPSPs. The values do not mirror the quantitative relations in the individual motoneurons, since convergence onto them is characterized by an enormous interindividual variation. To show the whole spectrum of possible connections Table 6 presents the convergence onto the individual Sup motoneurons ($n = 28$). Ia excitation was never contributed from EDC, EDL, ECU and EIP, from BRD and Ul in a single cell only. Comparable data were found in the APL nucleus. The sources of Ia excitation and the EPSP amplitudes were different between the motoneurons. No systematic rule was detected which could explain this variation

nor any statistical dependence between the different projections. However, our material is too small to be conclusive on this point. Furthermore, there was no evident correlation between the Ia convergence onto a motoneurone and the position of the cell in the respective nucleus.

The convergence pattern suggests that supination is the common mechanical action of both muscles. The APL participates since the muscle fibres from the ulna to the radius or to the distal APL tendon decrease the distance between the two bones. Some APL motoneurons lack the typical Sup convergence pattern. Perhaps the muscle units innervated by them originate from the radius.

Muscles extending or abducting the pollex. This synergistic group was formed on the basis of the bidirectional Ia connections between APL and EIP (Tables 2 and 5). As in the supinator group only a part (40–50%) of the motoneurons participated, but judging by the mean sizes of the Ia EPSPs, these bidirectional connections are balanced. Both APL and EIP extend the thumb (Reighard & Jennings, 1934), and in many cats both tendons are completely fused. This action may be the mechanical equivalent of the bidirectional connections between the motor nuclei. There are also clear differences between the two nuclei, both in the convergence they receive and in the projection they give. The EIP has strong relations with ECRB, EDC and EDL, which the APL has not. The APL, on the other hand, receives convergence from the triceps and biceps group, from Sup and from median afferents which are lacking in the EIP.

Part II: connections with muscles supplied by the median and ulnar nerves

Data are presented from 344 α -motoneurons with action potentials larger than or equal to 50 mV.

Amount of Ia excitation

The total aggregates of the Ia EPSPs (sum of heteronymous and homonymous EPSPs) ranged from 4.0 to 11.7 mV. The value was smallest in the UHd motor nuclei (barbiturate material: 4.7 mV, $n = 13$; chloralose material: 4.0 mV, $n = 3$). The heteronymous/homonymous EPSP relations varied between 3.9 (FP3) and 0.4 (FCUh). Values between 3.9 and 1.4 were present in the flexors of the digits (different FP heads), values between 0.5 and 1.0 in the wrist flexors (FCR, FCU). This distribution indicates an important Ia control of the FP nuclei from heteronymous sources (mainly from the other FP nuclei and from the PL).

Patterns of Ia connections

The number of neurones with monosynaptic EPSPs in the different nerve–nucleus combinations is listed in Table 7. Heteronymous Ia excitation has wide receptive fields and groups of motor nuclei exist in similar, if not identical, Ia patterns. As on the lateral side of the limb these nuclei are combined into ‘Ia synergistic groups’ (Fig. 7). Tables 8 and 9 give the mean amplitudes of the Ia EPSPs. Since the values differed slightly in the two anaesthetics, Table 8 contains the Nembutal, Tables 9 and 10 the chloralose material (this and the presence of neurones analysed only qualitatively explains the differences between Tables 7–9 in the number of tested cells; see Methods).

TABLE 7. Monosynaptic Ia excitation in identified forelimb motoneurons to the median, ulnar, Bi, Br and some deep radial muscles

Motoneurons		Nerves																					
Bi	Br	ECR	P _r T	PQ	FP5	FP1	FP3	FP2m	FP2u	FP4	PL	FCU _u	FCR	APL	Sup	ECU	Tri	MHd	UHD	M	U1	DR	
†	†	†	13	(15)	(14)	(18)	(23)	(18)	(23)	(18)	(23)	(18)	(18)	(24)	1	†	†	†	—	—	10	—	†
†	†	†	23	(23)	(15)	(16)	(18)	(16)	(18)	(16)	(18)	(16)	(16)	(22)	†	†	†	†	(9)	(18)	(19)	(18)	†
†	†	†	4	(7)	(5)	(6)	(7)	(6)	(7)	(6)	(7)	(6)	(6)	(7)	†	†	†	†	(7)	(16)	(23)	(16)	†
47	40	27	76	64	7	—	—	—	—	1	—	—	1	44	—	2	6	—	(3)	(6)	(5)	(6)	66
(70)	(71)	(27)	(76)	(66)	(68)	(7)	(9)	(8)	(8)	(10)	(7)	(10)	(9)	(75)	(52)	(66)	(70)	(4)	(4)	(4)	(76)	(74)	(68)
—	—	—	12	12	2	3	4	1	2	2	—	—	—	4	—	—	—	—	—	—	—	—	—
—	—	—	(12)	(12)	(10)	(7)	(11)	(11)	(7)	(11)	(12)	(11)	(11)	(12)	—	—	—	—	—	—	—	—	—
(2)	(2)	(1)	(14)	(12)	(14)	(12)	(12)	(6)	(13)	(13)	(13)	(13)	(12)	(14)	(1)	(1)	(1)	(3)	(12)	(7)	(14)	(12)	(12)
—	—	—	1	5	9	10	10	9	6	10	4	—	—	1	—	—	—	—	—	—	6	10	—
(1)	(1)	(10)	(10)	(8)	(10)	(10)	(10)	(6)	(10)	(6)	(10)	(10)	(10)	(10)	(10)	(10)	(10)	(1)	(10)	(7)	(7)	(10)	(10)
—	—	(6)	(8)	(8)	(8)	(4)	(8)	(6)	(8)	(8)	(8)	(8)	(7)	(8)	(6)	(6)	(6)	(1)	(6)	(5)	(8)	(6)	(6)
—	—	—	(7)	(7)	(7)	(2)	(7)	(7)	(3)	(7)	(5)	—	—	1	—	—	—	—	—	—	7	6	(7)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	(15)	(15)	(15)	(15)	(10)	(15)	(13)	(15)	(15)	(15)	(15)	(13)	(15)	(15)	(15)	(15)	(11)	(13)	(12)	(9)	(15)	(15)
—	—	(9)	(9)	(9)	(8)	(9)	(7)	(8)	(9)	(7)	(9)	(9)	(9)	(9)	(9)	(9)	(9)	(5)	(9)	(9)	(9)	(9)	(9)
—	—	(27)	(28)	(28)	(27)	(18)	(28)	(23)	(17)	(28)	(28)	(28)	(27)	(28)	(27)	(27)	(13)	(24)	(24)	(24)	(28)	(24)	(27)
(2)	(2)	(8)	(8)	(8)	(8)	(6)	(8)	(8)	(7)	(8)	(8)	(8)	(8)	(8)	(8)	(8)	(8)	(4)	(8)	(6)	(5)	(8)	(8)
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(1)	(1)	(12)	(12)	(12)	(12)	(9)	(12)	(12)	(8)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(2)	(2)	(11)	(8)	(9)	(12)	(12)
1	1	1	9	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
(42)	(42)	(20)	(47)	(46)	(5)	(4)	(2)	(6)	(3)	(2)	(9)	(11)	(49)	(32)	(39)	(33)	(45)	(4)	(5)	(49)	(45)	(37)	†
†	†	†	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
†	†	†	(10)	(6)	(4)	(1)	(7)	(7)	(1)	(7)	(7)	(1)	(1)	(10)	†	†	†	†	(2)	(9)	(7)	†	
†	†	†	—	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
†	†	†	(13)	(11)	(13)	(10)	(12)	(11)	(10)	(12)	(13)	(12)	(12)	(12)	†	†	†	†	(11)	(11)	(12)	(13)	
†	†	†	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	†	†	†	†	—	—	—	—	
—	—	—	3	1	4	5	1	2	—	—	3	1	4	—	—	—	—	—	—	—	—	—	
—	—	(19)	(18)	(19)	(12)	(19)	(19)	(15)	(19)	(19)	(19)	(19)	(19)	(18)	(5)	(5)	(5)	(5)	(18)	(19)	(19)	(19)	(18)

Material from part II. The motor nuclei are listed from top to bottom, the stimulated nerves from left to right. Upper row: number of cells with a monosynaptic Ia EPSP from the tested nerve; —, Ia excitation not found in any cell. Lower row (in parentheses): number of neurones tested. †, these combinations have been extensively investigated in part I; reference should be made to Table 2. Three of the Sup motoneurons and four of the ECU motoneurons recorded from were identified from their segmental location (Sup: C6-C7; ECU: C8-Th1) and their typical synaptic pattern (Sup, monosynaptic Ia excitation from Bi and Tri; ECU, monosynaptic Ia excitation from FCU, Tri and median nerve).

Long flexors of the digits. This group contains the FP1–5 and the PL muscles. All group members are bidirectionally interconnected. The frequency of these projections (60–100% between the different FP heads, 15–86% between the PL and the FP muscles) demonstrates a stronger linkage of the FP muscles with each other than with the PL (Table 7). This is paralleled by the amplitude distribution of the heteronymous Ia EPSPs (Table 8). Due to the small number of neurones the strength of the connections between the different FP heads is difficult to ascertain, but the relations between FP1 and FP5 appear stronger than those between the other FP heads. The excitation given from FP4 Ia afferents to other nuclei was always stronger than the heteronymous effects received by FP4 motoneurones.

All group members received weak Ia projections from the FCR. The number of cells recorded from is too small to allow a quantitative and more detailed description of these pathways, in particular with respect to a possible bidirectionality. On the other hand, FCR and the flexors of the digits have a common mechanical action on the wrist and the observed relations would correspond to this synergism. The group has interesting relations with the PQ. Muscles FP2–4 have weak, probably unidirectional, projections onto the PQ. The connections between PQ and FP1 and 5 are bidirectional and rather balanced, and point to a close functional association.

Flexors of the wrist. Tables 7 and 8 show the relations between FCR, PL, FCUh and FCUu. In most aspects the motor nuclei have similar Ia connections, but differences are present in the connections of the FCR and FCUu. All group members, except FCR and FCUu, are bidirectionally interconnected. The FCUu has balanced connections with the FCUh and skewed relations with the PL (FCUu receives stronger projections than it gives). The FCUu and FCUh evoke unidirectional excitation in the ECU motor nucleus, both heads with a comparable strength. Complex Ia relations exist with the ulnar motor nuclei to the intrinsic paw muscles. The FCR and FCU projected unidirectionally onto UHd motoneurones, but no excitation was found from PL (note that in the reverse direction excitation from UHd afferents was found in PL, but not in FCR and FCU motoneurones).

The absence of bidirectional Ia connections between FCUu and FCR is surprising. This is the first case reported in which two muscles acting in the same direction on the same joint are not connected by bidirectional Ia pathways. Furthermore, although the FCUu shares a common distal tendon with the FCUh it is not Ia connected with all group members in the same close way as the FCUh. There could be different mechanical actions since the FCUu does not originate from the humerus. A further specialization is indicated by the muscle unit composition, since the FCUu contains a higher proportion of fast muscle fibres than the FCUh (Gonyea, Marushia & Dixon, 1981).

Flexor carpi radialis. Although the FCR belongs to the group of the wrist flexors, this motor nucleus is in addition described separately, since its Ia connections differ in many aspects from those of the other muscles (Tables 7 and 8). It is the only palmar flexor which receives Ia excitation from the triceps group. The frequency of this projection and the EPSP amplitudes indicate a strong linkage. In the reverse direction four out of five TLo+TM motoneurones were Ia excited from the FCR (mean EPSP 0.4 ± 0.2 mV); no effect was found in the single TLa+An motoneurone recorded from. These findings suggest a bidirectional relation.

The FCR receives strong Ia excitation from the APL. We are not certain about the

TABLE 8. Mean amplitudes of the Ia EPSPs evoked in the motor nuclei to the long flexors of the wrist, of the digits, to the PQ, UHd and ECU muscles

Moto-neurons	Nerves													
	PQ	FP5	FP1	FP3	FP2m	FP2u	FP4	PL	FCU ^u	FCU ^h	FCR	MHd	UHd	DR
PQ	1.9 (1)	< 0.1 (4)	0.1 ± 0.1 (3)	— (4)	< 0.1 (4)	0.1 ± 0.1 (5)	— (4)	— (5)	— (4)	— (4)	— (5)	— (3)	0.1 ± 0.2 (4)	1.3 ± 0.6 (5)
FP5	0.1 ± 0.2 (3)	2.6 ± 0.3 (3)	2.1 ± 0.4 (3)	0.5 ± 0.1 (3)	0.7 ± 0.1 (2)	1.4 ± 0.9 (3)	1.5 ± 0.6 (3)	— (3)	— (3)	— (3)	— (3)	— (3)	— (3)	0.2 ± 0.3 (3)
FP1	0.2 ± 0.2 (3)	1.4 ± 1.0 (5)	3.7 ± 2.5 (3)	0.7 ± 0.5 (5)	0.7 ± 0.6 (5)	1.4 ± 0.8 (5)	0.8 ± 0.5 (5)	— (5)	— (5)	— (5)	— (5)	— (5)	— (4)	— (5)
FP3	— (4)	0.8 ± 0.2 (4)	0.9 ± 0.2 (2)	1.4 ± 0.3 (2)	0.5 ± 0.3 (3)	1.0 ± 0.6 (4)	2.0 ± 1.2 (4)	0.1 ± 0.2 (4)	— (4)	— (3)	0.1 ± 0.2 (4)	— (3)	— (3)	— (3)
FP2m	— (3)	1.3 ± 0.7 (3)	1.0 ± 0.5 (2)	0.7 ± 0.4 (3)	0.9 ± 0.2 (2)	1.6 ± 1.0 (3)	0.8 ± 0.3 (3)	0.1 ± 0.2 (3)	— (3)	— (3)	— (3)	— (3)	— (3)	— (3)
FP2u	— (11)	0.9 ± 0.3 (11)	2.4 ± 1.9 (7)	0.6 ± 0.3 (11)	0.7 ± 0.5 (9)	2.1 ± 0.7 (7)	1.2 ± 0.6 (11)	0.3 ± 0.3 (11)	< 0.1 (11)	< 0.1 (10)	0.1 ± 0.1 (11)	— (10)	0.2 ± 0.4 (11)	— (11)
FP4	— (8)	0.5 ± 0.4 (8)	0.3 ± 0.4 (8)	0.7 ± 0.4 (8)	0.1 ± 0.1 (6)	0.3 ± 0.2 (8)	2.9 ± 1.1 (4)	0.2 ± 0.3 (8)	— (8)	< 0.1 (6)	0.4 ± 0.4 (8)	— (8)	— (8)	— (8)
PL	— (16)	0.1 ± 0.1 (15)	0.1 ± 0.1 (9)	0.1 ± 0.1 (16)	0.1 ± 0.1 (11)	0.2 ± 0.2 (16)	0.5 ± 0.4 (16)	2.3 ± 1.0 (13)	0.1 ± 0.2 (16)	0.3 ± 0.3 (15)	0.5 ± 0.3 (16)	0.5 ± 0.6 (14)	0.3 ± 0.5 (15)	— (15)
FCU ^u	— (7)	< 0.1 (7)	0.1 ± 0.3 (6)	< 0.1 (7)	— (6)	< 0.1 (7)	< 0.1 (7)	0.3 ± 0.3 (7)	2.8 ± 0.8 (4)	1.4 ± 1.1 (7)	< 0.1 (7)	— (7)	— (5)	— (7)
FCU ^h	— (6)	— (6)	— (3)	— (6)	0.1 ± 0.1 (6)	— (6)	— (6)	0.5 ± 0.2 (6)	1.0 ± 0.7 (6)	4.3 ± 1.9 (3)	0.2 ± 0.2 (6)	0.1 ± 0.1 (5)	— (5)	— (6)
FCR	— (5)	0.1 ± 0.1 (6)	— (5)	— (4)	— (2)	— (6)	0.1 ± 0.1 (3)	0.1 ± 0.1 (2)	— (8)	0.3 ± 0.3 (10)	3.5 ± 1.4 (7)	0.2 ± 0.2 (3)	— (4)	0.5 ± 0.4 (4)
UHd	0.1 ± 0.2 (14)	< 0.1 (15)	0.1 ± 0.3 (9)	< 0.1 (15)	— (15)	0.1 ± 0.2 (15)	— (15)	— (15)	0.1 ± 0.3 (15)	< 0.1 (15)	0.1 ± 0.3 (14)	0.3 ± 0.6 (15)	3.6 ± 2.1 (7)	0.3 ± 0.7 (15)
ECU	0.2 ± 0.3 (7)	< 0.1 (9)	— (7)	— (9)	— (8)	< 0.1 (9)	— (9)	< 0.1 (9)	0.3 ± 0.4 (9)	0.3 ± 0.6 (8)	— (9)	0.1 ± 0.4 (7)	0.1 ± 0.4 (9)	— (9)

Material from part II (barbiturate material). The motor nuclei are listed from top to bottom, the stimulated nerves from left to right. Upper row: mean EPSPs in mV (± s.d.); —, Ia excitation was not present in any cell. Lower row (in parentheses): number of cells tested.

bidirectionality of this pathway, although convergence from median afferents is a regular finding in APL motoneurons (Table 2). In the only APL motoneuron, which was recorded in an experiment with complete median nerve dissection, monosynaptic Ia excitation was present from FCR, but not from the other median nerve branches. There are no experimental data which indicate that both muscles develop force in the same direction. Based on the anatomical course of the APL one could assume that activation of this muscle might cause a supinating force component, parallel to the extension of thumb and index. This undesired force vector could be counteracted by a co-contraction of the FCR. It is interesting that the FCR also projects onto Sup (0.3 ± 0.4 mV, $n = 9$), which has bidirectional relations with APL.

The relations between the FCR and the pronating muscles are similar to those with the supinating muscles. The connections with the PrT are bidirectional but skewed (FCR gives stronger excitation than it receives). A common mechanical action has not been described in the cat but, as in humans, it could consist of pronation in the supinated forelimb. The projection from FCR onto PQ is strictly unidirectional.

The FCR crosses the wrist on the radial side which is the appropriate place to monitor an insufficient wrist stabilization. The widespread projection field of this muscle covers most of the physiological extensors and is regarded as part of a general extensor synergism, serving the distribution of the length signal to the different antigravity muscles.

Pronator group. PQ and PrT are included in a common Ia synergistic group since they have regular bidirectional Ia connections. This correlates with the mechanical agonism of these muscles in pronation. The size of the Ia EPSPs indicates a strong but skewed linkage.

There are distinct differences in the further Ia relations of the nuclei. The Ia connectivity of the PrT is governed by the connections with the elbow flexors (Tables 7 and 9). Ia afferents from the PrT evoked substantial effects in Bi (0.3 ± 0.4 mV, $n = 22$), Br (0.7 ± 0.4 mV, $n = 20$) and ECR motoneurons (0.4 ± 0.3 mV, $n = 7$; excitation was present in both ECRL and ECRB motoneurons; compare Tables 2, 3 and 5 for the effects from the median nerve in the respective motor nuclei). In the reverse direction most PrT motoneurons received Ia excitation from the different members of the biceps group. The relations between PrT and Bi are balanced; those between PrT and Br are skewed (Br receives stronger Ia excitation from PrT than it gives). Because of the bidirectionality of these relations the PrT is included in the biceps group (Fig. 7). Six PrT motoneurons received Ia excitation from the triceps group ($n = 70$). The relation was unidirectional. Although the mean values were small, the individual EPSPs could reach considerable sizes (Fig. 5, *K-S*; mean of the positive cases from TLo+TM: 0.5 ± 0.5 mV, $n = 6$; from TLa+An: 0.7 ± 0.9 mV, $n = 4$). Convergence from the Tri-FCR muscles on one side and from the elbow flexors on the other seemed to exclude each other. The neurone of Fig. 5*A-J* received convergence from the elbow flexors, the neurone of Fig. 5*K-S* from the extensors. This finding was substantiated by correlation tests performed on the whole sample of PrT motoneurons (Table 4, Fig. 4*G-H*). The EPSPs from FCR were negatively correlated with those from Bi, Br (not illustrated) and the sum generated by BRD and ECR. The EPSP from PQ in PrT motoneurons was positively correlated to the

TABLE 9. Mean amplitudes of the Ia EPSPs evoked in the PrT, PQ and FCR motor nuclei

Moto- neurones	Nerves							
	Bi	Br	BRD	ECRL	ECRB	PrT	PQ	FP5
PrT	0.4 ± 0.4 (65)	0.4 ± 0.5 (65)	0.3 ± 0.3 (20)	0.3 ± 0.3 (27)	0.9 ± 0.5 (27)	4.8 ± 2.1 (51)	1.4 ± 0.9 (62)	< 0.1 (62)
PQ						2.4 ± 0.8 (6)	3.7 ± 1.5 (6)	0.2 ± 0.3 (6)
FCR	< 0.1 (35)	— (35)	— (14)	— (19)	< 0.1 (20)	0.1 ± 0.1 (35)	— (35)	— (27)

Moto- neurones	Nerves							
	FCR	APL	TLa + An	TLo + TM	Uhd	DR	M	U1
PrT	0.5 ± 0.6 (66)	— (52)	< 0.1 (66)	< 0.1 (66)	— (1)	1.3 ± 0.7 (54)	3.9 ± 1.4 (9)	— (65)
PQ	0.2 ± 0.2 (6)				0.2 ± 0.2 (5)	2.6 ± 1.1 (4)		1.7 ± 1.2 (5)
FCR	4.1 ± 1.2 (21)	0.8 ± 0.8 (30)	0.3 ± 0.4 (34)	1.0 ± 0.7 (34)		0.7 ± 0.8 (24)	2.0 (1)	0.8 ± 0.8 (29)

Material from part II (chloralose material). The motor nuclei are listed from top to bottom, the stimulated nerves from left to right. Upper row: mean EPSPs in mV (\pm s.d.); —, Ia excitation was not present in any cell. Lower row (in parentheses): number of cells tested.

different Ia inputs (note that the PQ EPSP is in a comparable range in both PrT motoneurones of Fig. 5). The different Ia patterns are possibly matched by different motoneurone types. When the fifteen PrT motoneurones in which the after-hyperpolarization (AHP) was determined are ranked with respect to the AHP duration, Ia excitation from the triceps group and FCR was present in neurones with longer AHP, convergence from the biceps group in neurones with shorter AHP (Table 10). The material is too small to draw firm conclusions, but it indicates a trend which might be interesting to pursue in further investigations.

In addition to its affiliation with the PrT the PQ is associated with some digit and wrist flexors (Tables 7–9). It is Ia receptive from all FP heads (Table 7). The relations with the intrinsic paw muscles innervated by the Uhd nerve are probably skewed; Ia excitation from the PQ was found in a single Uhd motoneurone ($n = 18$). In the reverse direction three of the eight recorded PQ motoneurones were Ia excited from Uhd afferents, and the size of the EPSPs points to a moderate strength of this connection. Tables 7 and 8 show the close relations of the PQ with the deep radial group. The PQ afferents excited 45% of the ECU motoneurones (note that there is Ia excitation from median afferent in EDC, EDL and EIP motoneurones; Table 2). All PQ motoneurones were Ia excited from the deep radial nerve. Additional experiments (N. Fritz, M. Illert & T. Yamaguchi, unpublished observations) revealed a unidirectional excitation of the PQ (four cells) from ECU, EDC and EDL; no effects were found from the ECR, Sup, APL, EIP, Bi and Br muscles.

Intrinsic paw muscles. The Ia connectivity of the intrinsic paw muscles was only cursorily investigated, since the complex anatomical situation in the paw did not allow an extensive nerve dissection of the intrinsic muscles combined with dissection

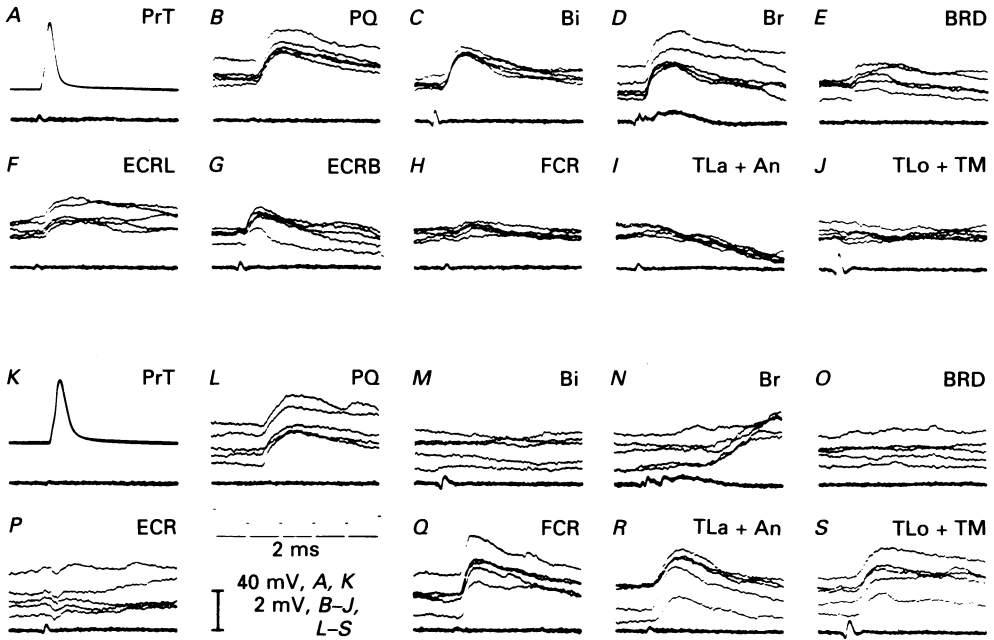


Fig. 5. Intracellular records from two PrT motoneurons. The neurone shown in A-J received Ia excitation from the biceps group; the neurone in K-S excitation from the triceps group. Construction of the figure as in Fig. 3.

TABLE 10. Ia convergence on to PrT motoneurons

Unit	AHP	Bi	Br	BRD	ECRL	ECRB	ECR	FCR	TLa + An	TLo + TM	AP	HEP
1	90	—	—	—	—	—	—	2.2	2.0	1.5	70	2.9
2	60	—	0.3	—	—	0.5	—	0.1	0.2	—	65	6.5
3	60	—	—	—	—	—	0.3	0.7	—	—	74	3.0
4	60	0.1	—	—	—	—	0.6	—	—	0.2	87	1.9
5	58	—	—	—	—	—	0.3	0.4	—	0.2	81	2.8
6	56	—	—	—	—	—	0.8	1.3	0.3	—	78	+
7	55	—	1.4	0.8	0.3	0.8	—	—	—	0.2	78	5.0
8	55	0.7	0.6	—	0.2	0.5	—	0.2	—	—	79	4.0
9	55	0.5	1.0	0.5	—	—	1.7	—	—	—	82	4.5
10	54	0.7	1.1	0.3	0.2	0.7	—	—	—	—	75	+
11	50	0.4	—	0.8	—	—	2.5	0.7	—	—	81	+
12	50	0.2	0.4	—	—	—	0.9	—	—	—	74	1.6
13	50	0.7	0.5	0.3	0.2	0.6	—	—	—	—	65	3.4
14	45	0.6	0.5	0.2	—	0.3	—	—	—	—	84	3.0
15	40	0.8	0.6	1.1	0.6	0.8	—	—	—	—	74	+

Material from part II (chloralose anaesthesia). The neurones are listed from top to bottom. The amplitude of the antidromic action potential (AP), the size of the maximal homonymous Ia EPSP (HEP) and the amplitude of the Ia EPSPs evoked from the different nerves is given in mV, the duration of the after-hyperpolarization (AHP), in ms. +, size of the Ia EPSP could not be established; —, no Ia convergence; no entry, combination was not tested.

of the forearm nerves. The connection patterns are displayed in Table 7. The MHd and UHd afferents projected in many cases to different forelimb muscles. Thus MHd afferents excited the wrist flexors except FCUu, and a projection from UHd afferents onto that group was only present in PL motoneurons. The connections of both nerves with the FP heads were unobtrusive: MHd afferents did not project into that group at all, UHd afferents only onto the FP2u. Both nerves projected onto the ECU motor nucleus. Excitation of UHd motoneurons originated from a variety of forelimb muscles, but since the motoneurons belong to different motor nuclei the presence of these projections was irregular and the amplitudes of the mean EPSPs small. The occurrence of Ia excitation from the deep radial nerve stem was surprising, but there is unfortunately no indication from which muscle this excitation originated. Stable intracellular recordings from MHd motoneurons were obtained in a single cell only. It received convergence from the PrT, FCR and UHd afferents.

DISCUSSION

Principles of Ia connections in the forelimb

Myotatic principle

It has been postulated that muscles acting in the same direction onto a common joint have bidirectional relations with each other (Lloyd, 1946*a, b*). Most of the Ia connections of the cat hindlimb follow this rule (Eccles *et al.* 1957; Eccles & Lundberg, 1958). In the forelimb the criterion of a similar mechanical action onto a common joint is fulfilled in several cases: Bi, Br, BRD; TLo, TM, TLa, An; SUP, APL (fibres coursing from ulna to radius); PrT, PQ; FCUh, FCUu. The Ia connections between these muscles are mostly bidirectional and balanced. Apparently the myotatic organization is optimally suited for the mechanical situation at joints with one degree of freedom where the synergistic-antagonistic relations are stereotyped and fixed.

Neighbouring principle

The mechanical situation is much more complex at joints with several degrees of freedom, like the wrist. Movements into a specific direction require the balanced shortening of two or more muscles, as isolated contraction of just one muscle (e.g. during load compensation) would disturb the balance and impress its characteristic direction on the intended movement. At the lateral side of the forelimb this graded mechanical synergism is reflected in graded Ia connections between the extensor muscles acting on the wrist. This graded pattern may be regarded as a modification of the myotatic principle. In this manner bidirectional heteronymous Ia pathways connect immediate anatomical neighbours which differ only slightly in their mechanical action onto the common joint. Muscles, which may change their synergistic-antagonistic relations (e.g. ECR and ECU), are thus only indirectly connected by the Ia system.

It is an interesting question if this organization is of general relevance for ball-like joints or specific for the extensors of the wrist. The palmar wrist muscles do not show a comparable pattern. No information is available on the intrinsic paw muscles. A comparable mechanical situation is present at the ankle (tibialis anterior, extensor

digitorum longus and peroneus muscles). The analysis is not so complete as in the forelimb, but the data of Eccles *et al.* (1957) indicate that the Ia relations crossing this joint may follow the proximity of the muscles, thus reflecting a graded mechanical synergism.

The modification of the strict myotatic principle to more extended patterns which are related to different mechanical actions of the involved muscles is present in other Ia systems as well (neck muscles: Anderson, 1977; Rapoport, 1979; Brink, Jinnai & Wilson, 1981; back muscles: Jankowska, Padel & Zarzecki, 1978). However, interpretation is more difficult in these cases since the mechanical situation is not as clear as in the case of the extensors of the wrist.

Unidirectional and skewed Ia relations

The large number of such projections in the distal forelimb differs from their rarity in the hindlimb. The numerous unidirectional projections onto the supinator and pronator muscles are viewed under the common aspect of a stabilization of the radio-ulnar plane. Since the forearm rotates around the ulna, forces applied to the paw will change the radio-ulnar angle. When, for example, the elbow extensors increase their force during the yield (English, 1978; Miller & van der Meché, 1975), unidirectional Ia excitation of the Sup, APL, PrT and PQ muscles from the triceps group (and from the other physiological extensors) will stabilize the radio-ulnar plane. Indeed, EMG studies in the unrestrained cat show that Sup, APL, PrT and PQ are active in the respective phases of the step cycle (English, 1978; Hoffmann, Illert & Wiedemann, 1987 and to be published) which supports this hypothesis. It is postulated that unidirectional Ia projections from a prime mover will assist the readjustment of the position of a distal joint which may be secondarily affected by contraction of the prime mover ('readjustment hypothesis').

Projections from the biceps and triceps groups may be present in one and the same motoneurone of the Sup, APL and PrT motor nuclei, but is also distributed to different neurones of one motor nucleus which could reflect an extensor- or flexor-coupled activation of the respective motor units. During locomotion the Sup and APL muscles are in fact active during the flexion and extension phases (English, 1978), with a preponderance in the extension phase (Hoffmann *et al.* 1987). However, there is no indication so far that the two motor nuclei are composed of different cell populations activated in different phases of the step cycle as was observed for the sartorius muscle in the cat hindlimb (Hoffer, Loeb, Sugano, Marks, O'Donovan & Pratt, 1987).

The readjustment principle may explain the unidirectional excitation of the ECU from the different physiological extensors. This muscle inserts on the fifth metacarpal bone. It abducts the wrist and wedges the metacarpal bones against each other. The latter action will secure the stiffness of the palmar arch, which is endangered during the support phase of the gait.

The relations between the wrist and digit extensors may serve a similar purpose. Contraction of the wrist extensors leading to wrist dorsiflexion will influence the proper action of the digit extensors: the tendons of the latter muscles will slacken and the grip will become loose. In such a case the skewed or unidirectional Ia projections from the wrist extensors onto the digit extensors may increase contraction of the latter and thus readjust the constant position of the phalanges. On the other hand, digit movements will not seriously affect the wrist position, since the reverse projections are weaker or non-existent.

Negative correlated projection strength

Burke (1968) showed that positive correlations between homonymous and heteronymous Ia EPSPs reflect the relation between membrane resistance and EPSP size. Therefore they cannot be used to investigate the relations between two inputs to a motor nucleus. Before this background the negative correlations found in the EDC, EDL, ECU and PrT motor nuclei indicate a functionally important internal organization of these motoneuronal pools. There is no strict separation of the nuclei into discrete subpopulations of motoneurons with qualitatively different heteronymous Ia inputs, but the distribution of the EPSP amplitudes points to a continuous transition between the cells. The motor nuclei with negatively correlated Ia inputs innervate multifunctional muscles. Fritz & Yamaguchi (1985, 1986) found that the heteronymous Ia input to EDC motoneurons is correlated with the direction of the force output of the respective muscle unit. This would suggest that the organization of the heteronymous Ia input to the EDC motor nucleus, and eventually also to the EDL, may be a consequence of the different mechanical actions of the motor units. Since the intramuscular mechanics of the ECU and the PrT are unknown it must remain open whether this explanation could apply for these muscles as well.

In a broader context these findings belong to the sensory partitioning phenomenon (survey in Vanden Noven, Hamm & Stuart, 1986) originally described for homonymous Ia projections (Botterman, Hamm, Reinking & Stuart, 1983). The presence of such an organization also for the heteronymous Ia projections, as now suggested for the EDC, EDL, ECU and PrT motor nuclei, would support the hypothesis that partitioning is a more general phenomenon.

Nuclei with negatively correlated Ia inputs are organized in a two-dimensional way: one dimension is given by parameters such as motor unit type or membrane resistance, the other dimension results from the source of the major Ia input. This must have consequences for the recruitment of motoneurons in reflex actions and suggests that multifunctional muscles have a changing recruitment order (e.g. Thomas, Schmidt & Hambrecht, 1978; see also ter Haar Romeney, Denier van der Gon & Gielen, 1982, 1984, 1984; van Zuylen, Denier van der Gon, Gielen & Jongen, 1986). In humans a changing recruitment order has been demonstrated in the EDC muscle (Thomas *et al.* 1978). This is interesting since the EDC motor nucleus displays a negative correlation of its Ia inputs in the cat.

Functional synergies

In the early investigations on the organization of the Ia pathways in the cat hindlimb it was found that the Ia receptiveness of most motor nuclei was restricted to agonists at the same joint (Lloyd, 1946*a, b*; Laporte & Lloyd, 1952; Eccles *et al.* 1957). The more detailed experiments by Eccles & Lundberg (1958) at the hip and knee joints revealed more distributed patterns which suggested that the Ia pathways support movements of a the whole limb, for example, during locomotion (Eccles & Lundberg, 1958; Lundberg, 1969). The functional interpretation of the Ia relations now described for the forelimb suggests that a combination of the different basic Ia

pathways outlined above could assist muscular synergies in complex forelimb movements.

Ia synergistic groups

To structure the widespread heteronymous Ia relations, motor nuclei with similar Ia patterns were combined into 'Ia synergistic groups'. This grouping was done on the basis of bidirectional, desirably balanced Ia pathways between the different

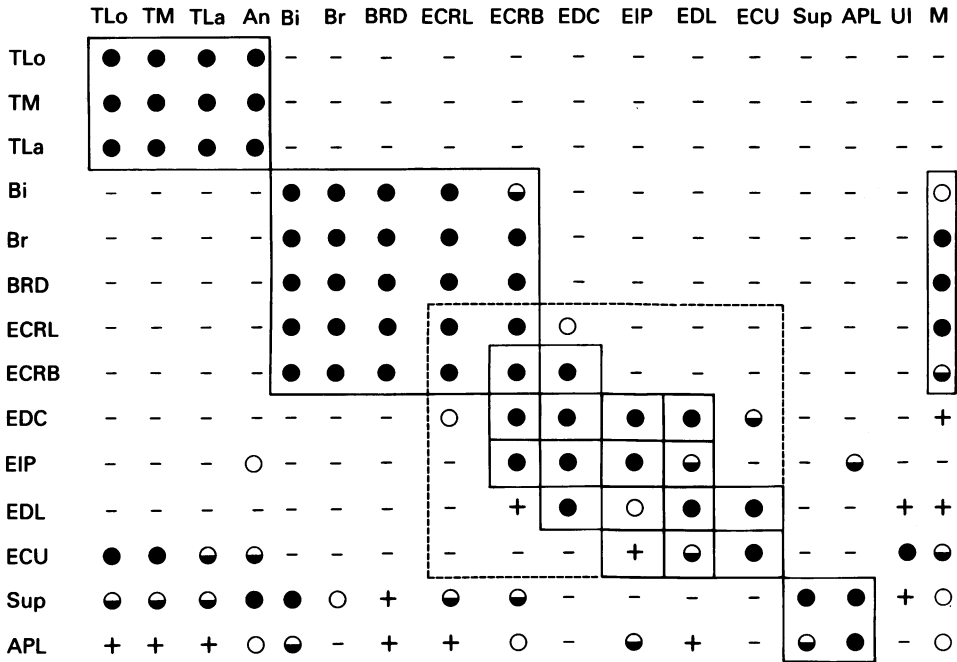


Fig. 6. Ia synergistic groups at the elbow and on the lateral side of the forelimb. The figure is based on Table 2 with the modification that only combinations with five or more cells are given. The motor nuclei are listed from top to bottom, the nerves from left to right. The occurrence of the projections is given as a percentage but for an easier survey the values are grouped in five different classes. The Ia synergistic groups are indicated by continuous lines, the group of the extensors of wrist and digits by a dashed line. ●, > 61%; ○, 31-60%; ○, 11-30%; +, 1-10%; -, < 1%.

motor nuclei. Figure 6 covers the material of part I. One group contains the elbow extensors, a second one the elbow flexors together with the PrT muscle. Several small groups cover the relations between the extensors of wrist and digits. Since these connections follow the neighbouring principle the nuclei are combined into a common group (dashed line). We have included the EIP in this group since the Ia connections of this motor nucleus closely resemble those of the EDC and EDL. This should not obscure the bidirectional relations between EIP and APL which might serve a local synergism in extension of the pollex. Supinator (Sup) and APL form a further Ia synergistic group. On the palmar side (Fig. 7) the Ia relations are dominated by the

flexors of the digits and the flexors of the wrist. The small number of neurones recorded from in some palmar motor nuclei does not allow the establishment of more differentiated subgroups, but there are indications that such subgroups may exist. It seems that the relations between PQ and FP1-5 are closer than those between PQ and the other FP muscles, that the relation between FCR and APL might be bidirectional and that there may be a bidirectional linkage between PQ and ECU, EDC and EDL.

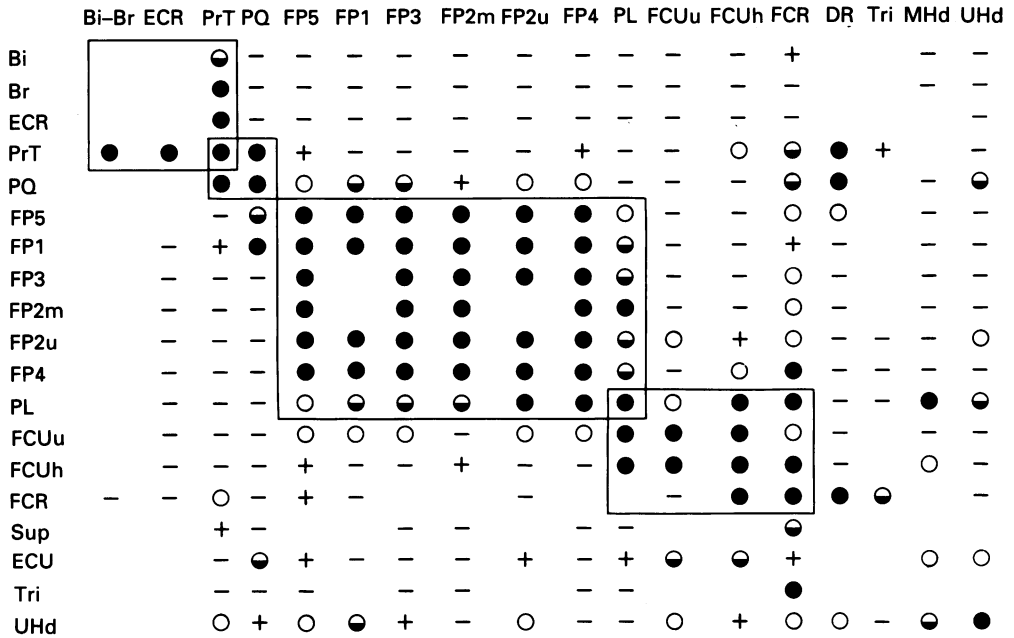


Fig. 7. Ia synergistic groups at the palmar side of the forelimb. Construction of the figure as in Fig. 6. The figure is based on the material of Table 7 with the following modifications: only combinations with five or more cells are listed; the effects evoked by separate stimulation of the Bi and Br nerves have been grouped together (Bi-Br); the actions from the APL, Sup and ECU nerves have been omitted; the combinations indicated in Table 7 by a † have been omitted. ●, > 61%; ◐, 31-60%; ○, 11-30%; +, 1-10%; -, < 1%.

This classification reveals the interesting aspect that the muscles composing one Ia synergistic group have, in addition to their bidirectional relations, two further characteristics of their Ia connections in common: the pattern of heteronymous Ia excitation received from muscles outside the group is very similar for the different group members; the pattern of heteronymous excitation given from the different group members onto motor nuclei not belonging to the group is nearly identical. One muscle may belong to several Ia synergistic groups. The described similarities raise the question whether the grouping of motor nuclei as Ia synergists may reflect a common behaviour in movements (Hoffmann *et al.* 1985, 1986; Illert, 1986 and to be published).

Extensor synergism

During locomotion forelimb muscles belonging to the following groups are activated during the stance phase: triceps group, group of wrist flexors, group of digit flexors, supinator group, pronator group and ECU (English, 1978; Hoffmann *et al.* 1985, 1987). The co-ordinated activation of these muscles may be supported by three sets of Ia pathways. The basic set of connections corresponds to the internal pathways within the triceps, the wrist and the digit flexor groups. These groups control the position of the large forelimb joints and their Ia connections follow the myotatic principle. The second set of relations interconnects these three Ia synergistic groups. The pathways between the wrist and digit flexors reflect the proximo-distal level of the muscular insertions: the central position of the PL is mirrored by the mainly bidirectional relations of this muscle with the proximally inserting wrist flexors and the distally inserting FP muscles; the linkage between the more distant wrist flexors and the FP muscles is substantially weaker and mainly unidirectional. The elbow extensors are isolated from the distal groups; the FCR is the only palmar physiological extensor they are connected with. The third set of Ia connections incorporates the ECU, the supinator and the pronator group in the extensor synergism. Each of these muscles receives Ia excitation from the distal physiological extensors and from the triceps group. These connections probably secure the position of the radio-ulnar plane and of the metacarpal arch during transmission of force to the ground.

The organization of the Ia connections subserving a comparable extensor synergism in the cat hindlimb is less differentiated (Eccles *et al.* 1957; Eccles & Lundberg, 1958). The basic set of relations is similar, i.e. presence at each joint of muscles interconnected in groups according to the myotatic principle. Regarding the pathways between the groups a possible parallelism is less obvious. The anatomical situation between wrist and ankle is too dissimilar to make a detailed comparison reasonable. Similarities exist between elbow and knee since in both cases only one connection crosses the joint from proximal to distal. It is unidirectional in the hindlimb (from vastocruureus to soleus, Eccles *et al.* 1957), but probably bidirectional in the forelimb (Tri-FCR). Unidirectional pathways serving a readjustment principle have so far not been described in the hindlimb.

Flexor synergism

The Ia connections of the biceps group represent a generalized flexor synergism of the forelimb. The group is comprised of muscles with different mechanical actions: flexion of the elbow, extension of and radial abduction of the wrist, pronation of the forearm. The myotatic agonists in these different actions are interconnected by bidirectional and balanced pathways (Bi, Br, BRD; ECRL, ECRB; PrT, PQ). The bidirectional connections between the elbow flexors and the wrist extensors reflect the in-series arrangement of the elbow and wrist joints. Indeed, limb lifting is characterized by a synchronous activation of the elbow flexors and the wrist extensors (Hoffmann *et al.* 1985, 1986). The inclusion of the PrT muscle in the biceps group is surprising and difficult to interpret. The bidirectional relations indicate a close synergism which is supported by the regular activation of the PrT in the paw lifting behaviour (Hoffmann *et al.* 1986, 1987). Since the PrT has an only minimal elbow flexing function (F. Caliebe, J. Häussler & M. Illert, unpublished observations)

readjustment of the radio-ulnar plane during paw lifting would be the most likely explanation for these connections. X-ray cinematography during locomotion has shown that the forearm is supinated when the paw is lifted from ground (F. Caliebe, J. Häussler & M. Illert, unpublished observations), possibly due to a supinating action of the biceps muscle. The Ia projections onto the PrT would help to counteract this undesired movement.

Synergisms subserving manipulatory paw movements

Several of the described Ia relations may support the manipulatory capacity of the paw. This is evident in case of the Ia relations organizing the neighbouring principle, which sculpture subsets of two or three muscles out of the layer of the wrist and digit extensors. One subset represents a defined sector of the space, and the balanced and co-ordinated contraction of all subset members is needed to place and keep the limb in that area. Each subset member belongs to other subsets as well, which ensures that each part of the space made available by the ball-like construction of the wrist joint is matched by an appropriate combination of muscles. The synergism of the neighbourhood principle is supplemented by the presence of negative correlations between heteronymous Ia inputs (EDC, ECU and probably also EDL). They organize a motor nucleus into subpopulations of motoneurons according to the force vector of the muscle units (Fritz & Yamaguchi, 1985, 1986). This supports the finely tuned selection of force vectors which is necessary in manipulatory movements.

The unidirectional or skewed bidirectional relations between the extensors of wrist and digits reflect a further synergism which may support the manipulatory capacity of the paw. They provide an independent function of the interconnected muscles rather than subordinating them into a common movement pattern. This secures independence of the distal joints from interference of reflex actions onto proximal muscles.

There remain several questions regarding the contribution of Ia mechanisms to grasping and object manipulation. There is the interesting finding that the Sup and PrT muscles, which actively participate in all aspects of delicate paw movements (English, 1978; Hoffmann *et al.* 1986), have only weak Ia connections with the intrinsic paw muscles. There are also the astonishing Ia relations between PQ and EDC/EDL, which may assist in exploratory movements. In any case, concepts on the organization of manipulatory forelimb movements must remain incomplete as long as systematic investigations on the Ia relations between the intrinsic paw muscles are not possible. Concerning the few observations in the present paper on the connections between the intrinsic and extrinsic paw muscles it is our impression that these pathways support an extensor synergism rather than assisting manipulatory paw movements.

Adjustment of reflex pathways to versatile forelimb movements

The cat forelimb shows a differentiated and complex mechanical behaviour. The ball-like construction of the distal joints together with the possibilities for pronation/supination makes a large part of the space available for the paws (Leyhausen, 1979). This versatile capacity must have important consequences for the organization of motor programs in the brain as well as for the 'functional units'

at the spinal level (Baldissera, Hultborn & Illert, 1981). It is a most important aspect in this context that the synergistic-antagonistic relations between the forelimb muscles are not constant but change according to the intended movements. The present paper shows that patterns of heteronymous Ia connections have developed which support the organization of these changing synergies. This suggests that the central organization of the many different synergies which are necessary for the large repertoire of movements indeed are matched by corresponding patterns of Ia connections. Such a comprehensive capacity of the Ia system was not realized in the early investigations which suggested that the Ia system mainly supported simple and stereotyped movements.

Evidence is accumulating that other spinal functional units have also adapted to the versatile movement repertoire of the distal forelimb. Illert, Lundberg & Tanaka (1976) have reported that the Ib actions seem to be larger in the forelimb than in the hindlimb segments. They have also shown the presence of a short latency cutaneous pathway which was discussed in connection with the manipulatory capacity of the paw. A recent study on the distribution of the recurrent inhibition from motor axon collaterals to motoneurons suggests that some motor nuclei to extrinsic paw muscles lack recurrent axon collaterals (Hahne, Illert & Wietelmann, 1988). It is to be expected that a more detailed analysis will reveal further modifications of the spinal functional units in the brachial segments.

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