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Monosynaptic Ia pathways and motor behaviour of the cat distal forelimb

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Review

Abstract. The projection pattern from large muscle spindle afferents (Ia) onto cat α-motoneurones innervating the elbow, wrist and digit muscles is correlated with new electromyographical and x-ray kinematic data on the motor behaviour of the forelimb. This correlation suggests that the Ia-synergistic groups may be one substrate to organize movement components mobilized in motor behaviour. This hypothesis is based on the data on the active stabilization of the radio-ulnar joints during the stance phase, on the data on the Ia-organization of a motor nucleus taking part in different motor behaviours and on the results showing how the Ia convergence onto the long digit extensor muscles fits the execution of finely tuned movements at ball joints.

Key words: forelimb muscles, forelimb motoneurones, x-ray cinematography, food taking movement, target reaching movement, treadmill locomotion

INTRODUCTION

In motor research increasing efforts are concentrated on the experimental investigation of how a certain neuronal system contributes to the execution of an integrated motor behaviour. A typical example for this research strategy is the investigation of the C3-C4 propriospinal system (Alstermark et al. 1981). In this system the anatomical location of the descending axons allows their rather selective abolition, thus giving the possibility to study the resulting deficit symptoms as a sign of their normal function. Other examples of this research strategy are discussed in Hultborn and Illert (1990).

Another way to investigate the contribution of a neural system to motor control is to correlate the architecture of its connections with the activation patterns of the respective muscles in unrestricted motor behaviour. This research strategy is based on the observation that the execution of even the simplest movements involves a large number of muscles, but that the pattern of muscle activity is very consistent for a defined type of movement. Beevor (1904) claimed that the neuronal arrangements for such stereotyped movements are laid down in the spinal cord. These various muscle synergies would thus be represented by different sets of spinal connections. They have been termed "spinal functional units" (Baldissera et al. 1981, Hultborn and Illert 1990) and are thought to be mobilized during ordinary voluntary movements (cf. Foster 1879).

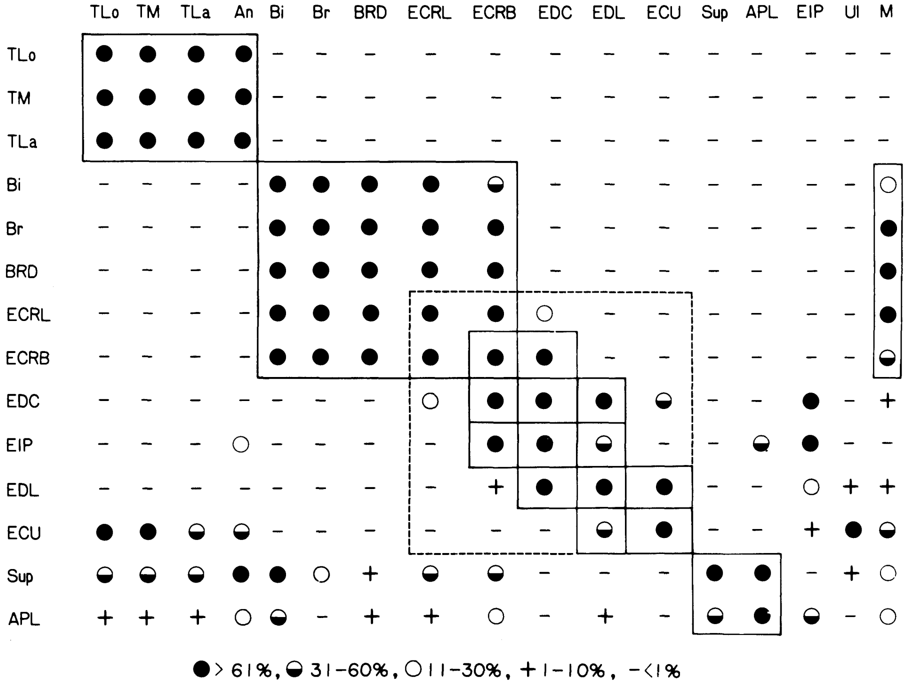
One of the best examples of such spinal functional units is the monosynaptic excitatory connection from Ia afferents to heteronymous α-motoneurones. The pattern of these connections has been investigated in detail in the different limbs of various species (early ref. in Baldissera et al. 1981, recent experiments in the cat: Fritz et al. 1989, in the monkey: Hongo et al. 1984, in humans: Pierrot-Deseilligny et al. 1981, Mao et al. 1984, Cavallari and Katz 1989, Cavallari et al. 1992). There is general agreement that the Ia interconnected muscles are closely associated in function. Since the pioneering studies of Laporte and Lloyd (1952) it is established that bidirectional and balanced Ia relations reflect a tight mechanical agonism of the interconnected muscles (acting into the same direction onto a common joint). However, already the early investigations in the cat hindlimb (Eccles at al. 1957, Eccles and Lundberg 1958) have shown that the synergism represented by this functional unit is by no means restricted to the mechanical agonists, but may include distant muscles acting at different joints. When they correlated the architecture of the heteronymous Ia connections with the activation patterns of the hindlimb muscles during locomotion Engberg and Lundberg (1969, see also Lundberg 1969) concluded that in this extremity the Ia connections may assist locomotion or, in more general terms, may organize a generalized flexion - extension synergism.

These results promoted the view that the synergism represented by the spinal functional unit of the Ia system is rather rigid and that, by not allowing much flexibility, is optimized for assisting stereotyped flexion-extension movements, like locomotion.

ORGANIZATION OF THE Ia SYSTEM OF THE CAT FORELIMB

Fritz et al. (1989) investigated the monosynaptic Ia connections in the cat forelimb and found an extended, but highly organized pattern. It is summarized in Fig. 1. Bidirectional pathways (e.g. interconnecting the different triceps muscles) are present, as are unidirectional ones (e.g. from the triceps heads onto the extensor carpi ulnaris [ECU] or onto the supinator [Sup] neurones). In many cases the convergence pattern onto a motor nucleus includes muscles acting at different joints (e.g. extensor carpi radialis [ECR] motoneurones receive Ia convergence from biceps [Bi], brachialis [Br] and extensor digitorum communis [EDC] afferents). The connections of one muscle are not necessarily restricted to one side of the limb, but can cross the radio-ulnar plane (e.g. Br motoneurones receive Ia excitation from median [M] afferents, ECU motoneurones from ulnaris [Ul] afferents).

Based on these findings it was argued that the Ia system of the forelimb is much more complex than



	TLo	TM	TLa	An	Bi	Br	BRD	ECRL	ECRB	EDC	EDL	ECU	Sup	APL	EIP	Ul	M
TLo	●	●	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-
TM	●	●	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-
TLa	●	●	●	●	-	-	-	-	-	-	-	-	-	-	-	-	-
Bi	-	-	-	-	●	●	●	●	◒	-	-	-	-	-	-	-	○
Br	-	-	-	-	●	●	●	●	●	-	-	-	-	-	-	-	●
BRD	-	-	-	-	●	●	●	●	●	-	-	-	-	-	-	-	●
ECRL	-	-	-	-	●	●	●	●	●	○	-	-	-	-	-	-	●
ECRB	-	-	-	-	●	●	●	●	●	●	-	-	-	-	-	-	◒
EDC	-	-	-	-	-	-	-	○	●	●	●	◒	-	-	●	-	+
EIP	-	-	-	○	-	-	-	-	●	●	◒	-	-	◒	●	-	-
EDL	-	-	-	-	-	-	-	-	+	●	●	●	-	-	○	+	+
ECU	●	●	◒	◒	-	-	-	-	-	-	◒	●	-	-	+	●	◒
Sup	◒	◒	◒	●	●	○	+	◒	◒	-	-	-	●	●	-	+	○
APL	+	+	+	○	◒	-	+	+	○	-	+	-	◒	●	◒	-	○

●> 61%, ◒ 31-60%, ○ 11-30%, + 1-10%, -<1%

Fig. 1. Ia synergistic groups at the elbow and on the lateral side of the forelimb. The figure summarizes the projection frequencies presented in the work of Fritz et al. (1989). The motor nuclei are listed from top to bottom, the stimulated nerves from left to right (abbreviations are given in the text). The occurrence of the projections is given as percentage, but for an easier survey the values are grouped in five different classes (symbols in the lower row). The Ia synergistic groups are indicated by continuous lines, the group of extensors of wrist and digits by a dashed line. (Reproduced from Fritz et al. 1989).

that of the hindlimb and that it should be capable to cope with and assist the differentiated repertoire of manipulatory paw movements (Fritz et al. 1989). It was suggested that the Ia pathways assemble the forelimb motor nuclei into Ia synergistic groups and that these groups represent the neural substrate to organize the synergisms needed for a coactivation of the respective muscles in motor behaviour. These Ia synergistic groups are outlined in Fig. 1.

One group contains the elbow extensors, the other one the elbow flexors together with the median pronator teres [PrT] muscle. Both groups organize elbow extension and flexion, they are interconnected *via* reciprocal Ia inhibitory pathways (Illert and Tanaka 1978). The flexor group includes the radial wrist extensors, and thus coordinates elbow flexion and wrist extension. An extended Ia synergistic group combines the different wrist and digit extensors. It is composed by small groups between the immediate neighbours, and thus ideally suited to cover paw movements into different sectors of space. The group combining the Sup and abductor pollicis longus [APL] muscles receives a broad convergence from many other forelimb muscles.

A lot of experimental evidence has been accumulated in the last years in our lab which supports the above hypothesis. The direct correlation of kinematic and electromyographical data with the results obtained with intracellular techniques on the organization of the Ia system shows that the Ia synergistic groups are a spinal functional unit and may be one substrate for the organization of simple movements or movement components mobilized in motor behaviour. Some of the respective data will be reviewed in the following.

ACTIVE STABILIZATION OF THE RADIO-ULNAR JOINT DURING THE STANCE PHASE

Figure 1 shows the Ia convergence onto Sup and APL motoneurones, as revealed with intracellular recordings (Fritz et al. 1989). Both nuclei have a very large Ia receptive field. There is convergence from all the different triceps heads. In addition from Bi, Brachioradialis [BRD] and Br (in case of the Sup), from the ECR and from M afferents. The frequency of projections is higher onto the Sup than

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	–				–	–

Fig. 2. Ia convergence onto supinator motoneurones. The neurones are listed from top to bottom. The amplitude of the antidromic action potential (AP), the size of the maximal heteronymous 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. (Reproduced from Fritz et al. 1989).

onto the APL nucleus. The qualitative aspects of the convergence are, however, similar in both nuclei. The striking feature is the co-projection from the elbow antagonists, the different triceps and the Bi muscles onto both nuclei. This co-convergence is a regular finding in the single Sup and APL motoneurones (Fig. 2 for our sample of 28 Sup motoneurones). It indicates that in this way Sup / APL motoneurones will receive exact information about the position of the elbow joint.

Figure 1 also shows the interesting finding that the Ia projections of the Sup and APL nuclei are very limited, in contrast to their wide receptive field. Beside their reciprocal interconnection they have no Ia projections onto other distal forelimb muscles (the additional reciprocal connections of the APL with the extensor indicis proprius [EIP] nucleus reflect a local synergism of both muscles). The figure further shows that the Sup motoneurones, apart from their global pattern, display a differentiated Ia convergence from the different forelimb muscles, indicating a functionally heterogeneous pool of motoneurones. This is in contrast to the findings from the hindlimb, which suggest that within a motor nucleus about 60% of the motoneurones are reached by heteronymous Ia afferents.

Co-convergence from the elbow antagonists was also found in the PrT motoneurones (Fritz et al. 1989). In this case, however, the co-convergence was not present in the single motoneurones, but the nucleus consisted of two different pools of neurones. All PrT motoneurones received Ia projection from the pronator quadratus [PQ] muscle. In the further Ia projections to the PrT neurones there were distinct differences. The Ia connectivity was governed by the connections from the elbow flexors Bi (67% of the neurones), Br (56%) and ECR (100%). Six PrT motoneurones (sample 70) received Ia excitation from the triceps muscles. Although the mean value of this projection was small, the individual EPSPs could reach considerable sizes. Correlation tests indicated that the convergence from the triceps and flexor carpi radialis muscles on one side and from the elbow flexors on the other seemed to exclude each other. These different Ia patterns are possibly matched by different motoneurone types. The Ia excitation from the triceps and flexor carpi radialis muscles was present in the PrT neurones with longer afterhyperpolarization, the convergence from the elbow flexors in the neurones with a shorter one. If this will be corroborated in further investigations (the sample presented by Fritz et al. 1989 is small) this result would indicate a division of the PrT motor nucleus in two different functional pools of α-motoneurones.

From this convergence pattern it was hypothesized that the co-convergence from the elbow antagonists could serve to stabilize the radio-ulnar plane during forward movements of the animal, e.g. during the stance phase of locomotion. 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 (Miller and van der Meché 1975, English 1978), unidirectional Ia excitation of the Sup, APL, PrT and PQ motoneurones from the elbow extensors (and from the other physiological extensors) would stabilize the radio-ulnar plane.

Kinematic recordings support the hypothesis that the radio-ulnar angle of the distal forelimb is actively maintained and controlled during the stance phase of locomotion. Figure 3C shows tracings of the radio-ulnar angle at the transition from swing to stance (upper record) and stance to swing (lower record). The angular tracings were obtained with x-ray cinematography (Caliebe et al. 1991, cf. Boczek-Funcke et al. 1994). A maximal supination angle of approximately 50° is reached during the swing phase, about 100 ms before touch-down. Then a gradual pronation starts and the limb is placed with a supination angle of 30°. A supination angle of around 20° is maintained during the stance phase until 100 ms before lift-off. A second pronation phase starts at that time and extends into the first 50 ms of the swing phase, when supination takes over.

During most of the stance phase passive forces will endanger the stability of the radio-ulnar joint position. Since the force vector transmitting the body weight onto ground is oblique to the axis of the forelimb bones (Caliebe et al. 1991), there is a continuous tendency to rotate the forelimb during the stance phase. This rotational component is not constant, but depends on the elbow and the ulnar deviation angle of the wrist which both change during stance (elbow angle: Miller and van der Meché 1975, English 1978, ulnar abduction angle: Caliebe et al. 1991). The finding that the supination angle is kept at 20° during that period indicates that this rotational component is counteracted by active forces and carefully controlled by neuronal commands.

Indeed, EMG studies in the unrestrained cat show that Sup, APL, PrT and PQ are active in the respective phases of the step cycle (F. Caliebe, M.

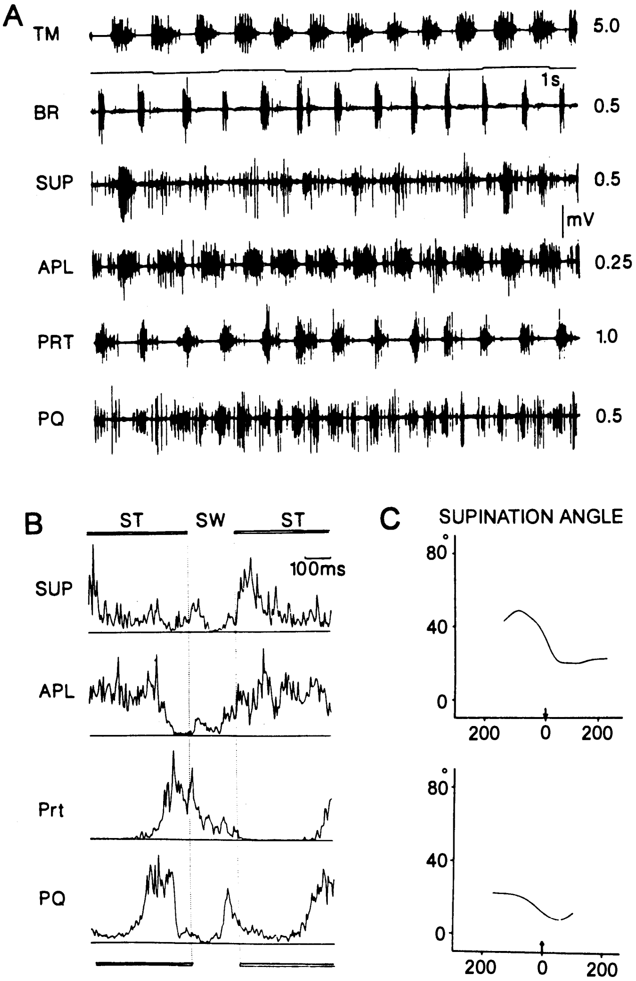


Fig. 3. Activation patterns of the supinator and pronator muscles and angular excursion of the radio-ulnar joints during treadmill locomotion. A, recordings from a cat walking at 1.2 m/s. The activity of the TM (triceps medialis) and Br muscles indicates the stance and swing phases. The calibration is given in mV. B, EMG records averaged from 15 steps of a locomotor sequence (1.0 m/s). The stance (ST) and swing (SW) phases are indicated. C, supination angle of the forelimb. x-ray data (100 frames/s) from a single step (treadmill velocity 1.0 m/s). The supination angle (upwards) is plotted against time at the transition from swing to stance (upper record) and from stance to swing (lower record). (A and B reproduced from Häußler and Illert 1991, C reproduced from Caliebe et al. 1991).

Illert and E. Wiedemann, unpublished results). This is illustrated with the EMG recordings of Fig. 3A. In contrast to the regular and stereotyped activation of the elbow and wrist muscles (Caliebe 1993), the activity of the muscles acting on the radio-ulnar joints displays variable patterns which virtually change from step to step. This is particularly evident in case of the Sup, and applies to the strength of the discharge and the detailed timing within the step cycle. The variability indicates that the control of the radio-ulnar joint reacts in a highly responsive way to the mechanical demands which change during the execution of the movement.

In Figure 3B the activity pattern of the muscles is displayed as averaged records. During the stance phase the APL is continuously active at a high level until the pronator muscles PrT and PQ take over. The Sup muscle has a pronounced discharge at the beginning of the stance phase, but then the activity declines and stays at a low level. In single steps the Sup activity was rather high in some cases, but virtually absent in others (Fig. 3A). This was similar in case of the PQ which, in the averaged records, also displayed a continuous, low level discharge throughout two thirds of the stance phase.

These results show that during stance the supination angle of 20° is maintained by the cocontraction of the supinating and pronating muscles. It seems reasonable to assume that the pronation extending from the swing into the stance phase is terminated by the brisk activation of the Sup. The continuous activity in the APL would then take over and set a certain degree of supination which would be finely tuned and adjusted by the cocontracting Sup and PQ muscles.

The second pronation at the end of the stance phase is parallelled by a strong activation of the PQ and PrT (note that in PQ the activity starts and peaks earlier than in PrT). There is no comparable intense activation of Sup and APL which would correlate with the supination in the first half of the swing phase. Either the moderate discharge in the Sup suffices for this rotation, or the supination is supported by a coactivation of agonists (refs. in Basmajian and de Luca 1985) or by inertial forces. The pronation at the end of the swing phase just before touchdown is parallelled by a short and intense discharge in the PQ which is in all likelihood responsible for this movement.

There are interesting differences in the EMG patterns of the proximal and distal pronators, PrT and PQ (Fig. 3B). There is no coactivation of both muscles during the second part of the swing (E1-phase, Caliebe et al. 1991) and the first part of the stance phase. During both these periods the physiological extensors are activated. Therefore the PrT muscle seems suited to support pronation movements during a general flexor pattern, whereas the PQ has a more general, extensor-related action. Both functions would be assisted by the respective Ia patterns.

From these findings it is postulated that unidirectional Ia projections from a prime mover, like the elbow muscles in case of the motor nuclei acting on the radio-ulnar joints, will assist the readjustment of the position of a distal joint which may be secondarily affected by the contraction of the prime mover. This readjustment principle seems to be of general validity, at least in the forelimb. It can explain the unidirectional Ia excitation of the ECU from the different physiological extensors. It is also valid at the proximal limb joints. At the shoulder a similar organization has been found in the motor nuclei to the supra- and infraspinatus and the subscapularis muscles (A. Hohn, R. Jänike and M. Illert, unpublished results), which all stabilize the position of the humeral head in the scapulo-humeral joint cavity.

Ia ORGANIZATION OF A MOTOR NUCLEUS TAKING PART IN DIFFERENT MOTOR BEHAVIOURS

It is characteristic for the forelimb that muscles acting on ball joints like the wrist take part in different motor behaviours. This is demonstrated in Fig. 4 for the ECU muscle (F. Caliebe, M. Illert and E. Wiedemann, unpublished findings). EMG recordings are displayed during a target-reaching (inset drawings 1-4) and a food-taking (inset drawings 5-8)

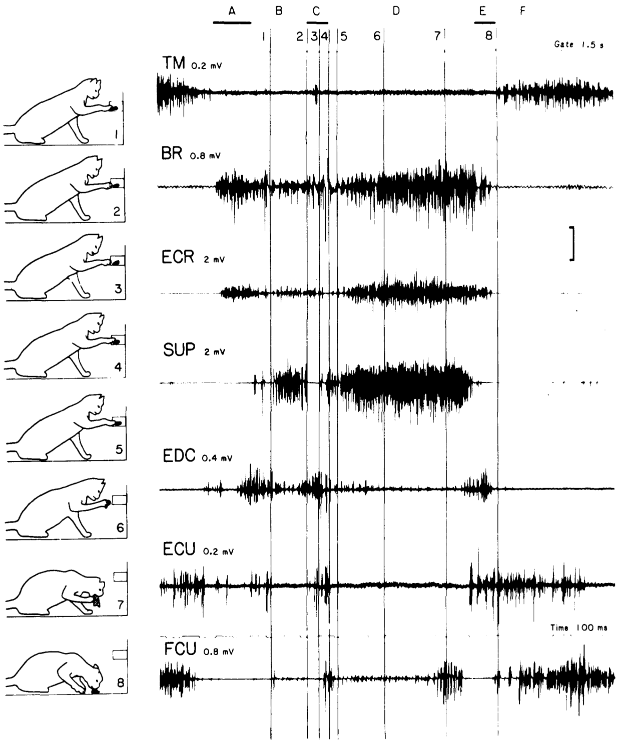


Fig. 4. Activation of forelimb muscles during a target reaching and a food taking movement of the cat forelimb. EMG recordings from different forelimb muscles, the calibration is given in mV. The inset drawings have been traced from high-speed film recordings, their timing is indicated in the EMG recordings by the vertical lines and the respective numbers. A, period of paw elevation; B, first target reaching trial and subsequent paw repositioning; C, second target reaching trial; D, food taking; E, extension of the digits and pronation of the limb; F, placing of the paw. (F. Caliebe, M. Illert and E. Wiedemann, unpublished material).

task (Górska and Sybirska 1980). During the stance phase of the right forepaw (no inset) the triceps medialis [TM], the ECU and the flexor carpi ulnaris [FCU] muscles are active. They silence when limb elevation starts with the activation of the Br and ECR muscles. The animal performed a first, but unsuccessful target reaching trial (inset 1). This trial was achieved by a temporally shifted activation of the ECR, extensor digitorum communis [EDC] and ECU muscles. In the following correction period the activity in the digit extensor muscles declines, there is a strong activation of the Sup. In the second target reaching trial (insets 3-4) the activation sequence of ECR, EDC and ECU is repeated. At the end the FCU is activated as well, which leads to the strong palmar flexion of the phalanges and of the metacarpo-phalangeal joints in this particular phase of the movement (A. Boczek-Funcke, M. Illert, B. Paschmayer and J. Raehtjen, unpublished results). Food taking is characterized by the strong activation of the Br, ECR and Sup muscles (insets 5-7). At the end of this period the limb is pronated and the paw is placed (insets 7-8). This goes together with an extension of the phalanges (activation of EDC and ECU) and the preparation for weight transfer during paw placing (activation of TM, ECU and FCU).

The records show that the ECU has two different functional tasks in this behaviour. At the end of target reaching it takes part in the digit and wrist extension (coactivation with ECR and EDC; note the same activation sequence during the pronation phase of the food taking movement), during paw placing it assists the general antigravity synergism (coactivation with TM and FCU). This double function is mirrored in the Ia convergence onto the ECU motoneurones. Figure 5 displays intracellular records from an ECU motoneurone. It receives Ia EPSPs from the different triceps heads (E-G), from the extensor digitorum longus [EDL] muscle (L) and from Ia afferents in the Ul and M nerve (O-P). The latter effects were shown to originate from the FCU, the PQ and the flexor carpi radialis muscles (Fritz et al. 1989). A survey of the ECU connections is given in Fig. 1. The convergence from the triceps, the Ul and the M Ia afferents reflect the antigravity synergism and thus correspond to the activation of the respective muscles during paw placing (inset 8 of Fig. 4), the convergence from EDL reflects the synergism in target reaching and thus corresponds to the coactivation of ECR, EDC and EDL during this period (insets 1, 3-4 of Fig. 4). To know if these two different Ia patterns are present in one and the same neurone Fritz et al. (1989) correlated the sizes of the Ia EPSPs generated from the different sources with each other. Figure 6 shows that the EPSPs from EDL were negatively correlated with the EPSPs generated from Ul, triceps longus [TLo] and TM (A,C,E). The correlation was positive between the

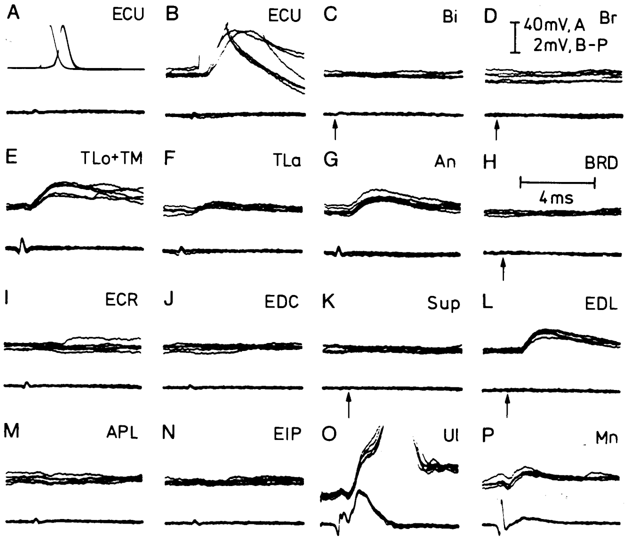


Fig. 5. Ia convergence onto ECU motoneurones. Intracellular records from an ECU motoneurone in a chloralose anaesthetized cat. The upper traces are intracellular records, the lower traces are from the dorsal root entry zone at the segmental level of the motoneurone (C8). The voltage calibration applies to the intracellular records. A-B, antidromic identification of the motoneurone, note the latency shift between the orthodromic and the antidromic spike (A) and between the homonymous Ia EPSP and the antidromic spike (B). C-P, supramaximal activation of the group I fibres (2 times threshold) in the indicated nerves. The segmental delay can be calculated from the time of arrival of the afferent summed action potential at the spinal cord (in some cases indicated by the arrows). Note the Ia excitation from the different triceps, the EDL, the Ul and the M nerves. (N. Fritz, M. Illert and P. Saggau, unpublished material).

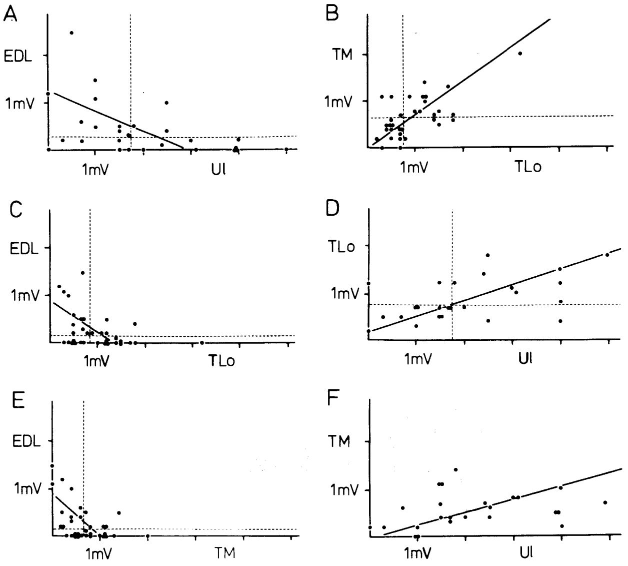


Fig. 6. Interdependence of the Ia inputs converging onto the ECU motoneurones. Each point represents one motoneurone; the coordinates give the size of the maximal Ia EPSPs evoked in that neurone from the indicated Ia systems. The dashed lines in A-E give the border lines for use in contingency tables. (modified from Fritz et al. 1989 and unpublished material).

EPSPs from the TLo, TM and Ul nerves. This suggests that Ia activation of the ECU muscle is achieved from two different functional groups of motoneurones, and that the single neurone is under the strong influence of either the one or the other source. This corresponds to the EMG pattern displayed in Fig. 4 and demonstrates that the ECU motor nucleus consists of two pools of motoneurones with different Ia convergences. A similar finding has been made with respect to the convergence onto ECU motoneurones from Renshaw cells *via* recurrent axon collaterals (Hahne et al. 1988, Hörner et al. 1991). It remains to be shown that the ECU motoneurones with strong Ia activation from the physiological extensors are also those which receive recurrent inhibition, and that they are predominantly activated during the antigravity synergism of paw placing, but not during target reaching.

THE NEIGHBOURING PRINCIPLE AS A MECHANISM FOR FINELY TUNED MOVEMENTS AT BALL JOINTS

Figure 1 shows the convergence pattern onto the extensor muscles of the wrist and digits (long and short heads of ECR [ECRL, ECRB], EDC, extensor indicis proprius [EIP], EDL, ECU). They are assembled in an extended Ia synergistic group which is composed by several smaller Ia groups. When the amplitudes of the Ia EPSPs are considered it seems that the interconnections between these nuclei follow a neighbouring principle. This is shown in Fig. 7, which displays the amplitudes of the Ia EPSPs in relation to the topographical location of the muscles across the forelimb. The extensor muscles are boxed in by the hatched lines. It becomes evident

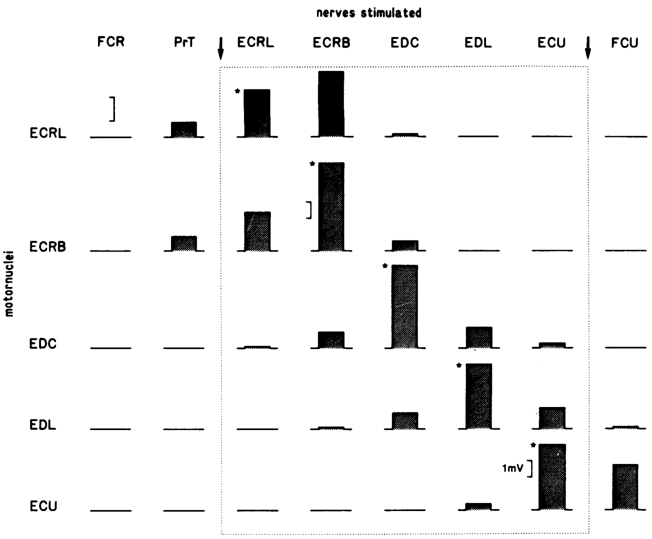


Fig. 7. Ia EPSPs in the motor nuclei at the dorsal and lateral sides of the forelimb. The motor nuclei are ranked from top to bottom (in the anatomical order from radial to ulnar), the stimulated Ia systems from left to right (starting at the palmar side and then crossing to the dorsal side from radial to ulnar). The columns display the Ia EPSPs recorded in the particular nucleus from the respective nerves (material based on the data reported in Fritz et al. 1989). The homonymous relations are marked by an asterisk. The Ia synergistic group combining the extensors of the wrist and digits is boxed in by the hatched lines and the arrows (compare also Fig. 1).

that only the neighbours are interconnected with each others, and that these interconnections are stronger between the close neighbours than between the more distant ones. There is the other interesting observation that this principle extends across the anatomical borders of the forelimb and includes the PrT, the FCR and the FCU muscles.

The muscles of this group are all wrist extensors, some also exert different degrees of ab- or adduction. Although the EDC and EDL affect the metacarpo-phalangeal and interphalangeal joints the wrist action is regarded the common feature of the group. In this respect the radio-ulnar position of the muscles in the forearm (as displayed in Fig. 7) represents the direction of their wrist action. Thus the neighbouring principle 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. These graded Ia connections reflect the peculiar mechanical situation of the wrist joint. Since it is a ball joint movements to a specific target in space require the balanced contraction of two or more muscles. The isolated contraction of just one muscle (e.g. during load compensation) would disturb this balance and impress its characteristic mechanical action on the intended movement. Is this organization of general relevance for ball-like joints, or is it specific for the extensors of the wrist? The detailed analysis of the Ia connections across the shoulder has revealed a similar organization at the scapulo-humeral joint (A. Hohn, R. Jänike and M. Illert, unpublished results), which would support the notion of a general relevance of the neighbouring principle in muscles steering movements at ball joints.

The motor nuclei taking part in the neighboring principle have subpopulations of motoneurones with different Ia patterns. This is exemplified in Fig. 8 for the EDC motor nucleus. The four EDC motoneurones illustrated in the figure were predominantly influenced from either the radial (neurone I and II) or the ulnar neighbouring muscles (neurone III and IV). The linear regression analysis shows that the size of the EPSPs generated in the EDC motoneurones by the radial neighbour ECRB is negatively correlated with the size of the EPSP generated by the ulnar neighbour EDL (Fig. 8, upper right hand diagram). On the other hand, correlation between the two ulnar neighbours EDL and ECU is positive (Fig. 8, lower right hand diagram). Similar findings were obtained for the other wrist and digit extensor motor nuclei (Fritz et al. 1989).

With regard to the functional task of the neighbouring principle in motor behaviour (i.e. organizing the combination of multifunctional muscles to reach a certain position in space) the presence of negative correlations between different Ia inputs in these motor nuclei is of importance. There seems to be no strict separation of these nuclei into discrete subpopulations of motoneurones with qualitatively different heteronymous Ia inputs, but rather a continuous transition between the cells. Negative correlated Ia inputs are specific for multifunctional muscles. Fritz and Yamaguchi (1985, 1986) dem-

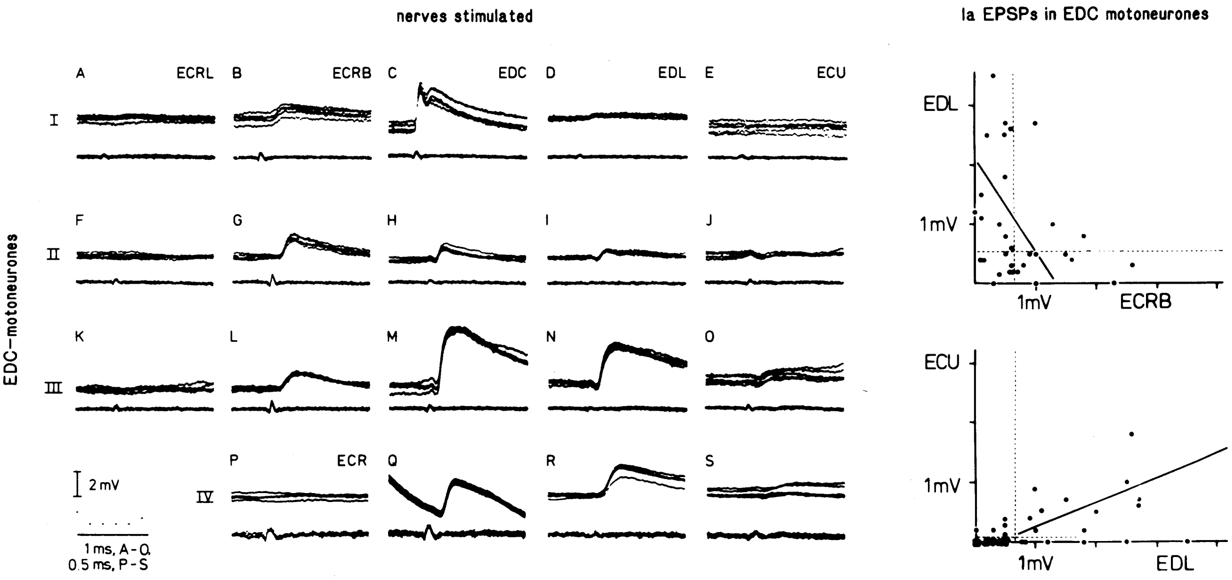


Fig. 8. Subdivision of the EDC motor nucleus into populations of motoneurones differing in their Ia receptiveness. A-S, intracellular recordings from four different EDC motoneurones. The motoneurones I-IV are indicated at the left of each row. The stimulated nerves are arranged in their radio-ulnar anatomical order and indicated above the specimen records A-E. Note that there is an M-spike in C. In Q the Ia EPSP is superimposed on the decay phase of an hyperpolarizing current pulse which was used to prevent antidromic invasion of the motoneurone. All Ia EPSPs are maximal. Construction of the figure as in Fig. 5. The two diagrams at the right hand side display the correlations in the EDC motoneurones between the Ia inputs converging from the radial and ulnar sides. Construction of the figure as in Fig. 6 (modified from Fritz et al. 1989).

onstrated that the heteronymous Ia input to EDC motoneurones is correlated with the direction of the force output of the respective motor unit. This suggests that the organization of the heteronymous Ia input to the EDC motoneurones may be a consequence of the mechanical action of the motor units. Thus it would support the functional demands fulfilled by the Ia connections behind the neighbouring principle.

CONCLUSIONS

The reviewed results show that the Ia system is much more flexible than it has been envisaged for many years. It is highly organized and seems to be optimally adjusted to fulfil all the demands posed on the muscles by the biomechanical constructions of the different joints. Whereas the Ia connections between muscles crossing hinge joints are rather simple and reflect the rigid and permanent division of the muscles into pairs of agonists and antagonists, those between multifunctional muscles are more complicated and allow a high degree of flexibility. Thus they are suited to take part in the organization of differentiated manipulatory movements. It seems that the connectivity principles which have developed at ball joints like the wrist (Fritz et al. 1989) and the shoulder (Hohn et al. 1993, A. Hohn, R. Jänike and M. Illert, to be published) represent general and very universal solutions, from which the more restricted patterns present at the hinge joints may have developed. The kinematic and the electromyographical studies show that the synergies provided by the Ia synergistic groups might be used and activated from the brain during motor behaviour. Thus they supply the central nervous system with a general set of spinal connections which can be used and will be combined with other spinal functional units for the execution of voluntary motor acts.

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