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SHARED REFLEX PATHWAYS OF GROUP I AFFERENTS OF DIFFERENT CAT HIND-LIMB MUSCLES

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SUMMARY

1. The convergence of group I muscle afferents of different muscle origin onto interneurones in spinal reflex pathways has been investigated using the technique of spatial facilitation of the transmission from afferents to motoneurones. The investigated pathways are those of non-reciprocal inhibition and of oligosynaptic excitation of motoneurones.

2. Extensive convergence has been found of group I afferents from muscles operating at the same and different joints onto the interneurones interposed in both excitatory and inhibitory, disynaptic and trisynaptic pathways to motoneurones.

3. Convergence has been found between muscle spindle Ia and/or tendon organ Ib afferents from different muscles, thereby extending observations on convergence of these subgroups of group I afferents from the same muscles.

4. The results show that group I afferents of different muscles influence motoneurones via shared neuronal pathways and that transmission from these afferents is influenced by afferents originating in other muscles. The afferent information forwarded to individual motoneurones is therefore the ensemble picture of the length and tension of many muscles.

INTRODUCTION

It is now well established that impulses from group Ib Golgi tendon organ afferents of one muscle affect motoneurones of a variety of other muscles and that the motoneurones of any muscle are under the influence of Ib afferents of a number of muscles (Laporte & Lloyd, 1952; Eccles, Eccles & Lundberg, 1957*a*, *b*; Eccles & Lundberg, 1959; Hongo, Jankowska & Lundberg, 1969; Lundberg, Malmgren & Schomburg, 1975, 1977, 1978; Jankowska, McCrea & Mackel, 1981*b*, *c*). Any discussion on the role of reflexes from tendon organs focussed on the control of the homonymous muscles thus takes into account only a limited part of their actions. The present study further investigates the widespread actions of Ib afferents, with particular reference to the convergence of afferents of different muscles onto the interneurones mediating these actions, as described by Lundberg *et al.* (1975). The finding that Ib afferents of different muscles may affect motoneurones via the same interneurones is of special interest in relation to the nature of the feed-back signal provided by Ib afferents. If the information forwarded by the afferents of several muscles is fused together before it reaches the motoneurones, the information received by individual motoneurones is the ensemble picture of the activity of many muscles and since muscles are not normally activated in isolation, the Ib system is unsuitable for providing local (homonymous) feed-back to single muscles. We have, therefore, extended the observations of Lundberg *et al.* (1975) by investigating in greater detail than before the characteristics of the excitatory convergence from Ib afferents of different muscles. In particular, it has been investigated whether actions of all Ib afferents are linked to the actions of afferents of other muscles and whether the linked Ib actions are directed at particular or at all species of target motoneurones. We have also investigated whether the actions of Ia muscle spindle afferents linked with actions of Ib afferents of the same muscles, as described in the accompanying paper (Jankowska & McCrea, 1983), are likewise linked with the actions of Ia and Ib afferents of other muscles. It will be shown that this is indeed the case and that the picture of activity of many muscles received by motoneurones includes information on both the length and tension developed by these muscles. An abstract of some of these results has been published (Harrison, Jankowska & Johannisson, 1982).

METHODS

Preparation. The successful experiments were performed on twelve cats under chloralose anaesthesia (50–60 mg/kg. I.V. initial dose) after initial dissection under ether anaesthesia. The animals were paralysed with gallamine triethiodide and artificially ventilated; eight of the animals were spinalized at Th 13.

A number of hind-limb muscle nerves were prepared and mounted on pairs of silver electrodes for stimulation. Among the nerves which were always cut were those to quadriceps, posterior biceps and semitendinosus, and anterior biceps and semimembranosus muscles. In five of the twelve experiments triceps surae and plantaris nerves were dissected in continuity with the muscles innervated by them to allow selective activation of Ia and Ib afferents as described in the accompanying paper (Jankowska & McCrea, 1983). Otherwise, gastrocnemius–soleus and plantaris nerves were also cut. A consequence of preparing these muscles for selective activation of the afferents was that the variety of other nerves available for stimulation was restricted. Among these other nerves were the nerves to peroneus longus, tertius and brevis, the distal part of the tibial nerve, the nerves to the two heads of flexor digitorum longus (often referred to as flexor digitorum and hallucis longus; see however Hunt & McIntyre, 1960) which were dissected free of the interosseus branch, and the nerve to popliteus.

L7 and S1 ventral roots were cut to avoid recurrent inhibition evoked by stimulation of motor axons within the peripheral nerves. The proximal ends of the ventral roots were mounted on stimulating electrodes to aid the location and identification of motoneurones.

Stimulation and recording. Observations were made by intracellular recording from motoneurones penetrated with potassium citrate-filled electrodes. The motoneurones selected for analysis were those in which distinct post-synaptic potentials (p.s.p.s) were evoked by group I afferents and generally, in which the p.s.p.s were not preceded by significant monosynaptic excitatory p.s.p.s (e.p.s.p.s). Additionally, if stimulation of a nerve produced a reciprocal inhibitory p.s.p. (i.p.s.p.) then this nerve was not tested for convergence in a given motoneurone or motoneurone species. For the purposes of the present analysis a maximum of 1·5 times threshold stimulus was used for activation of group I afferents in order to avoid the possibility of activating group II afferents (cf. Jack, 1978). However, optimal conditions for demonstrating a common pathway were usually achieved with lower stimulus intensities than this (1·2–1·3 times threshold) since the largest subliminal fringe would be expected when as large a number of interneurones as possible were brought below threshold for firing on separate stimulation of each of the tested nerves.

P.s.p.s were attributed to the Ia afferents of knee and thigh muscles if they were evoked by stimuli below threshold for the second component of the group I volley recorded from the entry zone of L6 or L7 dorsal roots (Bradley & Eccles, 1953; Eccles *et al.* 1957*a*).

The technique of selective activation of Ia and Ib afferents of triceps surae and plantaris has been used as described previously (Fetz, Jankowska, Johannisson & Lipski, 1979) and in the accompanying paper (Jankowska & McCrea, 1983). Briefly, group Ia muscle spindle afferents were activated by short duration stretches of amplitude less than 35 μm, and at an initial tension of 5·0–5·5 N. Under these conditions activation of Ib afferents was previously found to require more than 40 μm stretch. Group Ib afferents were stimulated electrically after having increased the threshold for excitation of group Ia afferents by electrical stimuli above that for group Ib afferents using the method of Coppin, Jack & McLennan (1970). This involved vibration of triceps surae and plantaris until the threshold for all group Ia afferents was increased above their original threshold. By recording from a triceps surae or plantaris motoneurone the effectiveness of the selective activation of Ib afferents was judged by the absence of monosynaptic e.p.s.p.s.

Data analysis. Convergence onto common interneurones was tested using the technique of spatial facilitation. Two test nerves were stimulated in a sequential mode and the post-synaptic potentials stored, averaged and arithmetically manipulated using a Nicolet (Model 1170) averager, as described by Jankowska & McCrea (1983). It was concluded that group I afferents from different muscles converged onto the same interneurones when p.s.p.s evoked by combined action of these afferents were larger than the arithmetic sum of p.s.p.s evoked by each of them separately and when this was repeatable. This technique has only been used to detect facilitation; inhibitory convergence could not be interpreted unambiguously since a result of combined stimulation smaller than the sum of the two nerves stimulated separately could also have been due to occlusion in excitatory convergent pathways at the interneuronal level, or to non-linear summation of p.s.p.s in motoneurones.

The easiest pathways to investigate were those mediating p.s.p.s evoked by the most potent afferents; ankle, knee and toe extensors (Eccles *et al.* 1957*b*). The greatest amount of data was therefore collected regarding these. Fewer observations were made regarding group I afferents of flexor muscles, since these have not only weaker but also less frequent reflex effects. This bias reflects the often little appreciated, relative potency of group I afferents of different origin.

RESULTS

The investigated pathways were from a variety of hind-limb muscles to various ipsilateral hind-limb motoneurones. Systematic tests of spatial facilitation were made of transmission from several afferent combinations in 166 motoneurones. These included 52 gastrocnemius–soleus, 18 plantaris, 12 flexor digitorum longus, 15 quadriceps, 22 posterior biceps–semitendinosus, 20 anterior biceps–semimembranosus, 5 tibial, 4 peroneus longus, tertius or brevis, and 18 partially identified motoneurones.

Convergence in inhibitory pathways

Fig. 1 illustrates the procedure of collecting the data and the principal findings of the present investigation. Fig. 1 *A* shows the synaptic effects in a plantaris motoneurone evoked by volleys in plantaris and gastrocnemius–soleus nerves. Activation of plantaris afferents evoked a homonymous monosynaptic e.p.s.p. that decayed faster than normal owing to autogenetic inhibition, while activation of gastrocnemius–soleus afferents evoked a negligible monosynaptic e.p.s.p followed by a large i.p.s.p. The third record shows effects of stimulation of the two muscle nerves together. Recruitment of additional interneurones due to the combined action of afferents from the two nerves manifested itself as a p.s.p. larger than the sum of the p.s.p.s initiated by stimulation of the two nerves separately. In the fifth trace a sum of separately evoked group I p.s.p.s has been superimposed on traces showing the combined action of two muscle nerves stimulated together; the difference being shown in the bottom trace. This series of records illustrates facilitation of autogenetic (plantaris) inhibition by afferents from a close synergist (gastrocnemius–soleus).

An alternative explanation for these observations is that the gastrocnemius–soleus i.p.s.p. is larger when evoked together with the plantaris nerve since the driving potential for the i.p.s.p. would be larger when superimposed on an e.p.s.p. This was

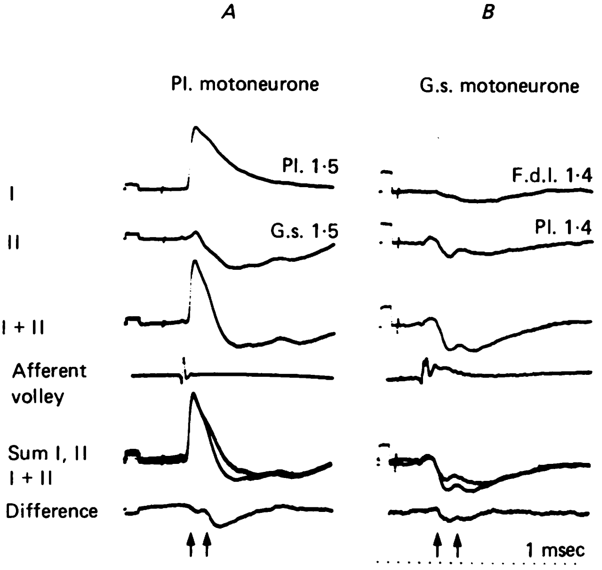

Fig. 1. Mutual facilitation of transmission from group I afferents of two synergists to motoneurones. The first two traces in each column (and for Figs. 2, 3 and 8) show averaged intracellular records of p.s.p.s evoked by group I afferents of different muscle origins when stimulated separately, and in the third traces when stimulated together. The fourth traces are records of afferent volleys recorded from the dorsal root entry zone. The lower traces show arithmetically derived sums of the p.s.p.s evoked by separately activated group I afferents superimposed on p.s.p.s evoked by combined action of these afferents to visualize the differences between them. The arithmetically derived differences are displayed on the bottom traces. *A*, mutual facilitation of autogenetic (Pl.) and non-autogenetic (G.s.) inhibition in a plantaris motoneurone. *B*, facilitation of actions evoked from close synergists in a gastrocnemius–soleus motoneurone. The arrows indicate the onset of separate components of the p.s.p.s attributed to interneurones recruited in di- and trisynaptic pathways. Both in this and in the following Figures calibration pulses are 200 μV. *Abbreviations for legends:* plantaris, Pl.; gastrocnemius–soleus, G.s.; medial gastrocnemius, M.g.; flexor digitorum longus, F.d.l.; quadriceps, Q.; anterior biceps–semimembranosus, A.b.s.m.; posterior biceps–semitendinosus, P.b.s.t.; peroneus longus, tertius and brevis, Per.; popliteus, Popl.; distal part of tibial, Tib.

not the main factor, however, since when large depolarizing currents were injected to *decrease* the amplitude of the e.p.s.p., the amplitude of the 'difference' *increased* in parallel with the increase in amplitude of the i.p.s.p. Such true facilitation is unambiguously observed in the absence of monosynaptic excitation as in Fig. 1 *B* for two synergists.

The facilitation shown in Fig. 1 may have been expected *a priori* since the i.p.s.p.s were evoked from close synergists acting at the same joint which are, therefore, subject to the same external disturbances. The pathways mediating I b reflex actions are, however, associated with several joints (Eccles *et al.* 1957*b*). The evidence presented in Fig. 2*A* shows, in agreement with the data of Lundberg *et al.* (1975), that the pathway of non-reciprocal inhibition to motoneurones acting at another joint may similarly be shared by afferents of synergists at the first joint. In this case the afferents of ankle extensors (gastrocnemius–soleus and plantaris) evoked inhibition in a knee extensor (quadriceps) motoneurone; the facilitation manifested itself primarily in shortening the latency of the i.p.s.p. evoked from the gastrocnemius–soleus nerves. Observations showing that interneurones may be activated by afferents from muscles operating at different joints are illustrated in Fig. 2*B*. The Figure shows inhibition of a gastrocnemius–soleus motoneurone from an ankle extensor (plantaris) which was facilitated by afferents of anterior biceps–semimembranosus; hip extensors. This is further exemplified in Fig. 2*C* where afferents of hip extensors (anterior biceps–semimembranosus) and of knee extensors (quadriceps) are mutally facilitating each others actions in the pathway to an ankle extensor (gastrocnemius–soleus). In this example the interneurones were associated with three joints.

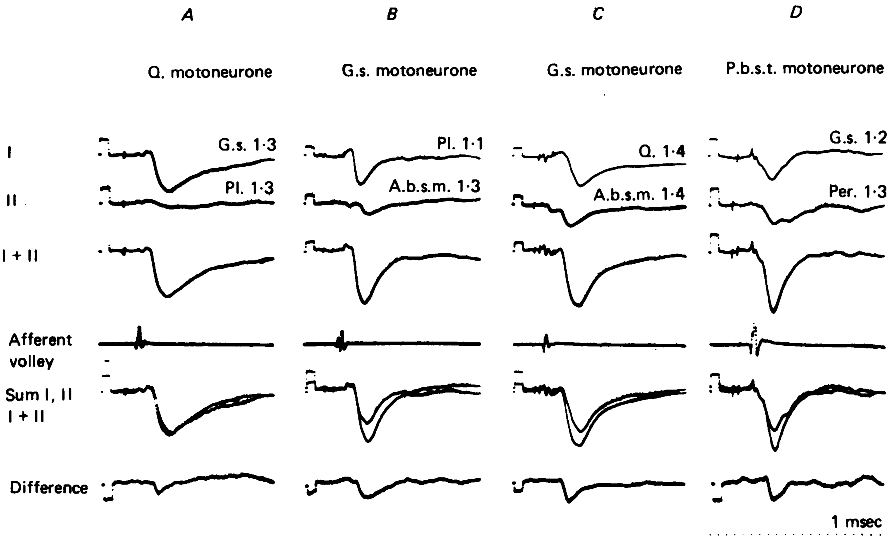

Fig. 2. Mutual facilitation of transmission from afferents of muscles acting at different joints (*B*, *C*) or onto motoneurones innervating a muscle at a different joint than the muscles of origin of both afferents (*A*, *B*, *C*, *D*). The format is as in Fig. 1.

The less frequent inhibitory pathways from extensor group I afferents to *flexor* motoneurones have also been found to be shared by afferents of various muscles. Fig. 2*D* shows an example of this with the i.p.s.p evoked from ankle extensors (gastrocnemius–soleus) in a knee flexor (posterior biceps–semitendinosus) motoneurone, which was facilitated by afferents of peroneus longus, tertius and brevis.

It should be noted that the amplitudes of the components of the i.p.s.p.s evoked by shared interneurones (the differences) were often comparable to the amplitudes of i.p.s.p.s evoked by the tested nerves when stimulated alone.

Convergence in excitatory pathways

The analysis of excitatory actions of group I afferents to motoneurones was restricted to excitatory effects recorded in thirteen knee flexor (posterior biceps–semitendinosus) motoneurones and the convergence was tested only for a smaller number of combinations. Fig. 3 exemplifies the data with records from two motoneurones in which the convergence was observed of group I afferents from the plantaris and the peronei muscles, and from the plantaris and flexor digitorum longus muscles, respectively.

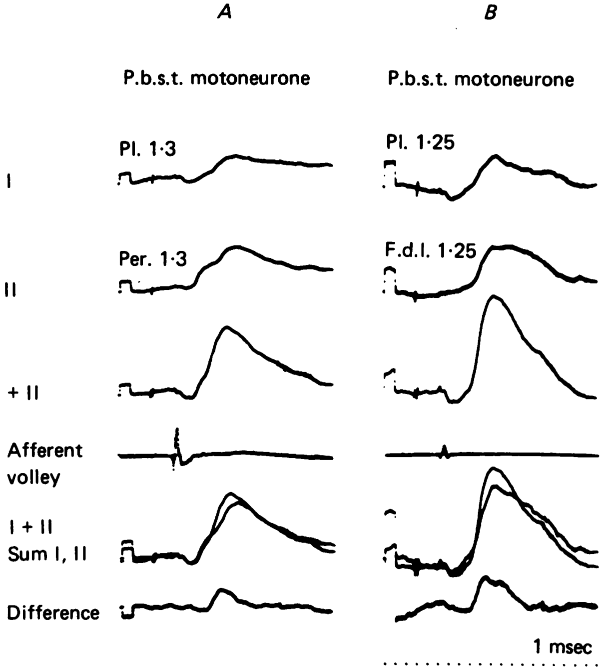

Fig. 3. Mutual facilitation of transmission from group I afferents in excitatory pathways to two flexor (P.b.s.t.) motoneurones. The format is as in Fig. 1.

The frequency and extent of the observed convergence

The spatial facilitation of synaptic actions of Ib afferents shows that the interneurones mediating non-reciprocal inhibition may have receptive fields not restricted to single muscles. In order to investigate the generality of this phenomenon the mutual facilitation has been tested for the twenty-eight possible combinations between the afferents of the eight muscles considered in the present study, while analysing transmission in reflex pathways to many motoneurone species. We found evidence of convergence in inhibitory pathways in twenty-six of the twenty-eight combinations (see Fig. 4*A*) and in excitatory pathways in fourteen of fifteen combinations tested (Fig. 4*D*, hatched). The convergence from afferents of different origin is thus not restricted to a few particular connections but may be quite a common phenomenon.

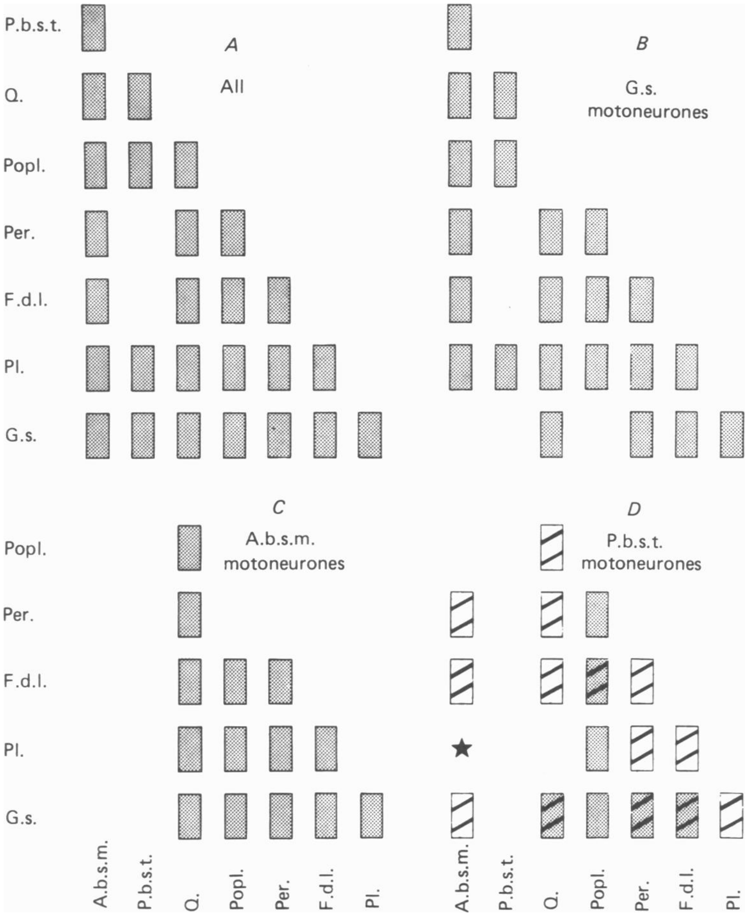

Fig. 4. Shared reflex pathways to various species of motoneurones. The shaded areas are for the convergence in inhibitory reflex pathways whereas the hatching is for excitatory reflex pathways. *A*, the pattern of convergence obtained when all motoneurone species are considered together. *B*, *C* and *D*, the convergence found when G.s., A.b.s.m. and P.b.s.t. motoneurones are considered separately. The missing combinations include combinations in which no convergence was found or (usually) in which it was not tested. The missing combinations indicated by * in *D* was tested only for excitation, with negative results.

In order to get more quantitative information of the occurrence of convergence the following approach was adopted. Nerves which produced distinguishable p.s.p.s when stimulated separately were selected for this purpose. Usually, a pair of nerves were tested under several different conditions, such as different stimulus strengths or timing interval, and if spatial facilitation revealed a shared pathway under some conditions, but in a repeatable way, then it was counted as: convergence present. If facilitation tested under similar conditions in other motoneurones was not observed then it was counted as: no convergence. Fig. 5 summarizes the degree of convergence estimated in this way for the inhibitory pathways. It is evident that

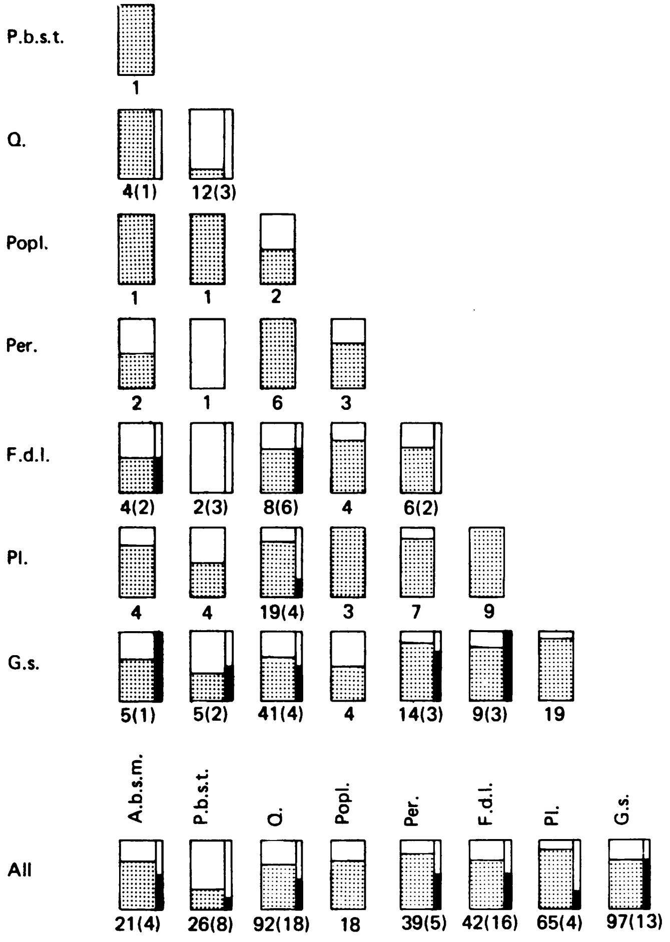

Fig. 5. The observed convergence in inhibitory reflex pathways of group I afferents from different muscles in the whole sample of the tested motoneurones. For each combination the shaded area represents the proportion of motoneurones in which evidence of convergence was found. The figures indicate the number of motoneurones in which each combination was adequately tested. The bottom row shows the pooled data for each nerve. The narrow columns and numbers in parentheses are from unpublished data of E. Jankowska, A. Lundberg, K. Malmgren & E. D. Schomburg (see Lundberg *et al.* 1975).

facilitatory interaction between group I afferents (shaded) was found in a large proportion of many combinations studied. Totally it was found in seventy % of tests ($n = 200$) in these pathways and in sixty-eight % of tests ($n = 28$) in the excitatory pathways. These proportions were, in addition, likely to be an underestimate of the true degree of convergence as a lack of spatial facilitation could not be used to exclude the presence of common interneurones; it might primarily have been due to inadequate parameters of stimulation, such as the strength of electrical stimuli and time interval between them. Even having adjusted the parameters of stimulation to make the maximum number of interneurones just subthreshold for firing, the lack of spatial facilitation may not reveal convergence, despite its presence, since on combined stimulation of the two nerves the action of the recruited interneurones would be negated by the occlusive action of any interneurones that are discharged by both of the tested nerves stimulated separately, and by non-linear summation of p.s.p.s (see Discussion). Comparison with the unpublished data of A. Lundberg, K. Malmgren & E. D. Schomburg, and of E. Jankowska & A. Lundberg, represented by narrow columns to the right, shows that the two sets are generally in agreement. These previous also included observations on convergence between afferents of the deep peronei and (i) posterior biceps–semitendinosus (in one of three cells) and (ii) flexor digitorum longus (in two of three cells), and between quadriceps and sartorius (in one cell).

With regard to the two combinations for which we failed to find convergence in inhibitory pathways, we feel that this reflects primarily the weaker potency of the involved afferents, in particular afferents of posterior biceps–semitendinosus (flexor muscles). Stimulation of nerves which produced no post-synaptic effect alone at 1·5 times threshold only very rarely facilitated group I actions of another origin, while it was relatively easy to show convergence when the p.s.p.s produced by the two test nerves alone were large. If a large p.s.p reflects the actions of a greater number of interneurones, it must be easier to obtain a significant subliminal fringe under these conditions and therefore to demonstrate a common pathway. Thus the apparent low occurrence of convergence for afferents of posterior biceps–semitendinosus may only have been due to their actions being less potent and therefore more difficult to demonstrate.

Convergence in pathways to various species of motoneurones

The analysis of the inhibitory pathways has so far been restricted to demonstrating that group I afferents of different muscles share common pathways regardless of motoneurone species in which this was tested. For the interpretation of the functional meaning of such common pathways it is important to know whether or not the various combinations of convergence were specific to particular species of motoneurones. Fig. 4*B–D* shows the combination in which we found convergence for the three most extensively studied species of motoneurones. For gastrocnemius–soleus motoneurones convergence was demonstrated in all combinations in which it was adequately tested. The major difference between the combinations observed for these motoneurones and for all motoneurones (Fig. 4*A*) is the lack of combination incorporating gastrocnemius–soleus afferents. Since, however, they evoke large homonymous monosynaptic e.p.s.p.s in gastrocnemius–soleus motoneurones, i.p.s.p.s superimposed on these e.p.s.p.s cannot be readily investigated. Similarly for anterior biceps–semimembranosus and posterior biceps–semitendinosus motoneurones, extensive convergence was observed for practically all the afferent combinations studied; the major omissions were in the data involving homonymous e.p.s.p.s or flexor afferents (posterior biceps–semitendinosus) (see above).

The occurrence of the convergence in pathways to various species of motoneurones is further illustrated in Fig. 6, where the most extensively studied afferent combinations

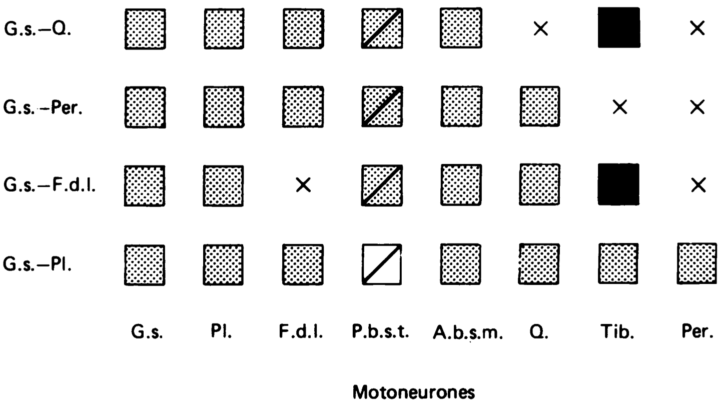

Fig. 6. Shared inhibitory and excitatory reflex pathways to all species of motoneurones studied, for the most extensively studied afferent combinations involving G.s. The missing combinations (crosses) largely reflect technical limitations (see text) and the small number of Tib. and Per. motoneurones from which recordings were made. The combinations marked as filled squares are from the unpublished data of E. Jankowska, A. Lundberg, K. Malmgren & E. D. Schomburg. Other symbols as in Fig. 4.

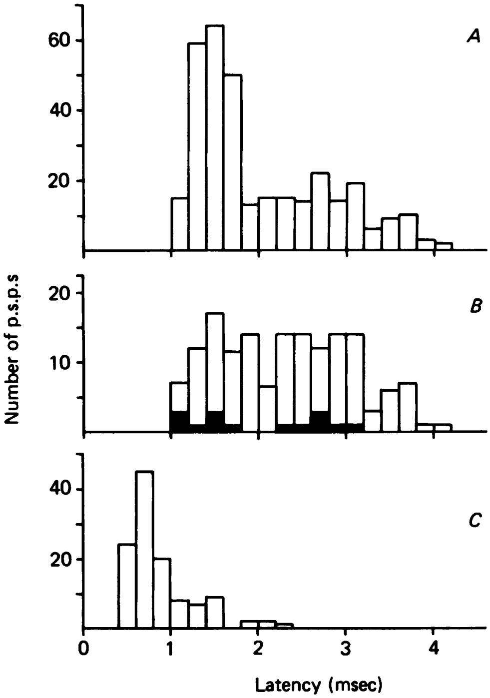

Fig. 7. *A*, histogram of the latencies of the p.s.p.s recorded from motoneurones upon activation of a single muscle nerve. Time zero corresponds to the time of arrival of the afferent volley at the dorsal root entry zone. *B*, histogram of the latencies of the p.s.p.s due to the interneurones recruited by combined actions of afferents from the two test nerves (i.e. latencies of the differences in Figs. 1–3). The shaded section indicates the latencies of the separate components of the p.s.p.s showing two components. *A* and *B* are for the data in both i.p.s.p.s and e.p.s.p.s. *C*, histogram of the latencies of e.p.s.p.s recorded from the interneurones mediating these actions (P. J. Harrison & E. Jankowska, unpublished).

involving gastrocnemius–soleus afferents are shown for all tested motoneurone species.

Taken together the present data indicate no systematic differences with regard to convergence in inhibitory pathways to the various motoneurones' species.

Convergence in both di- and trisynaptic pathways

The distribution of the central latencies of the p.s.p.s investigated in this series of experiments is illustrated in Fig. 7*A*, and is similar to that of Eccles *et al.* (1957*b*) who concluded that the p.s.p.s were di- and trisynaptically mediated. The latencies of the facilitated components of the p.s.p.s are shown in Fig. 7*B*. Since the latencies cover the same range, the recruited interneurones are also taken to be in di- and trisynaptic pathways. Additional evidence for this conclusion comes from observations of facilitated p.s.p.s showing two components with latencies corresponding to di- and trisynaptic pathways (means of 1·4 and 2·7 msec respectively), as in Fig. 1. Furthermore, this is in keeping with the latencies of the e.p.s.p.s observed in the last order interneurones mediating these actions (Fig. 7*C*) (P. J. Harrison & E. Jankowska, unpublished).

Convergence of group Ia and/or Ib afferents of different muscles

With only a few exceptions electrical stimulation of muscle nerves, even at low strengths, indiscriminately activates group I nerve fibres regardless of their receptor origin. The reflex actions evoked by such stimulation were originally attributed to the actions of I b afferents. However, it has since been demonstrated that some reflex actions of group I a afferents may be similar to the reflex actions of group I b or whole group I afferents (Fetz *et al.* 1979; Jankowska *et al.* 1981*b*, *c*) and the observations described in the accompanying paper (Jankowska & McCrea, 1983) show that p.s.p.s from group I a and I b afferents of the *same* group of muscles are evoked via shared pathways. One of the aims of this study has, therefore, been to investigate whether convergence of group I afferents of different muscles represents convergence of group I a afferents alone, group I b afferents alone, or I a afferents one muscle and I b afferents of another muscle. While investigating convergence of I a afferents we activated them either electrically, taking advantage of the different thresholds of the I a and I b afferents in certain knee and hip muscles (Bradley & Eccles, 1953), or using stretches of triceps surae and plantaris (Lundberg & Winsbury, 1960).

The only previous indication that I a afferents are involved in this convergence comes from the original observation that I a afferents of quadriceps facilitate the reflex actions of group I afferents of gastrocnemius–soleus (Lundberg *et al.* 1977). This observation has now been extended to afferents of muscles with widely differing function in fifteen cases.

Convergence of I a afferents of one muscle with I a afferents of another muscle was seen in six motoneurones. Fig. 8*A* shows i.p.s.p.s evoked by stimuli below threshold for the I b components of the incoming volleys from quadriceps and anterior biceps–semimembranosus in a gastrocnemius–soleus motoneurone, and spatial facilitation reveals that the pathway is shared. Combining electrical stimulation below threshold for I b afferents of quadriceps with adequate activation of I a afferents by brief stretch of triceps surae, the I a non-reciprocal inhibitory pathways from these afferents are again shown to be shared in Fig. 8*B*. Thus, the convergence reported in this paper can, at least partly, be explained by shared pathways from group Ia afferents.

In order to selectively activate the Ib afferents (of gastrocnemius–soleus and/or plantaris) the technique of Coppin *et al.* (1970) together with the previously introduced control procedure (Fetz *et al.* 1979, Jankowska & McCrea, 1983) have been used. In order to study the convergence of Ia and Ib afferents on common interneurones it was simplest to record from triceps surae and plantaris motoneurones since the selectivity of Ib activation could then be monitored without the need to record from another motoneurone simultaneously (cf. Jankowska & McCrea, 1983). Fig. 8*C* shows a homonymous Ib i.p.s.p. uncontaminated by Ia actions, recorded from a gastrocnemius motoneurone, after a period of muscle vibration; the Ia afferents from quadriceps facilitated this pure Ib action and thereby demonstrated convergence between Ia and Ib afferents of different muscles. Similar results were observed in eight other motoneurones.

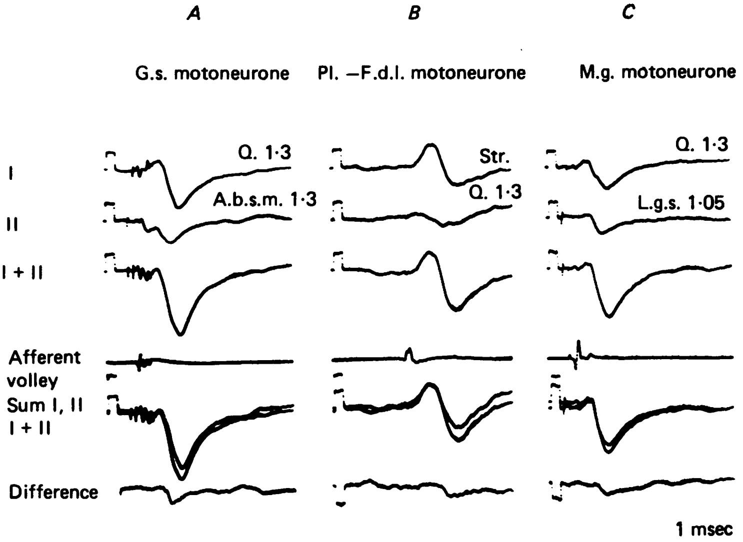

Fig. 8. Mutual facilitation of transmission from subgroups (Ia and Ib) of group I afferents. *A* and *B*, in reflex pathways of non-reciprocal inhibition activated by group Ia afferents of different muscles. *C*, in reflex pathways activated by group Ia afferents of one muscle and group Ib afferents of a different muscle. Selective activation of group Ia afferents was achieved by stimulating the quadriceps (in *A*, *B* and *C*) and anterior biceps–semimembranosus (in *A*) nerves below threshold for the second component of the group I afferent volley (Bradley & Eccles, 1953), and by small amplitude, short duration stretch of triceps surae (in *B*, str.). For selective activation of group Ib afferents (in *C*) see text. The format of the illustration is as in Fig. 1.

Thus, extending the observations reported in the accompanying paper (Jankowska & McCrea, 1983), it can be concluded that not only Ia and Ib afferents of the same muscle but also Ia afferents of one muscle and Ib afferents of another muscle share a common pathway.

With regard to the question of convergence of Ib afferents of different muscles, the evidence is scanty. We could selectively activate the Ib afferents of only one closely related group of muscles, and therefore observations made on these cannot readily be extrapolated to Ib afferents of all muscles. We could, nevertheless, easily facilitate Ib actions of one head of triceps surae with Ib actions from the other head. It was also rather easy to facilitate pure Ib actions with whole group I actions of other muscles; certainly easier than with just group Ia actions. Thus, although it seems highly likely that the Ib afferents of various muscles share common reflex pathways, the proof will have to wait until adequate activation of several populations of Ib afferents becomes a technical possibility.

DISCUSSION

The results of this study indicate extensive convergence on interneurones in reflex pathways from group I muscle afferents to motoneurones and as such extend the observations of Lundberg *et al.* (1975). While the existence of shared pathways does not exclude the possibility of additional parallel (private) pathways, it is essential in considering the importance of this convergence to ascertain whether such private pathways are subsidiary to more substantial shared pathways or vice versa. The following arguments indicate that the former possibility is the case: The p.s.p. evoked by activation of a single nerve is the result of the activity of a number of interneurones. Since on many occasions the facilitated p.s.p. (the differences in Figs. 1–3) was of a similar amplitude as that evoked by a single nerve alone, the number of recruited interneurones must have doubled. We can, therefore, conclude that on these occasions about half of the activated interneurones must have had a shared input. The present quantitative estimates cannot be more precise than this but the true proportion of shared interneurones is likely to be greater than half. Thus we do not know what proportion of the interneurones made to fire by one nerve alone were also excited from the second nerve, since combined action of the two nerves would produce only one action potential. Furthermore, if any interneurones were made to fire by both nerves when each was stimulated alone, then occlusion would result when they were stimulated together and the effect of this would be to subtract from the action of interneurones recruited from the subliminal fringe. Non-linear summation of the p.s.p.s at the motoneuronal level would further subtract from the observed facilitation. In conclusion, a large proportion of the interposed interneurones must be shared by afferents of the two nerves examined to account for our observations. In addition, any interneurones not shared by a given pair of test nerves may well have been excited from other nerves since convergence could be found from several pairs of nerves in any one motoneurone.

In harmony with this reasoning, the majority of laminae V–VI interneurones, functionally unidentified (Czarkowska, Jankowska & Sybirska, 1981; Jankowska, Johannisson & Lipski, 1981*a*), as well as those recognised as mediating the non-reciprocal inhibition (Brink, Harrison, Jankowska, McCrea & Skoog, 1982), show group I input from several muscles (P. J. Harrison & E. Jankowska, in preparation). A number of group I actions are thus subserved by the same interneurones.

Despite this convergence being extensive we are far from claiming that information forwarded by all tendon organs (not even those of muscles investigated in the present study) is completely mixed up before it reaches the motoneurones. Neither do we claim that all interneurones interposed between tendon organs and motoneurones receive information of the same kind and distribute it in an indiscriminate way. On the contrary, one might expect the existence of separate functional groups of the involved interneurones, which would process information from different combinations of muscles and forward it to different combinations of motoneurones to ensure a co-ordinated movement.

The convergence of afferents from different muscles onto common reflex pathway supports the idea of 'I b linkage between co-contracting muscles' (Hongo *et al.* 1969; Lundberg *et al.* 1975) and reinforces the view that I b reflex actions are participating in the functional control of the limb as a whole (Engberg & Lundberg, 1969; Hongo *et al.* 1969; Lundberg, 1969, 1975; Bergmans, Burke, Fedina & Lundberg, 1974; Baldissera, Hultborn & Illert, 1981). This contrasts with the view that the function of I b afferents is to contribute to a feed-back system controlling the homonymous muscle (e.g. Houk, 1972). In the light of the widespread actions of I b afferents across the whole limb, and of the extensive convergence reported in the present paper, the possibility that I b afferents are involved primarily in local feed-back of homonymous muscles is precluded. Since motoneurones are under the influence of I b afferents of a number of muscles acting at different joints, they are receiving information about the force of contraction of many muscles and it is difficult to envisage how the information from individual muscles could be disentangled under other than very artificial experimental conditions. The convergence described in the present and in the preceding paper (Jankowska & McCrea, 1983) further indicates that the information provided by the I b afferents of one muscle is integrated with the information from I a afferents, of both the same and of other muscles, and consequently they receive an ensemble picture of both the length and tension of many muscles.

In trying to define the feed-back signal, and hence the controlled variable it is important to note that the *main* reflex actions of I b afferents are inhibition of extensor motoneurones and excitation of flexor motoneurones, and that they are primarily evoked by extensor afferents. The I b feed-back signal must then be a composite signal of the force of contraction of primarily extensor muscles and, similarly, the associated I a feed-back signal a composite signal of the length of primarily extensor muscles. Consequently, the controlled variable will be primarily some function of the length and tension of extensor muscles (in short; extension).

In summary, these findings place I b and I a-like-I b actions into a particularly useful framework for viewing their role in the control of posture and movement of the whole limb, rather than in the control of the force of individual muscles. In particular, the feed-back control of the limb as a whole places its control into better dynamic perspective and ensures that the activity of individual muscles is functionally coordinated with the activity of other muscles.

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