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OLIGOSYNAPTIC EXCITATION OF MOTONEURONES BY IMPULSES IN GROUP Ia MUSCLE SPINDLE AFFERENTS IN THE CAT

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SUMMARY

1. Intracellular recording from hind-limb motoneurones was used to investigate whether di- and trisynaptic (oligosynaptic) excitatory post-synaptic potentials (e.p.s.p.s) are evoked from group Ia muscle spindle afferents in those motoneurones in which such potentials are evoked from Ib tendon organ afferents or entire group I afferents. Ia afferents of triceps surae and plantaris were activated either selectively by single brief stretches of these muscles, or together with Ib afferents by electrical stimuli applied to the nerves.

2. Muscle stretches below threshold for Ib afferents (10–35 μm) evoked e.p.s.p.s which appeared with latencies compatible with disynaptic and trisynaptic coupling between the afferents and the motoneurones. The latencies of a majority of these e.p.s.p.s were too short to allow their mediation by group II afferents, if any were activated by the applied stretches. They were also too short to be compatible with effects attributable to dorsal root reflexes. These e.p.s.p.s are thus attributed to oligosynaptic actions of Ia afferents.

3. Stretch-evoked di- and trisynaptic Ia e.p.s.p.s were found in 83% of motoneurones in which e.p.s.p.s were evoked by stimuli which activated both Ia and Ib afferents; in five motoneurone species they were found in more than 90%. These observations lead to the conclusion that group Ia muscle spindle afferents evoke not only inhibitory but also excitatory actions in parallel with group Ib tendon organ afferents.

4. The distribution of Ia oligosynaptic stretch-evoked excitation from ankle and toe extensor muscles was compared with the distribution of Ia non-reciprocal inhibition as described by Jankowska, McCrea & Mackel (1981*b*). Excitation predominated in posterior biceps–semitendinosus motoneurones and inhibition in other species of motoneurones investigated, except those of intrinsic foot muscles (tibial motoneurones); similar proportions of the latter showed excitation and inhibition.

5. Occurrence of oligosynaptic e.p.s.p.s as well as inhibitory post-synaptic potentials (i.p.s.p.s) of Ia origin in some motoneurone species, and in particular in individual motoneurones, is indicative of a number of reflex pathways between group I afferents and these motoneurones. Furthermore, the disappearance of some of the e.p.s.p.s evoked by near-threshold electrical stimulation following stronger stimuli

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indicates interactions between various functional groups of interneurones mediating group I actions.

INTRODUCTION

The aim of the present study was to reinvestigate the existence of oligosynaptic (di- and trisynaptic) pathways mediating excitation of hind-limb motoneurones by impulses in group Ia muscle spindle afferents. Evidence has been given for both directly (Lloyd, 1943; Eccles, Eccles & Lundberg, 1957*a*) and interneuronally mediated excitation of motoneurones from these afferents. However, the evidence has been much stronger with respect to late polysynaptic (for references see Matthews, 1972, and Hultborn & Wigström, 1980) than di- or trisynaptic excitation.

Eccles, Eccles & Lundberg (1960) showed that e.p.s.p.s with monosynaptic as well as oligosynaptic components were evoked at threshold for Ia afferents, but from a nerve to flexor digitorum longus from which the interosseus nerve branch was not dissected. It cannot thus be excluded that the later components of the e.p.s.p.s were due to excitation of the interosseus nerve. In the study of Tsukahara & Ohye (1964) an attempt was made to separate effects of the Ia afferents from others by using a stimulus which was half-maximal for the group I fibres from the triceps surae and plantaris nerves. More recently Coppin, Jack & MacLennan (1970) have reported very low thresholds of Ib afferents of these nerves, so that oligosynaptic excitation evoked by stimuli only slightly above threshold may be attributed to Ib as well as to Ia afferents. Observations of Pacheco & Guzman-Flores (1969, their Fig. 4) are similarly difficult to interpret since they show oligosynaptic e.p.s.p.s with a lower threshold than the e.p.s.p.s classified as monosynaptic, and one would expect that the interneuronally mediated effects would have a higher, or at least the same threshold as the monosynaptic ones.

The phase-dependent late components of Ia e.p.s.p.s reported by Schomburg & Behrends (1978) to appear during DOPA-induced fictive locomotion have also been considered as Ia oligosynaptic e.p.s.p.s. They were evoked by weak (1·1 times threshold) stimulation of anterior biceps–semimembranosus nerve, and since increasing the stimulus strength to two or five times threshold did not change the effect appreciably it was concluded that Ia afferents were most likely responsible for it. However, the full report of the study has not yet been published and the authors state that before further control experiments have been done they cannot exclude the possibility that a phasic modulation of the resting potential of the Ia afferents during locomotion caused additional firing of the Ia afferents and hence the appearance of a series of monosynaptic e.p.s.p.s.

Finally, Watt, Stauffer, Taylor, Reinking & Stuart (1976; see also Mendel & Henneman, 1971, and Munson & Sypert, 1979) reported several cases of late depolarization of motoneurones following discharges of single Ia afferents of triceps surae isolated in continuity with their receptors of origin. They considered the depolarization which appeared with latencies of 1·2–1·5 msec as being evoked mono- or disynaptically and di- or trisynaptically, respectively. However, they were somewhat uncertain about its interpretation, finding it difficult to distinguish 'disfacilitation hyperpolarization from true i.p.s.p.s or disinhibition from true long latency e.p.s.p.s'.

Our interest in the oligosynaptic excitation of motoneurones of Ia origin arose from the recent observations that di- and trisynaptically evoked autogenetic and synergistic inhibition of motoneurones is evoked not only from Ib but also from Ia afferents (Fetz, Jankowska, Johannisson & Lipski, 1979; Jankowska *et al.* 1981*b*). Since impulses in Ib afferents have excitatory as well as inhibitory actions on motoneurones (Laporte & Lloyd, 1952; Eccles, Eccles & Lundberg, 1957*b*), the question was whether the Ia afferents contribute to both these actions or only to the inhibitory ones. Some of the preliminary observations of this study have been published in abstract form (Jankowska, Mackel & McCrea, 1980).

METHODS

The reported observations are from experiments performed on eighteen cats, the same ones which were used for the study of Ia non-reciprocal inhibition (Jankowska *et al.* 1981*b*). The preparation and the general procedures of recording and stimulation were thus as described in the preceding paper and by Fetz *et al.* (1979). All of the experiments were carried out under chloralose anaesthesia (50–60 mg/kg initial dose) in low spinal cats paralysed with gallamine triethiodide and artificially ventilated, 4-aminopyridine was used in twelve experiments while recording from about 60% of motoneurones.

Recording. The distribution of the Ia oligosynaptic excitation was analysed only in those preparations in which it was found in at least some motoneurones; negative results of other experiments have not been included. In the case of e.p.s.p.s of 100–150 μV amplitude (smaller ones were not taken into account) at least two or three series of averaged records were taken, to ensure that the responses were repeatable.

Observations were made while recording from motoneurones penetrated with potassium-citrate-filled micro-electrodes, to avoid reversal of i.p.s.p.s by diffusion of chloride ions from potassium-chloride-filled electrodes and their erroneous classification as e.p.s.p.s. To further avoid such errors records were taken only from motoneurones in which distinct disynaptic Ia i.p.s.p.s from antagonists were in the hyperpolarizing direction, since these i.p.s.p.s would be among those easiest to reverse (cf. Burke, Fedina & Lundberg, 1971). Effects of depolarization and of hyperpolarization of the motoneurones were also tested, but the majority of results are from non-polarized motoneurones with action or membrane potential > 50–60 mV.

Criteria for the selectivity of group Ia excitatory actions. Effects of Ia afferents activated by muscle stretches were differentiated from those of Ib and group II muscle spindle afferents using similar criteria to those for i.p.s.p.s (Jankowska *et al.* 1981*b*). Briefly, to Ia afferents were attributed only those e.p.s.p.s which (i) were evoked by muscle stretches below threshold for Ib afferents ($\leqslant 35$ μm, the threshold for Ib afferents being > 40 μm; see Fetz *et al.* 1979), (ii) were matched by e.p.s.p.s evoked by electrical stimulation of the corresponding nerves with stimulus intensities below threshold for group II afferents (< 1·5 times threshold for Ia afferents: cf. Fig. 1*C*, *D*, Fig. 2*B*, *C*), and (iii) appeared with latencies shorter than the shortest expected effects of group II afferents (< 3·7 msec in relation to the incoming volleys in stretch-activated Ia afferents). Considering the latencies of the earliest stretch-evoked e.p.s.p.s of group II origin we assumed that, as in the case of i.p.s.p.s, they would be evoked disynaptically. In the studies which analysed distribution of monosynaptic actions of group II afferents, such actions were found only (Kirkwood & Sears, 1975; Lundberg, Malmgren & Schomburg, 1977), or predominantly (Stauffer, Watt, Taylor, Reinking & Stuart, 1976; Munson, Fleshman & Sypert, 1980) in homonymous and close synergist motoneurones. In our sample of motoneurones any e.p.s.p.s which were evoked monosynaptically in other motoneurones appeared both upon stretch and upon electrical stimulation of the triceps surae and plantaris nerves at stimulus intensities below threshold for group II afferents. Control experiments on a possible contribution of panciniform corpuscles (cf. Jankowska *et al.* 1981*b*) to the stretch-evoked oligosynaptic e.p.s.p.s did not give any indications of their involvement.

The 3·7 msec limit for the stretch-evoked e.p.s.p.s also alleviated two other complicating factors. One of them was the possible effect of reactivation of Ia afferents caused by small length perturbations following the initial stretch (see Jankowska *et al.* 1981*b*). The second was the

occurrence of any e.p.s.p.s which might be due to interactions between Ia afferents, i.e. to dorsal root reflexes, and the subsequent monosynaptically evoked depolarization of motoneurones instead of the activation of interneurones between Ia afferents and motoneurones. Eccles, Kozak & Magni (1961) found that the dorsal root reflexes resulting from electrical stimulation of group I afferents never had a segmental latency less than 4 msec. In a separate series of observations we have measured the latency for such reflexes in preparations treated with 4-aminopyridine, which may shorten their latency (Jankowska, Lundberg, Rudomin & Sykova, 1977), and found similar minimum values. Since dorsal root reflexes are recorded some distance from the terminals of the depolarized afferents, excitation of the terminals would occur about 0·2 msec earlier, with synaptic effects on motoneurones after a further 0·3–0·5 msec, or at least 4·0 msec after the arrival of the incoming volleys to the spinal cord.

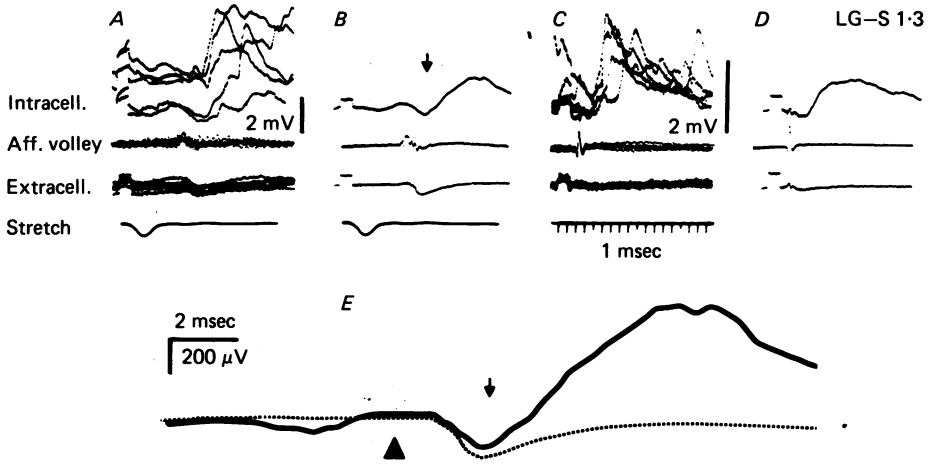

Fig. 1. Oligosynaptic e.p.s.p.s evoked by muscle stretches and by electrical stimulation of group I afferents. In *A* and *B* are records of e.p.s.p.s (top traces) evoked by 35 μm stretches of triceps surae and plantaris (bottom traces, with the increase in length upwards) and in *C* and *D* those evoked by electrical stimulation of the lateral gastrocnemius–soleus (LG–S) nerve, with stimulation intensity expressed as a multiple of nerve threshold. The corresponding records of the arrival of the afferent volleys to the dorsal root entry zone, and records of extracellular field potentials evoked by the same stimuli, are below the intracellular records. Single-sweep records to the left. Averaged (n = 128) records to the right. Calibration pulse: 200 μV (for averaged records), 1 msec. Superimposed tracings of averaged intracellular records in *B* are shown in *E*. Large arrowhead, onset of the group Ia afferent volley; arrows, onset of the e.p.s.p.s.

RESULTS

Ia oligosynaptic e.p.s.p.s evoked by small stretches of triceps surae and plantaris

Figs. 1–3 show three examples of stretch-evoked e.p.s.p.s attributed to Ia afferents. Muscle stretches usually evoked extracellular field potentials around the motoneurones recorded from (except those in L6) and the net post-synaptic potentials are given by the difference between the intracellular and extracellular records. In the large-scale superimposed tracings of the original records, the intracellular and the extracellular potentials are drawn in continuous and dotted lines, respectively.

Fig. 1 gives an example of stretch-evoked e.p.s.p.s (*A*, *B*, *E*) in a posterior biceps or semitendinosus motoneurone, with corresponding e.p.s.p.s evoked by electrical stimulation of the lateral gastrocnemius–soleus nerve (*C*, *D*). From the medial

gastrocnemius and plantaris were evoked similar, though smaller e.p.s.p.s. Both the longer latency and slower rise time of the stretch-evoked e.p.s.p.s are consistent with a less-effective activation of the interposed interneurones, and the interposition of an additional interneurone is not required to explain the differences between these stretch-evoked and electrically evoked e.p.s.p.s.

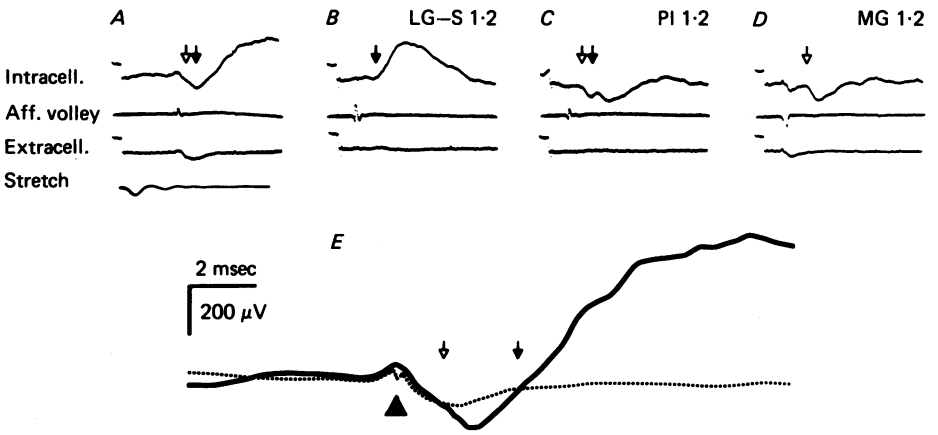

Fig. 2. Oligosynaptic e.p.s.p.s preceded by i.p.s.p.s. In *A* and *E* are responses to 25 μm stretches of triceps surae and plantaris and in *B–D* those to electrical stimulation of the lateral gastrocnemius–soleus (LG–S), medial gastrocnemius (MG), and plantaris (Pl) nerves. Intracellular records from a posterior biceps or semitendinosus motoneurone. Top traces in *A* and *B* and the continuous trace in *E* were taken at the neurone's resting membrane potential and those in *C* and *D* after it was depolarized by 50 nA current. Calibration pulse: 200 μV, 1 msec. Large arrowhead, onset of the group Ia afferent volley; filled arrow, onset of the e.p.s.p.s; open arrow, onset of the i.p.s.p.s. Other abbreviations as in Fig. 1.

Fig. 2*A* and *E* show a similar stretch-evoked e.p.s.p. but preceded by a small i.p.s.p. In this motoneurone electrical stimulation of lateral gastrocnemius and plantaris nerves evoked e.p.s.p.s (filled arrows) and i.p.s.p.s (open arrows) with latencies similar to those evoked by stretch. The electrically evoked i.p.s.p.s from these muscle nerves could, however, only be detected after depolarization of the motoneurone. Stimulation of medial gastrocnemius evoked an i.p.s.p. with longer latency (*D*); if this i.p.s.p. were evoked by Ia afferents it would be hidden by the rising phase of the stretch-evoked e.p.s.p.

Fig. 3*A*, *B* and *E* show stretch-evoked e.p.s.p.s in an anterior biceps–semimembranosus motoneurone. These e.p.s.p.s (filled arrows) appeared with a latency similar to the e.p.s.p.s evoked by stimulation of the lateral gastrocnemius–soleus nerves (*C*, *D*) as well as of medial gastrocnemius and plantaris nerves (not illustrated). No i.p.s.p.s preceding the e.p.s.p.s have been detected in this neurone. However, there were i.p.s.p.s (open arrows) which followed the e.p.s.p.s and cut short their falling phase.

Stretch-evoked Ia e.p.s.p.s, like those in Figs. 1–3, were seen in sixty-five motoneurones of various species (see below); the percentages of motoneurones with

e.p.s.p.s which were preceded or followed by i.p.s.p.s are given in Table 1. In the case of seventeen e.p.s.p.s effects of different amplitudes of stretches were tested. Sixteen of these e.p.s.p.s appeared in response to stretches of 10–20 μm.

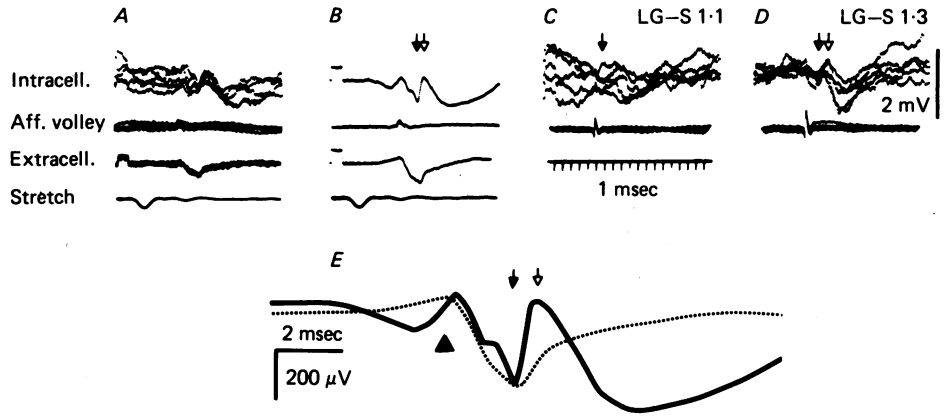

Fig. 3. Oligosynaptic e.p.s.p.s. In *A*, *B* and *E* are responses to 30 μm stretches of triceps surae and plantaris and in *C* and *D* those to electrical stimulation of the lateral gastrocnemius–soleus nerves. Intracellular records from an anterior biceps or semimembranosus motoneurone (top traces in *A–D* and the continuous trace in *E*) were taken after the motoneurone was depolarized by a 20 nA current. Calibration pulse: 200 μV, 1 msec. All abbreviations as in Figs. 1 and 2.

Ia oligosynaptic e.p.s.p.s evoked by electrical stimulation of nerves

Examples of oligosynaptic e.p.s.p.s following monosynaptic e.p.s.p.s evoked by electrical stimulation of Ia afferents are given in Fig. 4 *A–C* and *F–H*. The first series of records of Fig. 4 (*A–E*) shows e.p.s.p.s evoked in a posterior biceps–semitendinosus motoneurone by stimuli of increasing intensity, all of which were below threshold for the second (Ib) component of the incoming volley, which in this experiment appeared at a stimulus intensity 1·6 times threshold (*E*). The second series of records of Fig. 4 (*F–I*) is from a triceps surae motoneurone. In view of the low thresholds of some Ib afferents in gastrocnemius and soleus nerves it is difficult to exclude their activation by stimuli 1·15–1·2 times threshold (see Jack, 1978). However, similar late components of e.p.s.p.s were evoked both by stimuli 1·2–1·4 times threshold and by near-threshold ones (Fig. 4 *F*, arrow); at least in the case of the latter they could be attributed to Ia afferents. A particular feature of these e.p.s.p.s was that they did not have a counterpart in e.p.s.p.s of Ib origin. Similar oligosynaptic e.p.s.p.s, though evoked by an unspecified group of afferents of lateral gastrocnemius were seen by Carlen, Werman & Yaari (1980, see their Fig. 1). The third series of records of Fig. 4 (*K–O*) shows e.p.s.p.s evoked in another posterior biceps–semitendinosus motoneurone. They were evoked from plantaris and therefore the relative contribution of Ia and Ib afferents is similarly difficult to assess. Those evoked by near-threshold stimuli (*K*, *L*) should, however, be reasonably safely attributed to Ia afferents. It will be noted that a larger second and a third component of e.p.s.p.s were added with stimuli between 1·5 and 2·0 times threshold (*M*, *N*) and might be attributed to either Ib or

lowest-threshold group II afferents. Stimulation of a larger number of the latter did not change the effect substantially (*O*).

Oligosynaptic e.p.s.p.s following monosynaptic e.p.s.p.s like those in Fig. 4*A–J* were found in four hamstring, two tibial, one triceps surae and one quadriceps motoneurone. Oligosynaptic e.p.s.p.s evoked without a preceding monosynaptic e.p.s.p., as in Fig. 4*K–O*, were seen in six hamstring motoneurones.

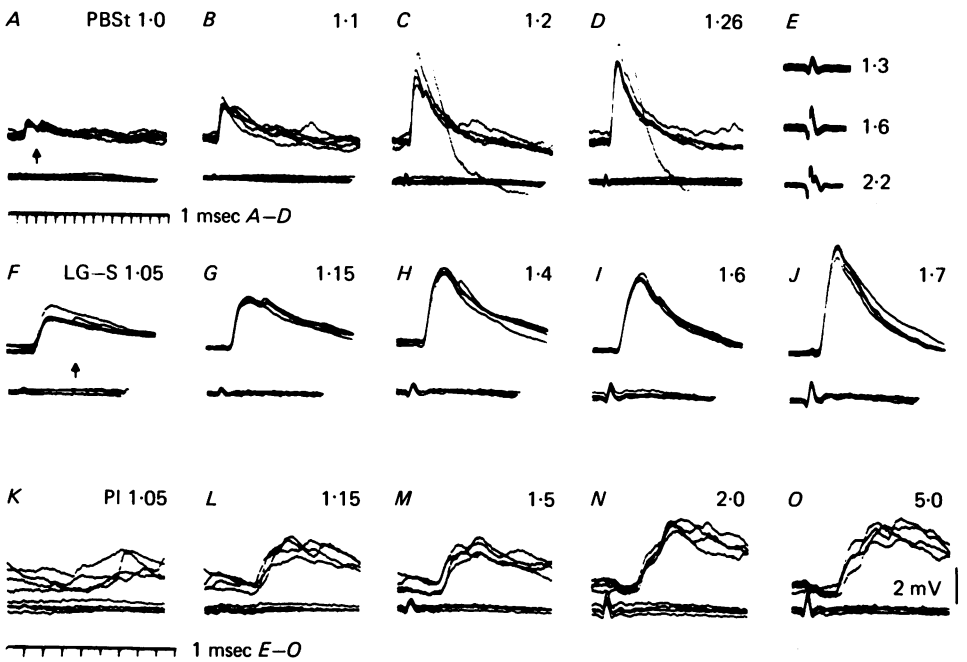

Fig. 4. E.p.s.p.s evoked by various fractions of group I afferents. In *A–D*, *F–J* and *K–O* are records from a posterior biceps–semitendinosus, a triceps surae and another posterior biceps–semitendinosus motoneurone, respectively. Note that in the first neurone oligosynaptic e.p.s.p.s (arrow) were evoked more effectively by lowest-threshold I a afferents (*A*, *B*) than when the stimulus intensity was increased (*C*, *D*), although it still remained within range for I a afferents. As shown in *E*, threshold for the I b component of incoming volleys was > 1·6 times nerve threshold. Similar higher effectiveness of weaker (arrow; *F*, *G*) than of stronger (*H–J*) electrical stimulation of group I afferents was found in the second neurone. *K–O* illustrate new later components of the oligosynaptic e.p.s.p.s added by higher threshold group I afferents (*L–N*) and group II afferents (*O*).

Latencies of stretch and electrically evoked e.p.s.p.s

E.p.s.p.s evoked by either stretch or electrical stimulation of various nerves appeared with latencies ranging between 0·5 and 5·0 msec, but for the reasons given above only those with latencies < 3·7 msec were included in the present material.

On the basis of previous studies (Eccles *et al.* 1957*b*; Fetz *et al.* 1979), latencies of < 1, 1–2 and < 2 msec were used to classify the e.p.s.p.s evoked by electrical stimuli as mediated by monosynaptic, disynaptic and trisynaptic pathways, respectively; those classified as di- or trisynaptic are plotted in the frequency histograms of latencies of e.p.s.p.s evoked by stimulation of nerves of triceps surae and plantaris

(Fig. 5*B*). Stretch-evoked e.p.s.p.s corresponding to the electrically evoked monosynaptic e.p.s.p.s were classified as monosynaptic even though their latencies were sometimes up to 1·2 msec; such e.p.s.p.s have not been included in the present material.

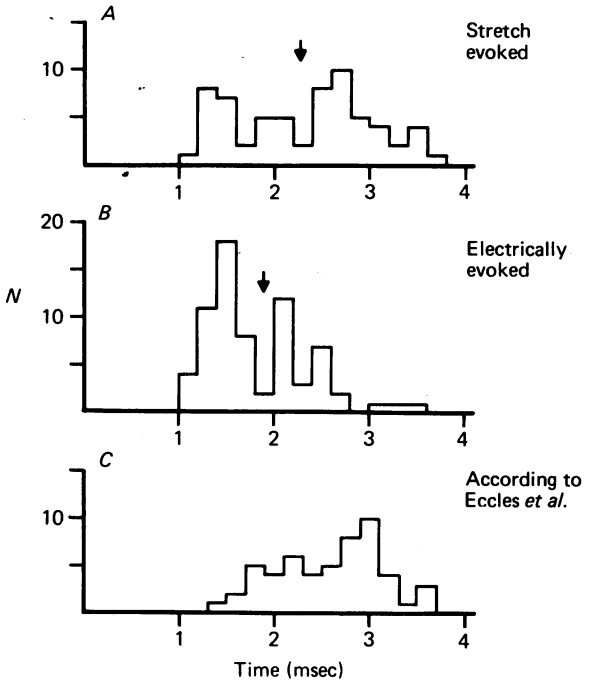

Fig. 5. Histograms of the distribution of latencies of e.p.s.p.s evoked by electrical stimulation of group I afferents of triceps surae and by muscle stretches. *A*, distribution of latencies of oligosynaptic e.p.s.p.s evoked by $\leqslant 35\ \mu$m stretches of triceps surae and plantaris in motoneurones listed in Table 1. *B*, distribution of latencies of e.p.s.p.s evoked in the same motoneurones by electrical stimulation of lateral gastrocnemius–soleus, medial gastrocnemius or plantaris nerve with intensity $\leqslant 1{\cdot}5$ times threshold. *C*, distribution of oligosynaptic e.p.s.p.s evoked in posterior biceps–semitendinosus and pretibial flexor motoneurones by electrical stimuli, according to Eccles *et al.* (1957*b*).

Histograms of the oligosynaptic e.p.s.p.s showed maxima at 1·2–1·6 and 2·0–2·6 msec for the electrically evoked e.p.s.p.s (Fig. 5*B*) and at 1·2–1·6 msec and 2·4–2·8 msec for the stretch-evoked e.p.s.p.s (Fig. 5*A*). Minima indicating a tentative border between di- and trisynaptic latencies are indicated by arrows. A comparison of histograms *B* and *A* shows a general tendency for the electrically evoked e.p.s.p.s to appear with shorter latencies than the stretch-evoked e.p.s.p.s; the differences in their distribution are probably due to the fact that electrical stimulation results in a greater synchronization of the afferent volley than does stretch. A comparison of the latencies of electrically evoked e.p.s.p.s with the latencies of I b e.p.s.p.s recorded by Eccles *et al.* (1957*b*) (Fig. 5*C*) reveals a higher proportion of e.p.s.p.s with shorter latencies in the present study.

The differences may be explained by a higher excitability of the interposed

interneurones which likewise resulted in a higher proportion of motoneurones with oligosynaptic e.p.s.p.s from Ib afferents of triceps surae and plantaris. Such e.p.s.p.s were found in, for example, quadriceps and flexor digitorum longus motoneurones in which there was no previous evidence for them. E.p.s.p.s in some other combinations, e.g. from posterior biceps–semitendinosus in flexor digitorum longus motoneurones, have earlier been seen only against the background of facilitatory supraspinal actions (cf. Hongo, Jankowska & Lundberg, 1969).

TABLE 1. The distribution of oligosynaptic stretch-evoked effects among various motoneurone species

	ABSm	Q	FDL	Tib	Grac	PBSt	TA, EDL	Per l	Per t, br	Total
% of motoneurones with Ib e.p.s.p.s showing Ia e.p.s.p.s	100	100	100	100	20	94	33	0	70	83
% of motoneurones tested showing Ia e.p.s.p.s (*n*)	26 (27)	7 (30)	28 (29)	33 (20)	6 (17)	94 (34)	9 (23)	0 (21)	23 (31)	28 (232)
% of motoneurones tested showing Ia i.p.s.p.s (*n*)	67 (27)	75 (36)	80 (24)	35 (20)	34 (17)	15 (34)	50 (14)	43 (21)	58 (24)	53 (217)
% of motoneurones with Ia e.p.s.p.s showing Ia i.p.s.p.s	86	100	50	33	0	16	0	0	57	35

The first row shows proportions of those motoneurones in which electrical stimulation $\leqslant 1{\cdot}5$ threshold evoked di- or trisynaptic e.p.s.p.s which displayed stretch-evoked Ia e.p.s.p.s. The second row gives the proportion of the total number of motoneurones tested in which these stretch-evoked Ia e.p.s.p.s have been detected. The third row gives corresponding data for stretch-evoked Ia non-reciprocal i.p.s.p.s described in the preceding paper. The fourth row shows in how many motoneurones stretch-evoked Ia non-reciprocal i.p.s.p.s were found in addition to stretch-evoked Ia e.p.s.p.s. In brackets are numbers of motoneurones of various species, those in the third row from Jankowska *et al.* (1981*b*). The motoneurones in which the distributions of Ia e.p.s.p.s and i.p.s.p.s have been analysed were partly the same and partly different since the distribution of i.p.s.p.s was investigated in a greater number of experiments and since the criteria for accepting failures of occurrence of e.p.s.p.s and i.p.s.p.s were less strict than those for accepting their presence. The failures were counted even if the tested stimuli were stronger than required by our criteria.

The latencies of oligosynaptic e.p.s.p.s evoked by electrical stimulation of Ia afferents in hamstring nerves ranged between 1·3 and 2·0 msec.

Contribution of group Ia muscle spindle afferents of triceps surae and plantaris to oligosynaptic excitation of motoneurones of various hip, knee, ankle and toe muscles

Di- and trisynaptic e.p.s.p.s attributable to Ia afferents were found in different proportions in the different motoneurone species. As shown in Table 1 (second row), these proportions ranged from more than 90% for posterior biceps–semitendinosus to 6% for gracilis motoneurones. However, the disclosure of the e.p.s.p.s was easiest when no other e.p.s.p.s were evoked in the same motoneurones. In those with monosynaptic e.p.s.p.s (e.g. anterior biceps–semimembranosus and flexor digitorum longus motoneurones) or with disynaptic reciprocal or non-reciprocal i.p.s.p.s (e.g.

pretibial flexors and quadriceps motoneurones) the occurrence of the oligosynaptic e.p.s.p.s was undoubtedly underestimated.

When distinct oligosynaptic e.p.s.p.s were evoked by electrical stimuli activating both Ia and Ib afferents, they were usually matched by stretch-evoked e.p.s.p.s (Table 1, first row). The matching appeared to be stronger in those motoneurone species in which the Ib excitatory actions were most pronounced, in particular in posterior biceps–semitendinosus motoneurones.

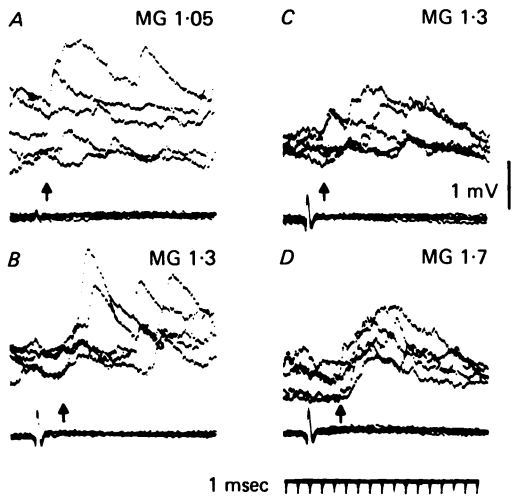

Fig. 6. Suppression of early oligosynaptic e.p.s.p.s by stronger stimuli. In *A–B* and in *C–D* are records from two posterior biceps–semitendinosus motoneurones. Upper and lower row records show e.p.s.p.s evoked by weaker and stronger stimuli, respectively. Note lengthening of the latencies of the e.p.s.p.s (arrows) evoked by stronger stimuli.

An examination of proportions of motoneurones displaying stretch-evoked Ia non-reciprocal i.p.s.p.s (Jankowska *et al.* 1981*b*) and e.p.s.p.s (second and third rows of Table 1) shows a tendency towards the predominance of either one or another of these effects in all but one of the motoneurone species analysed (tibial). In spite of this tendency both excitatory and inhibitory actions of Ia afferents have been found in all the motoneurone species. A comparison of stretch-evoked responses in two subgroups of quadriceps motoneurones identified on the basis of their monosynaptic excitation from anterior biceps–semimembranosus and disynaptic inhibition from posterior biceps as innervating rectus and vasto-crureus (cf. Eccles *et al.* 1957*a*) showed that also within these subgroups some motoneurones were excited while others were inhibited. A comparison of responses of anterior biceps and semimembranosus motoneurones identified by their input from quadriceps and gracilis led to the same conclusion.

Further evidence for both excitatory and inhibitory oligosynaptic pathways from Ia afferents to a given species of motoneurones comes from the observations that the two effects were seen in individual motoneurones, as illustrated in Figs. 2 and 3 and summarized in Table 1, last row. The e.p.s.p.s were evoked either with a shorter latency and were followed by an i.p.s.p., as illustrated in Fig. 3, or with a latency

longer than that of the i.p.s.p.s, as in the neurone of Fig. 2. The two effects were evoked by Ia afferents of the same muscle (Fig. 2*C*) as well as of one or two of the four synergists (Fig. 2*B* and *D*).

Possible interactions between effects of different groups of afferent fibres

The records in Figs. 4 and 6 illustrate that the di- and trisynaptic electrically evoked e.p.s.p.s may be more distinct at lower than at higher stimulus intensities (cf. Fig. 6*C*, upper and lower row records, and Fig. 4*F*, *G* and *I*, *J*). The decrease or disappearance of oligosynaptic e.p.s.p.s following monosynaptic e.p.s.p.s as in Fig. 4 might to some extent have been due to a shunting of the e.p.s.p. during a period of increased motoneurone membrane conductance, but a more likely explanation is an inhibitory effect of stronger stimuli on the interneurones mediating the e.p.s.p.s. The records in Fig. 6 are easier to interpret in this way. As seen in Fig. 6*A*, *B* the earliest e.p.s.p.s produced by threshold stimuli to medial gastrocnemius disappeared when stimulus intensity was increased to 1·3 times threshold. Records in *C* and *D* are from another posterior biceps–semitendinosus motoneurone and show a similar depression of the earliest e.p.s.p.s by an increase in either medial gastrocnemius or plantaris nerve stimulation. Since no attempt was made to activate selectively the Ib afferents without the Ia afferents, nor was a range of muscle stretches used in order to stimulate various proportions of the Ia afferents, we cannot conclude which afferent fibre systems are responsible for the effects demonstrated in Figs. 4 and 6.

DISCUSSION

The results of the present study agree fully with the previous postulates of the existence of oligosynaptic excitatory pathways between group Ia muscle spindle afferents and motoneurones (see Introduction), even if the earlier evidence for such pathways may not be quite conclusive. The precautions which have now been taken to differentiate between the oligosynaptic actions of Ia muscle spindle afferents and actions of other afferents, or other factors, have been discussed under Methods and in the preceding paper (Jankowska *et al.* 1981*b*). In view of these precautions we consider our observations as providing strong evidence that the Ia muscle spindle afferents may excite hind-limb motoneurones di- and trisynaptically, as well as monosynaptically. The evidence is for Ia oligosynaptic excitation when it is combined with Ib excitation as well as when it is evoked independently from it in homonymous motoneurones (see below). Recent observations of P. A. Kirkwood and T. A. Sears (personal communication) similarly give strong evidence for disynaptic excitatory effects of Ia afferents of intercostal muscles on their homonymous motoneurones. These authors found that monosynaptic e.p.s.p.s evoked by impulses in a Ia fibre may be followed by somewhat later e.p.s.p.s during the inspiration phase of the respiration, a double firing of the afferents being excluded. The dependence of these e.p.s.p.s on the phase of respiration might be considered as analogous to the dependence of the late homonymous Ia e.p.s.p.s in hind-limb motoneurones on the phase of locomotion (Schomberg & Behrends, 1978), supporting the conclusion that the latter are evoked oligosynaptically (see Introduction). Kirkwood & Sears' observations also strengthen the interpretation of Watt *et al.* (1976) of oligosynaptic

components of unitary Ia e.p.s.p.s detected with a spike-triggered averaging technique.

With respect to the problem of the relationship between the reflex actions of Ia and Ib afferents, the results of this study show that *the oligosynaptic excitation of motoneurones evoked by impulses in tendon organs is paralleled by excitatory actions of group Ia muscle spindle afferents*. The stretch-evoked Ia e.p.s.p.s as well as the Ia i.p.s.p.s have been found in a great proportion of motoneurones which displayed post-synaptic potentials evoked by electrical stimulation involving Ib afferents. The proportion might even have been underestimated in view of the fact that we have taken into account only those e.p.s.p.s which appeared with segmental latencies $< 3{\cdot}7$ msec. We might have also missed some oligosynaptic e.p.s.p.s, e.g. those evoked on the background of i.p.s.p.s. Combined actions of Ia and Ib afferents might thus be expected on practically all motoneurones with Ib e.p.s.p.s even if the effects of Ia afferents alone are weak or absent.

In addition to Ia e.p.s.p.s evoked in parallel with e.p.s.p.s of Ib origin, hereafter referred to as Ia-like-Ib e.p.s.p.s, we have seen some Ia e.p.s.p.s apparently not combined with Ib actions. Observations reported on pp. 417 and 421 of the Results indicate that occurrence of Ia oligosynaptic e.p.s.p.s following the monosynaptic e.p.s.p.s may even be prevented by Ib afferents. There is no information on Ib actions in motoneurones with such oligosynaptic e.p.s.p.s evoked by single Ia afferents (Mendell & Henneman, 1971; P. A. Kirkwood & T. A. Sears, personal communication) but Schomburg & Behrends (1978) reported that the e.p.s.p.s which they recorded during one of the phases of locomotion did not increase with stimulus strength above the strength required to activate Ia afferents. It is thus possible that the Ia oligosynaptic e.p.s.p.s in homonymous motoneurones represent reflex actions independent of or opposed to Ib actions, in contrast to Ia-like-Ib excitation evoked in other motoneurones.

Considering the relations between the oligosynaptic and polysynaptic excitation evoked from Ia afferents, one should first of all try to find out whether they may be mediated by the same or different interneurones. The results obtained in different preparations (e.g. human or animal, unanaesthetized decerebrate or anaesthetized spinal) and in which Ia afferents were activated in different ways (e.g. by single stretch, vibration, single or repetitive electrical stimuli) are rather difficult to compare. They indicate, however, that the Ia-like-Ib oligosynaptic excitation and the polysynaptic excitation are mediated by different, rather than the same interneurones. For example, according to Hultborn & Wigström (1975, 1980) the late long-lasting Ia excitation is evoked primarily in homonymous motoneurones and in motoneurones of Ia synergists (from ankle and toe extensors: soleus, gastrocnemius and plantaris, in soleus motoneurones), while the results presented in two previous papers (Fetz *et al.* 1979; Jankowska *et al.* 1981*b*) show that the predominant Ia oligosynaptic effects to ankle and toe extensors are inhibitory. Other characteristic features of the Ia oligosynaptic excitation, i.e. its facilitation by Ib, joint and cutaneous afferents (Jankowska & McCrea, 1980) were either not tested on the Ia polysynaptic excitation (Ib and joint effect) or the tests showed an opposite effect; Hultborn & Wigström (1980) have found that cutaneous nerve stimulation abolishes the Ia polysynaptic excitation. It may, however, be considered that the oligosynaptic

excitation evoked in homonymous motoneurones and the polysynaptic excitation are mediated by the same interneurones.

In view of the wide distribution of the parallel oligosynaptic excitatory actions of Ia and Ib afferents these actions may be of prime importance as a counterpart of the non-reciprocal Ia and Ib inhibition in movements involving several joints of a limb. Since various aspects of the interplay between Ia and Ib afferents have already been discussed (Fetz *et al.* 1979; Jankowska *et al.* 1981*a*, *b*; Czarkowska, Jankowska & Sybirska, 1981) or will be taken up in a forthcoming paper (E. Jankowska & D. McCrea, in preparation), we will now comment only on the problem of alternative reflex pathways between group I afferents and motoneurones (Hongo *et al.* 1969). Table 1 (bottom row) shows that fairly large proportions of our sample of motoneurones were both excited and inhibited by the applied stimuli, i.e. influenced by two neuronal pathways with opposite effects, although inhibition predominated in extensor and excitation in flexor motoneurones. Since the main aim of the present experiments was to detect the Ia-like-Ib actions, little attention was paid to determining the conditions under which the alternative pathways would operate. However, together with other observations our results show that there is a possibility of choice between these pathways, the final result depending on which of them are open and which closed. Direct records from individual Ia-excited laminae V–VI interneurones substantiate such a possibility, showing that these interneurones may be inhibited by group I afferents of the same or other nerves (Czarkowska *et al.* 1981; Jankowska *et al.* 1981*a*). Opening and closing of pathways of the oligosynaptic excitation from Ia afferents to homonymous motoneurones by other fibre systems has been demonstrated by the above-mentioned observations of Kirkwood & Sears and strongly suggested by those of Schomburg & Behrends (1978). A differential facilitation or depression of alternative pathways of Ia-like-Ib excitation and inhibition by various neuronal systems may be also expected in view of previously evidenced control of segmental reflexes from Ib afferents (for references see Hongo *et al.* 1969, and Lundberg *et al.* 1978).

The results presented in this and previous papers (Fetz *et al.* 1979; Jankowska *et al.* 1981*b*) lead to the general conclusion that *all the known reflex actions of Ib tendon organ afferents on ipsilateral motoneurones are also evoked from Ia muscle spindle afferents*, and a forthcoming paper (see Jankowska & McCrea, 1980) will present evidence that the parallel actions of Ia and Ib afferents are mediated by common interneurones.

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