SEGMENTAL ACTIONS OF AFFERENTS OF THE INTEROSSEOUS NERVE IN THE CAT

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SUMMARY

1. Electrical stimulation of the interosseous nerve evokes oligosynaptic inhibition of extensor motoneurones and excitation of flexor motoneurones. Lowest-threshold, shortest-latency post-synaptic potentials evoked at group I strength are attributed to the action of group I b afferents. Post-synaptic potentials evoked at slightly higher stimulus strengths (within the higher group I and the group II range) and at longer latency are attributed to the action of afferents of Pacinian corpuscles.

2. Facilitation of post-synaptic potentials evoked from afferents in the interosseous nerve by group I muscle afferents and by joint afferents is taken to indicate convergence of these afferents onto common interneurones in reflex pathways to motoneurones. Evidence is presented that afferents of Pacinian corpuscles project to the interneurones mediating group I (non-reciprocal) reflex actions to motoneurones.

3. Unitary monosynaptic excitatory post-synaptic potentials (e.p.s.p.s) evoked from the interosseous nerve are taken to indicate that only a very small number of muscle spindle I a afferents course through the interosseous nerve.

4. Dorsal root potentials evoked by low-strength electrical stimulation of the interosseous nerve are largely attributable to the action of afferents of Pacinian corpuscles.

INTRODUCTION

The interosseous membrane, lying between the tibia and fibula, is innervated by a small nerve which courses between the medial and lateral heads of flexor digitorum longus before merging with the nerves of this muscle. The interosseous nerve is exclusively afferent and has been shown to contain myelinated fibres supplying several types of receptor (Hunt & McIntyre, 1960; see also Silfvenius, 1970a). The group I component consists of afferents of about twenty unusually sited Golgi tendon organs (Barker, 1962; Boyd & Davey, 1968) together with a small number of I a afferents, while the group II component consists almost entirely of afferent fibres of Pacinian corpuscles and constitutes 35 % of the total myelinated fibres in this nerve (Boyd & Davey, 1968).

On a number of occasions previously, advantage has been taken of the high number of Pacinian corpuscles in the interosseous membrane to activate them either by electrical or natural stimuli in order to infer their central actions. In this way the cortical actions of Pacinian afferents have been established (McIntyre, 1962; Norrsell

& Wolpow, 1966; McIntyre, Holman & Veale, 1967; Silfvenius, 1970b). With respect to the segmental reflex actions of Pacinian afferents, however, there is some evidence of presynaptic actions (Jänig, Schmidt & Zimmerman, 1968; Yeo & McIntyre, 1976; Yeo, 1978) but investigations of reflex actions to motoneurones have failed to reveal any effect (Yeo & McIntyre, 1976; Ellaway & Murphy, 1978).

The aim of the present study was 2-fold. First, we wanted to study the segmental actions of afferents of the interosseous nerve, since this nerve may have been taken together with the nerve to flexor digitorum longus in some studies (e.g. see Hunt & McIntyre, 1960), and it was of interest to see how much the actions from the interosseous nerve could add to the actions of group I afferents of this muscle. Secondly, we wanted to attempt to define the segmental actions of afferents of Pacinian corpuscles by graded electrical stimulation of the interosseous nerve into the group II range.

METHODS

The experiments were performed on fourteen cats. The preparation and general procedures of motoneuronal recording, stimulating and data analysis were as described previously (Harrison, Jankowska & Johannisson, 1983) and some of the present material is drawn from those experiments.

Briefly, cats were under chloralose anaesthesia (initial dose 50–60 mg/kg, supplemented with two or three additional doses of 10–20 mg/kg), paralysed with gallamine triethiodide and artificially ventilated. Deep anaesthesia was assured by observations of pupil diameter, lack of movements during periods of recovery from the paralysis and from observations of adequate anaesthesia of non-paralysed animals during other experiments with an identical anaesthetic regime. Six of the animals were spinalized at Th13. In addition to the interosseous nerve (i.o.), the following nerves were cut and mounted on separate pairs of silver electrodes for stimulation and recording: quadriceps (q.), posterior biceps and semitendinosus (p.b.s.t.), anterior biceps and semimembranosus, sural, gastrocnemius and soleus (g.s.), plantaris (pl.), flexor digitorum longus (f.d.l.), peroneus longus, tertius and brevis (per.), popliteus (pop.), tibialis posterior and the posterior nerve to the knee joint (j.). In the present paper we will refer to the two heads of flexor digitorum longus collectively as flexor digitorum longus. In some studies these have been referred to as flexor digitorum and hallucis longus. However, since in the cat the two heads have a common tendon (Reighard & Jennings, 1934) the latter terminology is less appropriate (see Hunt & McIntyre, 1960). The interosseous branch of the nerve to flexor digitorum longus was traced distally between the medial and lateral heads of flexor digitorum longus to run alongside the tibia just dorsal to the interosseous membrane. As an additional control for the identification of the interosseous nerve the distal ends of the L7 and S1 ventral roots were stimulated while recording from its proximal end to ascertain that the nerve was purely afferent and lacking motor components. The proximal ends of the ventral roots were then mounted on stimulating electrodes to aid the location and identification of motoneurones. Motoneurones were assigned a species according to their pattern of Ia connectivity (Eccles, Eccles & Lundberg, 1957).

Stimulation and recording. Observations with intracellular recording from motoneurones were made with potassium-citrate-filled electrodes. The interosseous nerve was then activated from 1 to 20 times threshold for the lowest-threshold afferents in the nerve. Single and in some cases short trains of stimuli were used.

To evoke primary afferent depolarization, stimuli were delivered at about one per second. Single or double stimuli were used, and only occasionally short trains of three to five stimuli. With multiple stimuli, interstimulus intervals were 3·3 or 5·0 ms. Primary afferent depolarization was observed by recording dorsal root potentials from the most caudal L6 dorsal root filament. Most of the data were recorded as averaged records using 32 (but sometimes up to 256) single records for each average.

In order to test for convergence of other afferent systems on the interneuronal pathways mediating post-synaptic actions from the interosseous nerve, the technique of spatial facilitation was used. This consisted of stimulating the two test nerves in a sequential mode and storing the averaged post-synaptic potentials, which were then arithmetically manipulated using a Nicolet

(Model 1170) averager. It was concluded that afferents of different origin converged onto the same interneurones when post-synaptic potentials (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. The motoneurones selected for analysis were those in which distinct p.s.p.s were evoked by the tested afferents when stimulated alone, and generally, in which the p.s.p.s were not preceded by monosynaptic excitatory post-synaptic potentials (e.p.s.p.s).

The afferent systems tested for convergence were from group I muscle afferents and from joint afferents. For the purposes of activating group I muscle afferents stimuli did not exceed a maximum of 1·5 times threshold in order to avoid the possibility of activating group II muscle afferents (cf. Jack, 1978). In addition, the analysis of convergence from group I muscle afferents was restricted to the interneuronal systems mediating group I non-reciprocal inhibition: that is to say group I inhibition other than I a reciprocal inhibition. (For a detailed account of the term 'non-reciprocal inhibition' see Jankowska, McCrea & Mackel, 1981.) In testing for convergence with other afferent systems the interosseous nerve was activated with stimulus intensities up to 5 times threshold. However, optimum conditions for demonstrating a common pathway were usually achieved with lower stimulus intensities than this (typically less than twice threshold) since the largest subliminal fringe would be expected when as large a number of interneurones as possible were brought just below threshold for firing on separate stimulation of each of the tested nerves.

RESULTS

Post-synaptic potentials evoked in motoneurones

Recordings were made from a total of 105 hind limb motoneurones. These included twenty-six gastrocnemius–soleus, fifteen flexor digitorum longus, seven plantaris, ten anterior biceps or semimembranosus, sixteen posterior biceps or semitendinosus, seven quadriceps, four popliteus, ten common peroneal and ten unidentified motoneurones. Distinct p.s.p.s evoked from the interosseous nerve could be recognized in 70 % of the motoneurones, either with single-sweep records or with the use of averaging. The p.s.p.s were inhibitory in extensor motoneurones and generally, though not always, excitatory in flexor (posterior biceps–semitendinosus) motoneurones. In some flexor motoneurones the p.s.p.s were inhibitory, and in these motoneurones inhibition was also evoked from group I muscle (non-reciprocal) and joint afferents. Qualitatively similar results were obtained from spinalized and non-spinalized animals.

Fig. 1 illustrates the post-synaptic actions of afferents of the interosseous nerve, in a plantaris motoneurone (*A*). For comparison the actions of afferents of the flexor digitorum longus nerve are shown in *B*. As shown in *A*, the inhibitory post-synaptic potentials (i.p.s.p.s) evoked by the interosseous nerve followed the group I volley after a latency of 4 ms, which was in contrast to the presumably disynaptic, non-reciprocal i.p.s.p. evoked by flexor digitorum longus afferents at a latency of 1·7 ms. If the group I afferents in the interosseous nerve had evoked inhibition in this motoneurone then this would have been recorded at di- or trisynaptic latency (< 3 ms). Since this was not the case, the i.p.s.p.s may be attributed to the action of higher-threshold afferents in this nerve: afferents of Pacinian corpuscles.

That this inhibition was not of group I origin is illustrated in Fig. 2. Stimulation of the interosseous nerve at 1·5 times threshold evoked a group I volley which did not increase further as the stimulus strength was progressively increased. However, the long-latency i.p.s.p.s appeared at about 1·9 times threshold and increased to a maximum at about 5 times threshold. This is entirely compatible with their Pacinian

afferent origin since being largely in the group II range these afferents would generally have a higher electrical threshold with most of them being activated by a strength of 4 times threshold (Yeo, 1976). The segmental latency of these i.p.s.p.s estimated from the time of arrival of group II afferents would indicate a di- or trisynaptic action.

Activation of the interosseous nerve evoked a characteristic potential at the cord dorsum which also occurred later and at higher threshold than the group I volley.
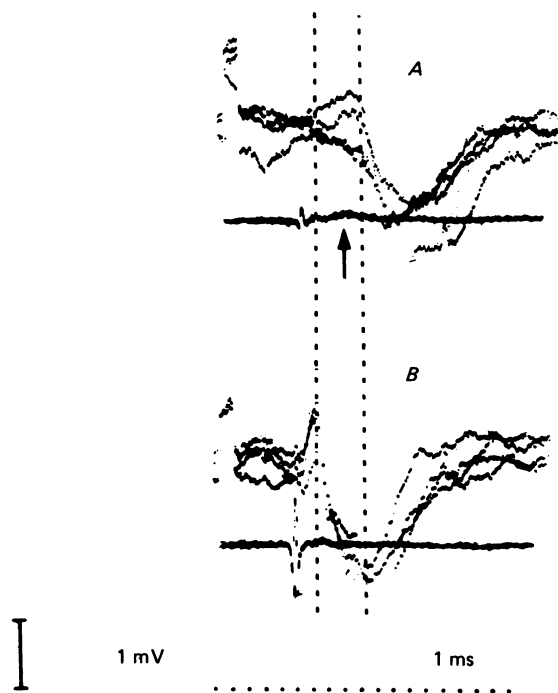
Fig. 1. Comparison of actions of interosseous afferents with those of flexor digitorum longus afferents in a plantaris motoneurone. Stimulating the interosseous nerve at twice threshold for the largest-diameter fibres evoked long-latency i.p.s.p.s (*A*) whereas stimulation of the flexor digitorum longus nerve at twice threshold evoked short-latency non-reciprocal i.p.s.p.s (*B*). In *A* note the potential in the cord dorsum record, following the group I volley and preceding the i.p.s.p. (arrowed). The difference in latency of the two i.p.s.p.s is indicated by the dotted lines which mark their onset.

This can be seen in Figs. 1 and 2 (arrowed) though it is more distinct after averaging (Fig. 3). Such potentials were not observed following stimulation of group I muscle afferents and correspond to the negative cord dorsum potential of the type evoked by cutaneous, joint and high-threshold muscle afferents. Their presence is attributed to the action of Pacinian corpuscles. Figs. 2 and 3 show that the longer-latency i.p.s.p.s appeared at about the same threshold and increased in parallel with these potentials as the stimulus strength was increased.

The i.p.s.p.s in Figs. 1, 2 and 3 were selected since they were not preceded by i.p.s.p.s of group I origin which would have occurred between 1·3 and 3·0 ms after the group I volley. Often such i.p.s.p.s were present, however, and on these occasions the

longer-latency components due to Pacinian afferents could not usually be distinguished since they simply added to, and blended with, the earlier i.p.s.p.s. Indeed the p.s.p.s attributed to Pacinian afferents could only be distinguished as occurring at longer latency and appearing at higher threshold than the group I component. Fig. 4 *A* shows the latencies of oligosynaptic p.s.p.s following activation of the interosseous nerve at or below twice threshold for the most excitable fibres. Since the distribution of
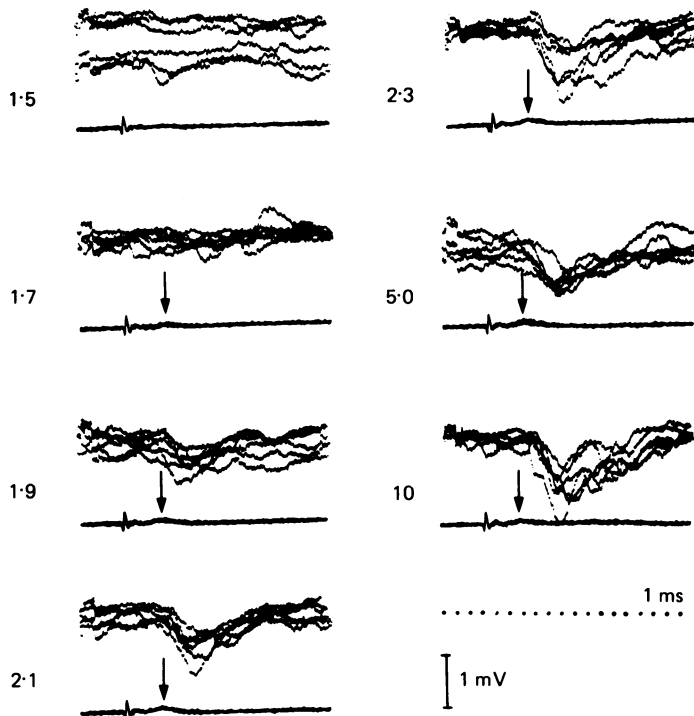

Fig. 2. The action of interosseous afferents at different stimulus strengths. Upper traces, intracellular i.p.s.p.s from a gastrocnemius–soleus motoneurone. Lower traces, cord dorsum potentials. The arrows indicate a small cord dorsum potential occurring after the group I volley (see text and Fig. 3).

latencies was a continuum no distinction could be made between p.s.p.s attributed to group I afferents and p.s.p.s attributed to Pacinian afferents, except for those occurring at latencies exceeding those of group I actions. In order to help in such a comparison the distribution of latencies for p.s.p.s evoked by afferents of flexor digitorum longus is shown in Fig. 4 *B*. For a more direct comparison, the latencies of p.s.p.s evoked in the same motoneurones are plotted in Fig. 4 *C*.

Thus, since the majority of p.s.p.s evoked from the flexor digitorum longus nerve occurred between 1·2 and 3·0 ms, we can be fairly confident that the majority of those p.s.p.s evoked by the interosseous nerve at latencies greater than 3·0 ms are of Pacinian afferent origin. On the other hand we cannot claim that those p.s.p.s evoked at latencies less than 3·0 ms are due solely to the group I afferents. If the minimal synaptic linkage from Pacinian afferents is disynaptic, and the volley from the more

slowly conducting Pacinian afferents arrives 0·5 ms later than the group I volley, then Pacinian afferents may evoke p.s.p.s as soon as 1·8 ms after the group I volley. Since this is the latency of the earliest interosseous i.p.s.p.s we cannot confidently attribute even the very shortest-latency p.s.p.s solely to group I origin.
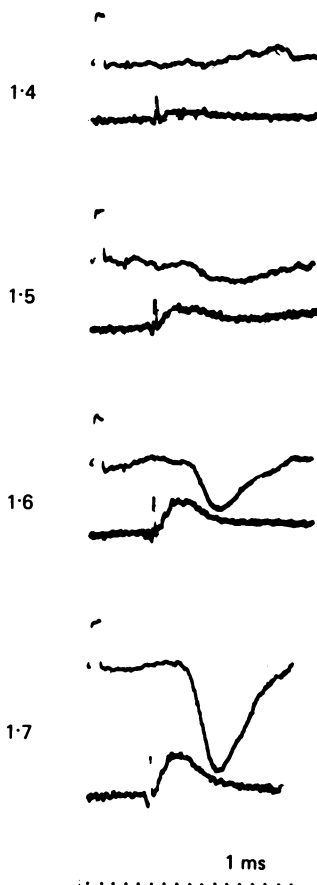

Fig. 3. Averaged records from an anterior biceps–semitendinosus motoneurone and from the cord dorsum following graded stimulation of the interosseous nerve. Note particularly the evolution of the late cord dorsum potential and the parallel changes in the i.p.s.p. as the stimulus strength was varied. The calibration pulse at the beginning of each trace is 200 μV.

Facilitation of transmission in Ib reflex pathways by afferents of the interosseous nerve

Recent studies have established a high degree of convergence from many descending and segmental systems onto the interneurones mediating reflexes from Ib afferents (Lundberg & Voorhoeve, 1962; Hongo, Jankowska & Lundberg, 1969; Lundberg, Malmgren & Schomburg, 1975, 1977, 1978; Jankowska & McCrea, 1983; Harrison *et al.* 1983). In the present study the interosseous afferents have been found to facilitate the non-reciprocal group I action of many muscles. Since the interosseous membrane has close anatomical relations with the two heads of flexor digitorum longus it was

of special interest to see to what extent the interosseous afferents can influence the actions of afferents of flexor digitorum longus. Fig. 5 illustrates the mutual facilitation observed between afferents of the interosseous nerve and flexor digitorum longus group I afferents in a variety of motoneurone species. The first two rows show the action, in different motoneurones, of afferents of flexor digitorum longus and the interosseous nerve when activated separately. The third row shows the effects of
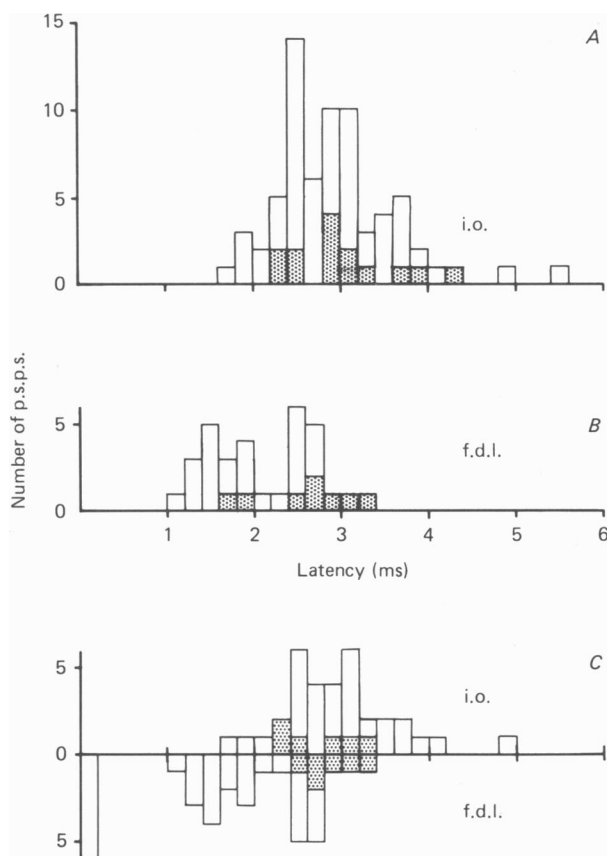

Fig. 4. Distribution of latencies of oligosynaptic p.s.p.s evoked by interosseous afferents (*A*) and flexor digitorum longus afferents (*B*), at or below twice threshold for the lowest-threshold fibres, measured from the cord dorsum group I volley. For a more direct comparison the bottom histogram (*C*) shows the distribution of latencies when the interosseous (i.o.) and flexor digitorum longus (f.d.l.) afferents were tested in the same motoneurones. The bin on the extreme left represents occasions when flexor digitorum longus did not evoke p.s.p.s. Open columns, i.p.s.p.s; stippled columns, e.p.s.p.s.

stimulating the two 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 the 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 is shown in the bottom trace.

In addition to facilitating reflex actions of flexor digitorum longus afferents, interosseous afferents were found to facilitate the reflex actions of group I afferents of many other muscle nerves. Fig. 6 shows such facilitation found in two gastrocnemius motoneurones in one experiment. Facilitation was sought on sixty-two occasions and was found on fifty-four of them. Mutual facilitation was found between interosseous and other afferents in both extensor and flexor motoneurones, as shown in Fig. 7.
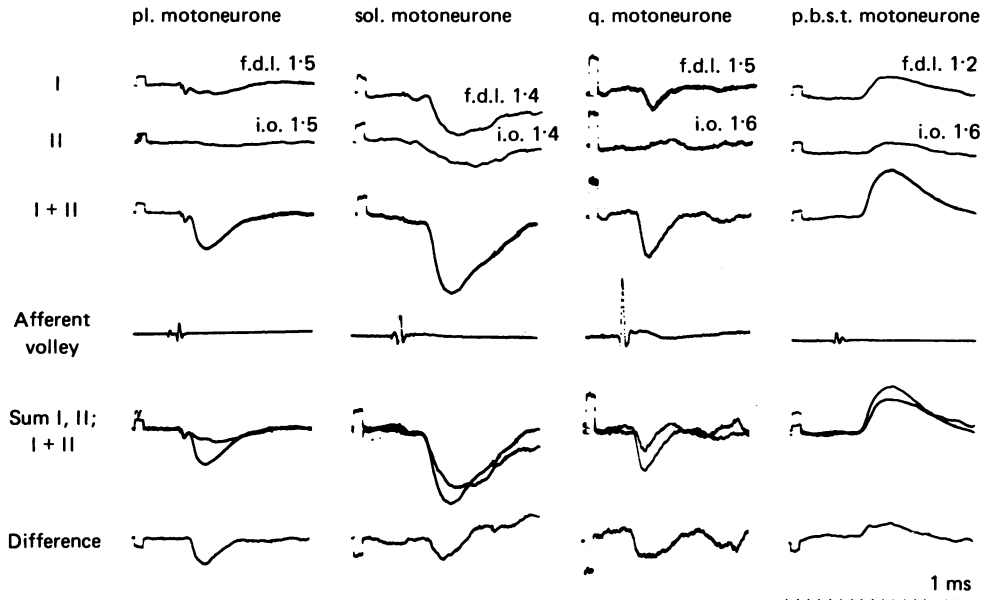

Fig. 5. Mutual facilitation of transmission from interosseous afferents and flexor digitorum longus group I afferents to four motoneurones. In the first two traces of each column are the averaged intracellular records of p.s.p.s of flexor digitorum longus and interosseous afferents when these are stimulated separately, and in the third traces the records when they are stimulated together. The fourth traces are of afferent volleys recorded from the dorsal root entry zone. The fifth traces show sums of the p.s.p.s evoked separately, superimposed on p.s.p.s evoked by the combined action of the two groups of afferents, in order to visualize the differences between them. The arithmetically derived differences are displayed on the bottom traces. The calibration pulse at the beginning of each trace is 200 μV.

The latencies of the facilitated p.s.p.s are shown in Fig. 8A. Such a wide distribution is expected since in searching for facilitation the timing of the afferent volleys was varied in order to achieve optimum conditions for observing facilitation. It was a common finding that the greatest facilitation was observed when the interosseous volley preceded the muscle nerve volley (see Fig. 6D), and this became standard protocol when searching for the facilitation. However, this would tend to increase the number of facilitated p.s.p.s with long latency when measured from the interosseous volley. In order to present an unbiased distribution of facilitated p.s.p.s, Fig. 8B shows the distribution of latencies when the two volleys arrived at the surface of the cord simultaneously. Since a significant proportion of these p.s.p.s exceeded 3·0 ms, afferents evoking actions at longer latencies have probably participated.
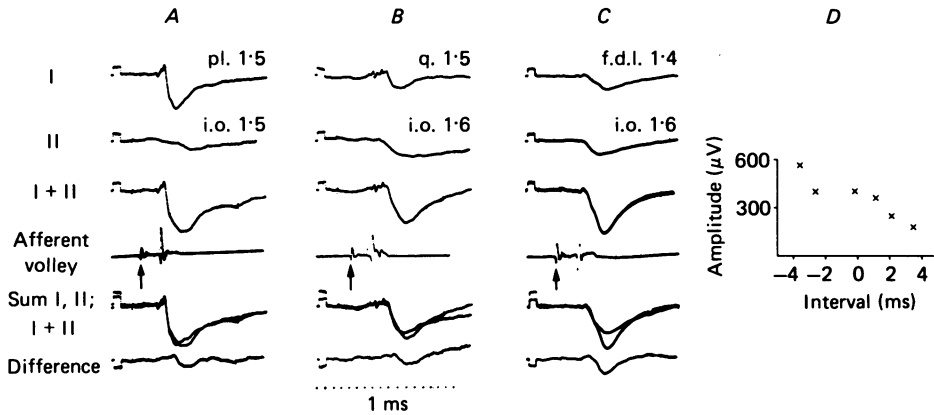
Fig. 6. Mutal facilitation of transmission from interosseous afferents and group I muscle afferents to gastrocnemius–soleus motoneurones. The format is the same as in Fig. 5. The records in *A* and *B* are from the same motoneurone. The arrows indicate the interosseous volleys recorded from the cord dorsum. *D* shows the influence of the timing of arrival of the two volleys at the surface of the cord on the degree of facilitation (the amplitude of the difference) for the example in *C*. Time zero corresponds to the flexor digitorum longus volley; thus the facilitation was larger when the interosseous volley preceded the flexor digitorum longus volley. The calibration pulse at the the beginning of each trace is 200 μV.
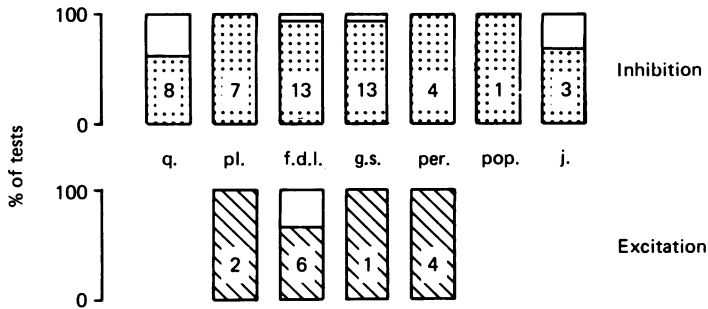

Fig. 7. Summary of observed convergence between interosseous afferents and group I muscle and joint afferents in reflex pathways to motoneurones. This representation is irrespective of motoneurone species although the data for inhibition are largely from extensor motoneurones whereas all the data for excitation come from flexor motoneurones (posterior biceps–semitendinosus). The stippled and hatched areas show the percentage of tests in which convergence was demonstrated. The numbers indicate the number of motoneurones tested in each case.

Independent evidence for long-latency actions of interosseous afferents facilitating group I muscle actions comes from an intracellular study of the last-order interneurones mediating group I non-reciprocal inhibition (Harrison & Jankowska, 1984). Fig. 8*C* and *D* shows the distribution of latencies of e.p.s.p.s evoked by interosseous afferents and group I flexor digitorum longus muscle afferents taken from that study. Many of the longer-latency (around 2 ms) e.p.s.p.s evoked by the interosseous afferents can be attributed to the actions of Pacinian afferents rather than group I afferents by the same reasoning as for the motoneuronal p.s.p.s. Thus, taken together, these
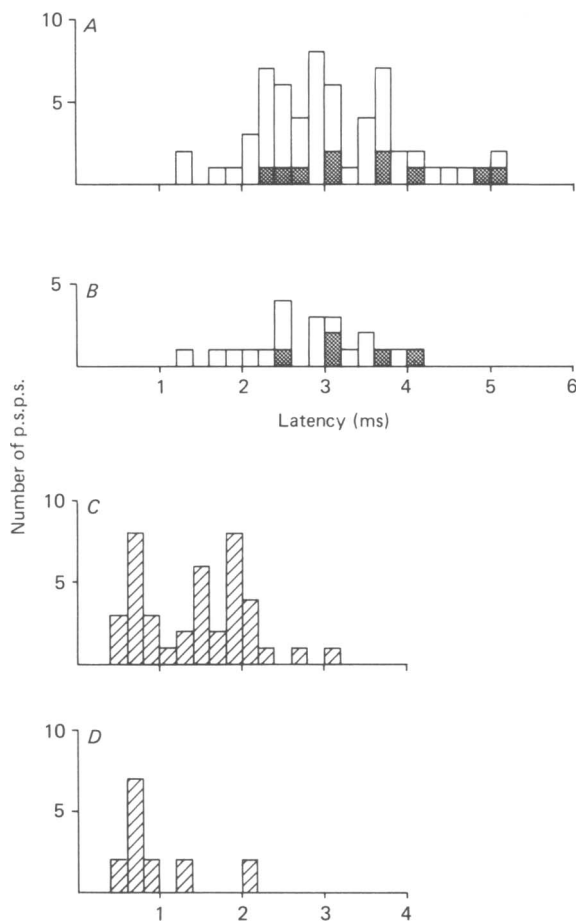
Fig. 8. Distribution of latencies of facilitated p.s.p.s measured from the group I interosseous volley (*A*) (the 'differences' in Figs. 5 and 6). Since some of the scatter in *A* is due to the interosseous and muscle nerve volleys arriving at the cord asynchronously, the latencies of the facilitated p.s.p.s obtained when the volleys were synchronous are shown in *B*. Since many of these latencies exceed 3·0 ms it is likely that afferents of Pacinian corpuscles contributed to the facilitation. The distribution of latencies of p.s.p.s evoked in last-order interneurones by interosseous and flexor digitorum longus afferents is shown in *C* and *D* (from the data of Harrison & Jankowska, 1984). The presence of long-latency p.s.p.s evoked by interosseous afferents is further evidence that afferents of Pacinian corpuscles facilitate group I reflex actions.

findings suggest that not only interosseous afferents in general, but specifically Pacinian afferents, facilitate group I non-reciprocal reflex actions.

Since interosseous afferents facilitate actions of group I muscle afferents, as do joint afferents (Lundberg *et al.* 1978), a possibility was considered that interosseous afferents facilitate actions of joint afferents. This is not necessarily to be expected *a priori*, however, since the interosseous afferents could act upon a different group of group I excited interneurones than do the joint afferents. Thus we also tested for mutual facilitation of actions of interosseous afferents and joint afferents in three

motoneurones. We detected mutual facilitation in two of them and records from these are shown in Fig. 9.

Monosynaptic e.p.s.p.s evoked in motoneurones

Electrical stimulation of the interosseous nerve was observed to evoke small monosynaptic e.p.s.p.s in a number of motoneurones. Of the motoneurones tested monosynaptic e.p.s.p.s were only detected in flexor digitorum longus motoneurones and of these in eleven of the fifteen. The e.p.s.p.s were of from 50 to 400 μV in amplitude.
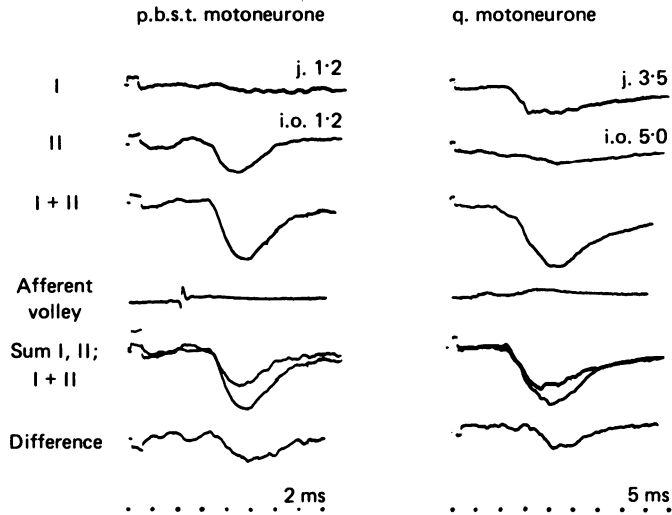

Fig. 9. Mutual facilitation of transmission from interosseous and joint afferents in reflex pathways to motoneurones. The format is the same as in Fig. 5. The calibration pulse at the beginning of each trace is 200 μV.

Fig. 10 illustrates the case for the largest monosynaptic e.p.s.p.s evoked by the interosseous nerve. The single-sweep records shown in A were obtained when the strength of stimulation of the nerve was such that the e.p.s.p. occurred in an all-or-none manner which corresponds to the action of a single I a afferent when the stimulus strength was straddling the threshold for initiating action potentials in its axon. Fig. 10B shows the averaged e.p.s.p. obtained when the stimulus strength was just above that required to evoke the e.p.s.p. in every sweep. (Note that the averaged e.p.s.p. is of the same amplitude as that of the single unitary e.p.s.p.s.) Fig. 10C shows the averaged e.p.s.p. when the stimulus strength is increased to 5 times threshold to ensure that all the Ia afferents are activated. Since at this stronger stimulus intensity the amplitude of the e.p.s.p. has remained constant then we can conclude that only one Ia afferent of the interosseous nerve projected to this motoneurone.

Since the monsynaptic e.p.s.p.s recorded in the other flexor digitorum longus motoneurones were smaller and also unitary, it is likely that they were likewise evoked by single afferents.
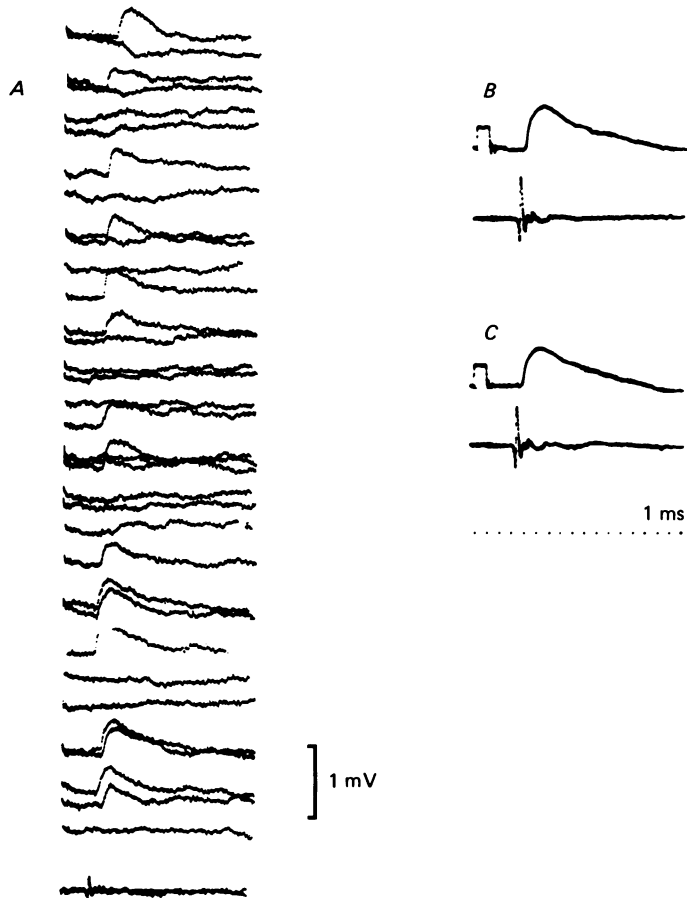
Fig. 10. Monosynaptic unitary e.p.s.p.s evoked by the interosseous nerve in a flexor digitorum longus motoneurone. The sequence of single sweeps is at threshold for the occurrence of the unitary e.p.s.p. An averaged record of the e.p.s.p. (when the stimulus was increased to evoke an e.p.s.p. on every sweep) is shown in B. Thus at this strength, since the averaged e.p.s.p. is of the same amplitude as the unitary e.p.s.p.s, it is concluded that this e.p.s.p. is due to the action of a single I a afferent. An increase of the stimulus strength to 5 times threshold would ensure that all of the I a afferents are activated. However, since at this strength (C) there appears to be no increase in the amplitude of the e.p.s.p. it is concluded that only one I a afferent terminated on this neurone. Calibration pulse in B and C: 200 μV.

Primary afferent depolarization evoked by interosseous afferents

Primary afferent depolarization evoked by interosseous afferents was recorded in seven cats. Fig. 11 shows dorsal root potentials evoked by graded electrical stimulation of the interosseous nerve. This experiment was exceptional in that the dorsal root potential was evoked by the lowest-threshold afferents, although generally it required stimuli at 1·2–1·3 times threshold to evoke dorsal root potentials from this nerve. For comparison, Fig. 11B shows the effects evoked by afferents of flexor digitorum longus at the same stimulus strengths, and Fig. 11C is a plot of the relative
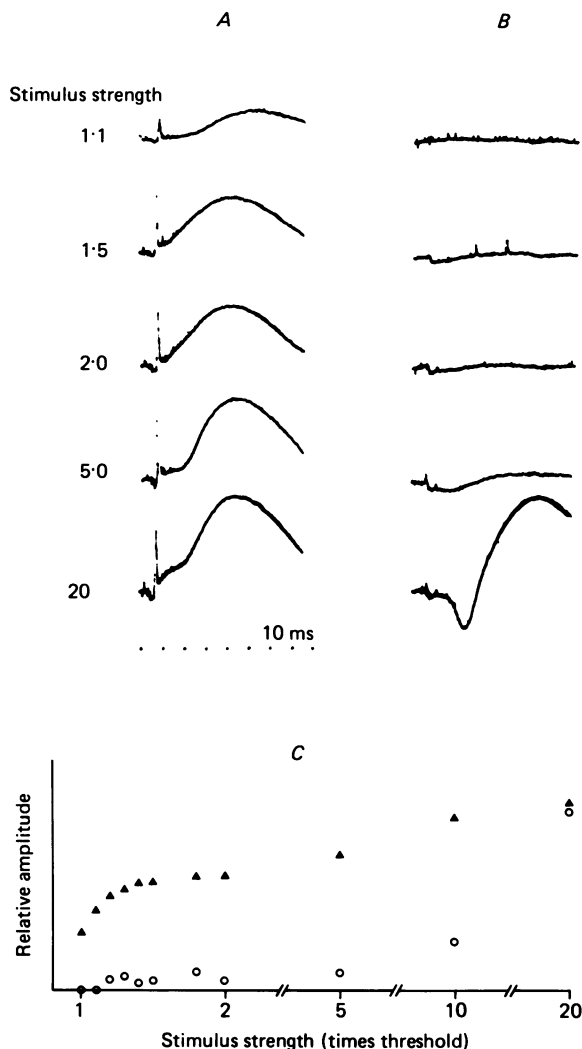
Fig. 11. Dorsal root potentials (in a spinalized cat) evoked by interosseous afferents (*A*) and flexor digitorum longus afferents (*B*). *C* shows the relative amplitude of the dorsal root potentials as the stimulus strength was increased. ▲, i.o.; ○, f.d.l.

amplitude of the dorsal root potentials throughout the range of stimulus strengths tested. It is clear that the dorsal root potentials evoked by the interosseous afferents were of larger amplitude than those of flexor digitorum longus afferents for stimulus strengths below those required to activate group III afferents. Since the major afferent species present in the interosseous nerve that is not present in the nerve to flexor digitorum longus is the afferents of Pacinian corpuscles, it is concluded that the major component of the dorsal root potential evoked by the interosseous afferents can be attributed to the action of Pacinian afferents.

DISCUSSION

Oligosynaptic post-synaptic potentials

The post-synaptic potentials reported in this paper were mainly evoked at or below twice threshold for the most excitable fibres and as such reflect the actions of only the fastest-conducting interosseous afferents. Comparison with the actions of the flexor digitorum longus afferents indicates that some of the p.s.p.s could be attributed to the action of the group I b afferents present in the interosseous nerve; the small number of I a afferents is unlikely to make a significant contribution to oligosynaptic pathways. However, the longer-latency (> 3 ms) and higher-threshold (> 1·5 times threshold) p.s.p.s would correspond to the action of afferents of smaller diameter and higher electrical threshold than the group I afferents.

The interosseous membrane is closely associated with many Pacinian corpuscles (Hunt, 1961; Barker, 1962), the afferents of which course through the interosseous nerve with conduction velocities in the upper part of the group II range (see e.g. Boyd & Davey, 1968; Yeo, 1976). They correspond to the vibration and tap receptors of the earlier studies (Hunt, 1961; see also Barker, 1962, 1967, 1974), comprise 35 % of the total myelinated fibres in the interosseous nerve, and form the whole of the group II component (Boyd & Davey, 1968). It would therefore seem highly likely that the longer-latency, higher-threshold actions that we report here are due to the action of afferents of Pacinian corpuscles.

While the evidence suggests that afferents of Pacinian corpuscles influence motoneurones (and as such have reflex actions) our present observations do not allow us to comment on the potency of their actions. However, it may be that these connexions function to *modulate* reflex pathways. In the present experimental situation, synchronous electrical activation of the Pacinian afferents was sufficient to make some last-order interneurones discharge, the actions of which were detected in motoneurones as p.s.p.s. However, under physiological conditions Pacinian afferents may fail to evoke firing in last-order interneurones by themselves, but rather modulate the excitability of the interneurones.

To put this into a functional context, it has been argued with respect to the cutaneous facilitation of I b reflex pathways that during an exploratory movement, when the limb comes into contact with an object the resulting cutaneous discharge modulates the activity of the I b reflex pathways so as to prevent forcing the object (Lundberg, 1975; Lundberg *et al.* 1977). The Pacinian afferents may be contributing in a similar way since they would be most effectively excited by the jarring action of the limb coming into contact with an object (and this would be particularly applicable to those situated on the interosseous membrane). Furthermore, since Pacinian corpuscles are widely dispersed in the dermis of the skin, the modulatory action of cutaneous afferents on reflex pathways could, at least partly, be attributed to the action of Pacinian corpuscles.

Monosynaptic e.p.s.p.s

In their studies of the afferent content of the interosseous nerve, Barker (1962) and Hunt & McIntyre (1960) described the presence of a small number (two or three) of muscle spindle afferents. More recently Yeo (1976) has claimed a larger incidence of

muscle spindle afferents (thirty-eight in a sample of 207 fibres) and therefore the present data relating to monosynaptic e.p.s.p.s were considered of value since they provide an independent estimate of the muscle spindle afferent content of the interosseous nerve. Since single muscle spindle I a afferents of cat hind limb muscles evoke e.p.s.p.s with a mean amplitude of 100 μV in a large proportion of their homonymous motoneurones (e.g. Mendell & Henneman, 1971), then each motoneurone will be influenced by a large proportion of homonymous I a afferents. Consequently, recording the monosynaptic action of the interosseous afferents is a simple way of assessing the muscle spindle I a afferent content without the sampling biases associated with fibre dissection techniques. Since only small monosynaptic, unitary e.p.s.p.s were recorded, this suggests that the interosseous nerve contains one or, at most, a very small number of I a afferents.

Our findings thus confirm the earlier reports of Hunt & McIntyre (1960) and of Barker (1962) and are at variance with those of Yeo (1976). In respect of Yeo's (1976) report it should also be noted that in addition to a larger number of I a afferents he observed large, early facilitatory actions from the interosseous nerve on flexor digitorum longus motoneurones with monosynaptic reflex testing, which would also be in accordance with his observed frequency of I a afferents. In our experiments the actions of the interosseous nerve were always inhibitory to extensor motoneurones (including flexor digitorum longus motoneurones) and the observed monosynaptic e.p.s.p.s were too small to facilitate monosynaptic reflexes substantially. In order to reconcile this discrepancy the following considerations may be of use. In the present experiments branches of the flexor digitorum longus nerve were sometimes observed to course between the medial and lateral heads before turning and entering one head, and it was important to exclude such branches before being satisfied with the identification of the interosseous nerve. However, if in the work of Yeo such branches were taken together with the interosseous nerve then a high number of I a afferents and a facilitation of monosynaptic reflexes would undoubtedly result.

Primary afferent depolarization

Graded electrical stimulation of the interosseous nerve evokes a dorsal root potential that appears at 1·2–1·3 times threshold, increases quickly up to about 1·7 times threshold and then increases only modestly until the group III afferents are activated at about 10 times threshold. Since group I afferents of extensor muscles evoke only weak primary afferent depolarization (Schmidt, 1971), the dorsal root potentials evoked by the interosseous nerve can largely be attributed to the actions of Pacinian afferents. Comment should be made, however, regarding the lower threshold at which primary afferent depolarization can be evoked relative to the threshold at which post-synaptic potentials attributed to Pacinian afferents are evoked in motoneurones. However, since primary afferent depolarization can be evoked by even a single Pacinian afferent (Jänig et al. 1968), the threshold at which the dorsal root potential appears may simply reflect the threshold of the lowest-threshold Pacinian afferent.

In conclusion, the results of this study show that afferents of the interosseous nerve evoke significant segmental actions both pre- and post-synaptically. Thus when these afferents are stimulated together with the nerve to flexor digitorum longus, the

observed actions cannot be attributed solely to afferents of flexor digitorum lòngus. Correspondingly, since Pacinian corpuscles evoke segmental reflex actions, and some of them have conduction velocities in the group I range (Silfvenius, 1970*a*; Yeo, 1976), the occasional Pacinian afferent found in muscle nerves (Boyd & Davey, 1968; Yeo & Sriratana, 1974) could conceivably contribute to group I reflex actions.

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