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REGENERATION OF AFFERENT AND EFFERENT FIBRES TO MUSCLE SPINDLES AFTER NERVE INJURY IN ADULT CATS

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SUMMARY

1. The nerves to cat peroneus longus and tenuissimus muscles were either cut or crushed close to the muscle and the afferent and efferent nerve supply to the muscle spindles was studied electrophysiologically between 2 and 32 weeks later.

2. Recovery was more rapid and complete after crush than section for both afferent and efferent fibres. After recovery from either procedure normal primary and secondary afferents and static and dynamic γ efferent fibres were found.

3. Some abnormally occurring neurones were found. One group consisted of β fibres which had a static action on muscle spindles. Static β fibres are very rarely found in normal muscles.

4. The results indicate that some guidance mechanism exists which after crush injuries of nerves may restore muscle receptor function almost to normal. Even after nerve section some muscle spindles may become correctly reinnervated.

INTRODUCTION

The complex afferent and efferent innervation of mammalian muscle spindles provides a severe test of the ability of reinnervating nerve fibres to reconnect in an appropriate way. Previous work on spindle reinnervation has been carried out either in very young animals where disruption of the nerve supply may have effects on the development of muscle spindles (Zelená & Hnik, 1960; Zelená, 1964; Werner, 1973) or in adult cats (Thulin, 1960; Bessou, Laporte & Pagès, 1966), where observations have been limited to finding out that afferent fibre response to stretch returns

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after injury and that fusimotor stimulation increases afferent discharge. Whether the behaviour of group I and group II afferent fibres is normal and appropriate for axons of their respective sizes has not been reported, nor has it been discovered whether static and dynamic γ fibre effects can be distinguished. The experiments described in this paper show that both afferent and efferent fibres to muscle spindles show preference for their original sites during reinnervation; preliminary reports of some of this work appeared previously (Brown & Butler, 1974, 1975).

METHODS

Twenty-three adult cats (> 9 months old) were used. An initial aseptic operation to cut or crush the nerve to either the tenuissimus or peroneus longus muscles on the right side was carried out under sodium pentobarbitone (Nembutal, Abbott) anaesthesia. For peroneus longus five nerves were crushed and five cut, and for tenuissimus eleven were crushed and two cut. The nerves were cut about 2 mm from the muscle and no attempt was made to hold the cut ends together. In tenuissimus this resulted in a gap of a few mm between the two cut ends, but in peroneus longus the two ends lay close together. For the crush operations a pair of fine watchmaker's forceps were used. These forceps were chosen with care to ensure that the two tips were in perfect visual register. The nerves were crushed 3 times. The first crush was made about 2 mm from the muscle, the second 1 mm nearer the muscle and the third 1 mm proximal to the first to demonstrate by the absence of muscle contractions that the two previous crushes had been effective. To check that this procedure was enough to lead to degeneration in all axons a subsidiary group of operations was done on a further three cats by one of us (R.G.B.). Using an identical procedure the nerves to the two muscles were crushed and 5 days later in an acute experiment the nerves were stimulated proximal to the cut. In none of the three cats were contractions observed, and in addition histology of the nerves distal to the crush site showed uniform Wallerian degeneration.

Acute experiments

Two to thirty-two weeks later under Nembutal anaesthesia reinnervation was investigated after widespread denervation of the right leg (apart from the nerve to either peroneus longus or tenuissimus) and a lumbar laminectomy. The muscle was connected via a myograph to a servo-controlled electromagnet (Ling Altec 407) which was used to stretch the muscle with constant velocity ramps (usually at 8 mm/sec). The final length at which the muscle was held, for about 1 sec, before being released at the same velocity, was carefully set to be equal to the maximum *in situ* length of the muscle, which was known by means of a marker thread sewn into the leg at the time of operation opposite the tie on the tendon. In the Figures the length records are diagrammatic; the starting and stopping points of the ramp were obtained for this from a tension record which was photographed at the same time as the instantaneous frequency display of afferent firing.

Afferent fibres

The first stage of each experiment was to isolate in dorsal root filaments as many single afferent fibres as possible. This was done by splitting dorsal root filaments until only a single action potential was present on stimulating the muscle nerve.

Those units which responded to stretch and/or contractions were then classified (see later) and the non-responsive afferents were removed after noting their conduction time. From each peroneus longus a total of about thirty-five afferents were usually isolated (maximum forty-six), a variable proportion of which would be unresponsive, and from tenuissimus about eighteen, again with a variable proportion of unresponsive units (the units which responded neither to stretch nor contraction also had no resting discharge). These numbers of isolated afferents represent a high proportion (*ca.* 60–70 %) of group I and II afferents known to originate in the respective muscles.

The classification of the afferent fibres on behavioural grounds as being typical or atypical primary or secondary spindle afferents or Golgi tendon organ afferents was made by observing the instantaneous frequency of their firing displayed on an oscilloscope with a long persistence phosphor during twitch contractions of the muscle and ramp stretches and releases. The normal behaviour of a primary ending was taken to be the following (Matthews, 1972): a silent period during muscle twitch contractions, a well marked dynamic sensitivity during ramp stretches shown as a sharp drop in firing frequency as the plateau length was reached at the top of a ramp stretch, and a silence during ramp release. Spindle afferents classified as secondary endings fired more regularly and showed much less dynamic sensitivity. Ideally, perhaps, a variety of strict quantitative criteria for normality should have been used. In practice the decision as to which type an afferent belonged and whether it was normal was made subjectively after watching several stretch and release responses. This method may have oversimplified classification but did not lead to any gross errors, and because it was quick it enabled more observations to be made on each cat than would otherwise have been possible. The conduction velocity of all afferents was calculated from the conduction time from the stimulating electrodes, which were placed central to the crush point on the muscle nerve, to the dorsal roots, and the conduction distance which was measured by laying a thread along the course of the nerve between the two electrodes. The nerve was *in situ* and exposed except in the pelvic region.

Motor fibres

The motor supply to stretch responding spindle afferents was then sought by stimulating thin ventral root filaments obtained after splitting the L7 and S1 ventral roots into twenty or more strands. Stimulation was at 150/sec and was carried out before and during a ramp stretch and release of the muscle. When an excitatory effect was found the effective filament was split until only a single all-or-none action potential could be recorded in the filament on stimulating the muscle nerve. The action of this motor fibre whether it was γ or β was classified as static or dynamic by observing its effect on the dynamic sensitivity of the afferent. Motor fibres classified as dynamic increased the dynamic index but did not enable the spindle firing to continue during release of the muscle (Crowe & Matthews, 1964; Lennerstrand & Thoden, 1968). Static fibres reduced the dynamic index and enabled the afferent to continue firing during release. As the response of the afferent unit to the same stretch in the absence of efferent stimulation was still visible on the long persistence phosphor of the oscilloscope, any change in dynamic sensitivity was readily detectable.

Once a motor fibre had been tested and classified on one afferent it was then tested on the other stretch responding afferents, and where it excited any other afferent its effect was again classified.

In experiments where there were few stretch responding afferents, it was possible

to search for the motor supply to all of them. Where the number of afferents was large this was not possible and usually only the most normal afferents were selected.

β fibres

To decide whether single motor fibres of α conduction velocity which besides generating tension also accelerated spindle firing were doing so via intrafusal contraction, the two techniques introduced by Bessou, Emonet-Dénand & Laporte (1965) were used. In tenuissimus topical application of gallamine triethiodide (2 mg/100 ml.) in Ringer solution in the leg-pool (see Fig. 6) was used to block extrafusal contraction. If spindle excitation persisted after the extrafusal contraction had stopped (myograph could detect tensions of > 10 mN) the fibre was classified as a β fibre. The extrafusal block occurred in 2–5 min and was quickly reversible on washing out the leg-pool with fresh Ringer solution.

In peroneus longus dissociation of spindle excitation from the strength of extrafusal contraction was shown by increasing the frequency of stimulation of the β fibre up to 200 sec^{-1}, and observing a continued rise in afferent excitation after extrafusal contraction had reached a plateau or even started to come down due to transmission failure (see Fig. 7). This technique is not quite so dramatic in separating intra- and extrafusal effects as it is in the lumbrical muscles for two reasons. First, the fusion frequency for extrafusal fibres in the reinnervated peroneous longus is about 150/sec and secondly the transmission at the new β junctions in the intrafusal fibres is not as secure as in normal cats. However, as can be seen in Fig. 7*C* and *D* there is an increase in firing frequency at 200/sec as compared with 143/sec stimulation, whereas the extrafusal tension is less at the higher frequency.

RESULTS

General observations

After crush injuries recovery was relatively rapid. This was most noticeable in peroneus longus, where at 2 weeks after crush some afferents responded to stretching and efferent effects on them were elicited. At this early time, however, most of the afferents were unresponsive, confirming that the nerve had indeed been crushed. Between 4 and 6 weeks after crush in peroneus longus many of the afferent fibres responded normally to stretching and there were many functional γ fusimotor fibres. Recovery after crush in tenuissimus was slower and more variable. Even at 32 weeks one cat had a very low percentage of normal afferent and efferent fibres, but in most tenuissimi the spindles were fairly normal by 10 weeks.

After nerve section recovery was much less complete but again better in peroneus longus than tenuissimus. The longest recovery period after section was 18 weeks and at this time both muscles were still far from normal, possessing few normal stretch responding afferent fibres, many non-responsive afferent fibres and very few functional γ motor fibres.

Afferent fibres

Fig. 1 shows the responses recorded from three different afferent fibres (conduction velocities in $m.sec^{-1}$ at the top right of each record) of

peroneus longus muscle 12 weeks after cutting the muscle nerve. These stretch-evoked responses from reinnervated receptors would be quite typical for fibres of these particular conduction velocities in normal cats. The fastest behaves like a primary ending with a large dynamic sensitivity, while the slowest fibre behaves like a secondary ending for it is not

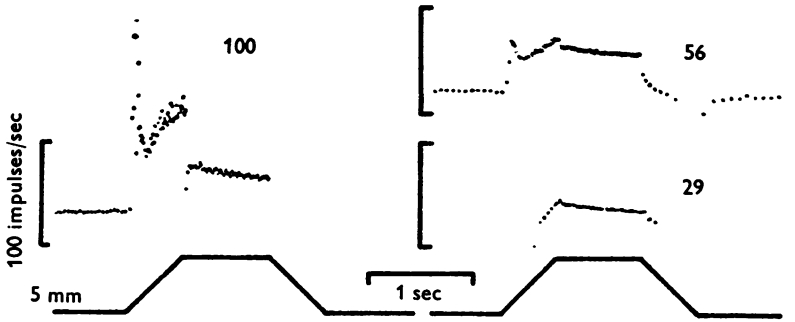

Fig. 1. Responses to stretch of three different afferent units (conduction velocities in m.sec^{-1} given beside each record) all from the *same* peroneus longus muscle recorded after 12 weeks regeneration following section of the muscle nerve. Above, instantaneous frequency; below, length record, diagrammatic.

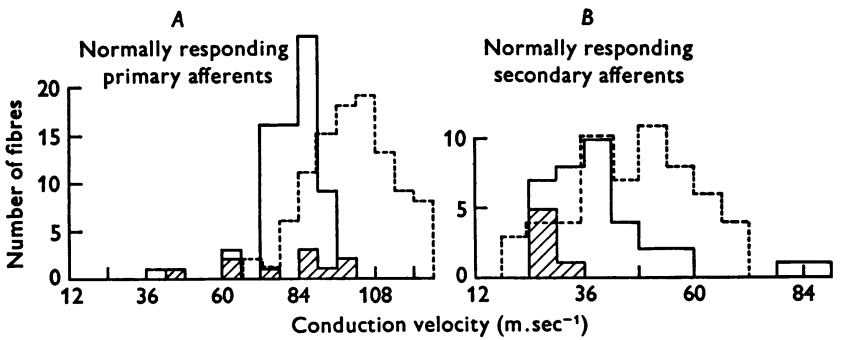

Fig. 2. Conduction velocity histogram of units which responded like normal spindle primary afferents (*A*) and normal spindle secondary afferents (*B*) after regeneration in peroneus longus. Cross-hatching indicates units found in animals in which the nerve had been cut; open areas indicate units found after crush operations. The dashed outline is for data obtained by MacLennan (1971) from the peroneus longus of normal cats.

dynamically sensitive and it also fires more regularly than the primary ending. The receptor connected to the fibre which conducted at 56 m.sec^{-1} has intermediate properties. Other examples of units which we classified as normal primary endings are given in Figs. 7 and 8.

In order to find out if reinnervated receptors which behaved like typical

primary and secondary endings were connected to the size of afferent fibres with which they are associated in normal cats, histograms of the conduction velocities of normally-responding primary and secondary endings were plotted (Fig. 2*A* and *B*). For comparison on these two histograms are given with dashed outline the data obtained by MacLennan (1971) from normal peroneus longus muscle. In her experiments single afferent fibres were isolated in dorsal root filaments to obtain a random collection of fibres of different conduction velocities in the group I and group II range, and their behaviour was then classified as that of primary or secondary endings by stretching and vibrating the muscle and studying the response to twitch contractions to differentiate spindle receptors and Golgi tendon organs.

It can be seen that the conduction velocities for our sample of primary and secondary endings are shifted towards lower than normal values after both crush and nerve section. But all but two of our primary endings conducted above 60 $m.sec^{-1}$ and only two of the units which we classified as secondaries conducted above 60 $m.sec^{-1}$. The difference between the normal and regenerated histograms is probably due not to a systematic difference in the measurement of conduction velocities by us and MacLennan, for data obtained by us for normal primary endings in other experiments fit well with her data. The explanation is more likely to be the reduction in conduction velocity of nerves proximal to the site of an injury which has been well described by Cragg & Thomas (1961). The conduction velocity histogram for non-responding units (not illustrated) was even further shifted to slower than normal values, but there was no difference between histograms for abnormally responding and normally responding units.

Not all the afferents which responded to stretch did so normally. Sometimes the units fired only during the dynamic phase of stretching. Others fired with far greater than normal frequencies and with excessive dynamic sensitivity. Some were far more irregular in their firing than normal. Some responded only to a direct tap over the muscle. An example of a unit which we classified as abnormal is given in Fig. 6*A*. The proportion of afferents behaving abnormally was higher at early times and also after nerve section. Our data also showed that abnormal afferents were less likely to have an efferent innervation, but our protocol (see Methods) may partly have given rise to this.

In reinnervated peroneus longus we found many Golgi tendon organs. We tested their responses to muscle twitches only, so we do not know if they would have behaved normally during tetani. Their conduction velocity histogram also showed a shift to slower than normal values, but most Golgi units still conducted within the normal range.

Efferent innervation

After crush injuries many normal static and dynamic fibres were found. For about half of these we were able to check their stimulating effect on more than one afferent fibre. The very striking observation was that only one of a total of fifty-six fibres checked in this way produced a different

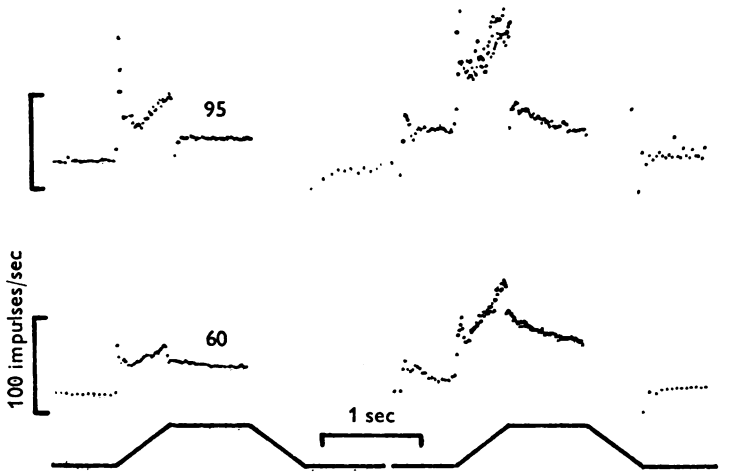

Fig. 3. An example of consistency of dynamic γ fibre action after regeneration following nerve section. Peroneus longus 12 weeks after nerve section with a single dynamic fibre (conduction velocity 28 m.sec^{-1}) acting on two afferent units (conduction velocities 95 and 60 m.sec^{-1}). On left, response to stretch of 5 mm alone. On right, response to same stretch, during stimulation of γ d at 143/sec. Frequency display as in Fig. 1. Time bar 1 sec. Length record diagrammatic.

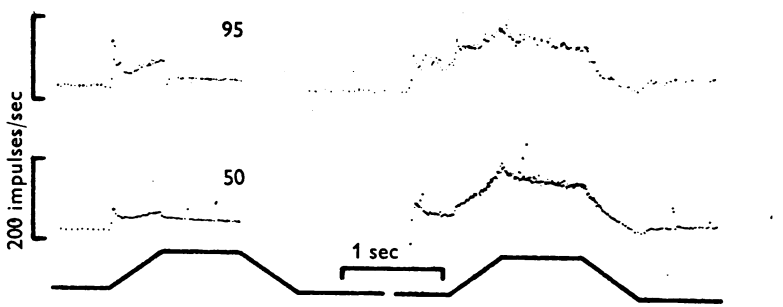

Fig. 4. An example of consistency of static γ fibre action after regeneration following nerve section. Same experiment as Fig. 3 and 95 m.sec^{-1} unit same as in Fig. 3. Left, response to stretch alone. Right, same 5 mm stretch during stimulation of γ s (conduction velocity 20 m.sec^{-1}) at 143/sec. Note gain for frequency display less than for Fig. 3.

excitatory effect on two different afferent fibres. The other fifty-five remained true to type, i.e. with either a static effect on all units or a dynamic effect on all units. All eleven γ fibres tested after nerve section on more than one afferent were also consistent in their actions. Examples of such consistency of action are given in Figs. 3 and 4, and the complete data is summarized in Table 1.

TABLE 1. Summary of data on γ and β fusimotor fibres. Unclassifiable motor fibres either had different actions on different afferent units or a mixed action of one unit

	Tenuissimus		Peroneus longus	
	Crush	Cut	Crush	Cut
Number of cats ...	11	2	5	5
Static γ fibres				
Total number	41	2	30	9
Number whose static action confirmed on 2 or more units	23	1	14	8
Number whose static action confirmed on 3 or more units	18	0	6	3
Number whose static action confirmed on 5 or more units	8	0	1	1
Dynamic β fibres				
Total number	11	1	14	3
Number whose dynamic action confirmed on 2 or more units	7	0	11	2
Number whose dynamic action confirmed on 3 or more units	2	0	5	2
Static β fibres				
Total number	11	5	0	11
Number whose static action confirmed on 2 or more units	1	0	0	2
Dynamic β fibres				
Total number	5	0	2	7
Number whose dynamic action confirmed on 2 or more units	1	0	0	2
Unclassifiable γ	0	0	1	0
β	2	0	0	1

The conduction velocities of the γ fibres found reinnervating peroneus longus are given in Fig. 5. The histogram with the dashed outline in this Figure is derived from Boyd & Davey's (1968) histological data for diameter of γ fibres in normal peroneus longus nerve, using a conversion factor of 4·5 $m.sec^{-1}$ per μm fibre diameter (Boyd & Davey, 1968). There does not seem to be any shift in the histogram towards lower than normal values for the conduction velocities.

β fibres

As well as excitation by γ fibres we found excitation of spindles by β motor fibres, that is fibres which innervate both extrafusal and intrafusal muscle fibres and which have conduction velocities > 45 m.sec^{-1}. The means by which their excitatory action was shown to be due to intrafusal fibre contraction are described in Methods. In Figs. 6 and 7 two examples of β fibres which had a static excitatory action are illustrated. We also found β fibres which had dynamic actions, and very occasionally β fibres whose action appeared to be a mixture of static and dynamic

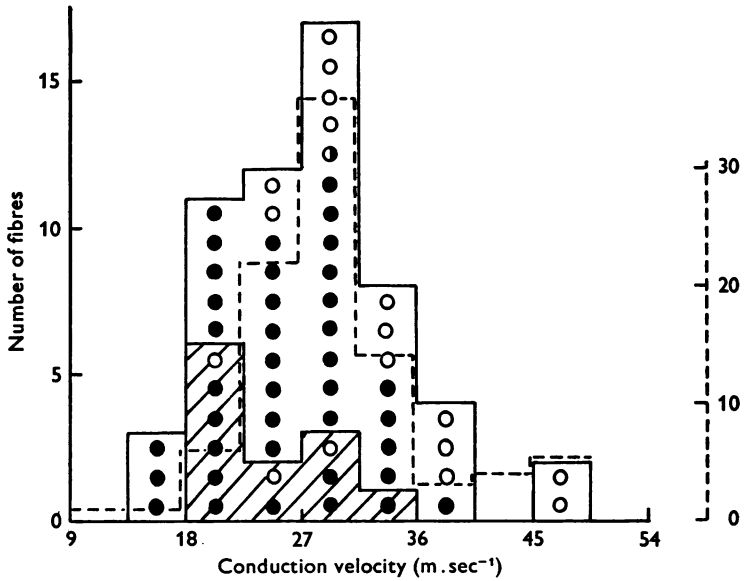

Fig. 5. Conduction velocity histogram for peroneus longus γ fibres (57 fibres from 10 cats) studied after nerve crush (open areas) or section (cross-hatched areas). ●, static γ fibres; ○, dynamic γ fibres. Histogram with dashed outline (ordinate scale to right) derived from histological data of Boyd & Davey (1968) – see text.

effects. Such a fibre is illustrated in Fig. 8. Table 1 gives the numbers of the various types of β fibres found. β fibres were found much more commonly after nerve section, where at early times they sometimes provided the sole intrafusal motor innervation. β fibres with a static action were found more commonly than β fibres with a dynamic action. Six of the β fibres acted on more than one unit. All of these were consistent in action. The conduction velocity histograms of the β fibres found in the two muscles are given in Fig. 9. There is no particular grouping of different β fibre types into different parts of the histograms.

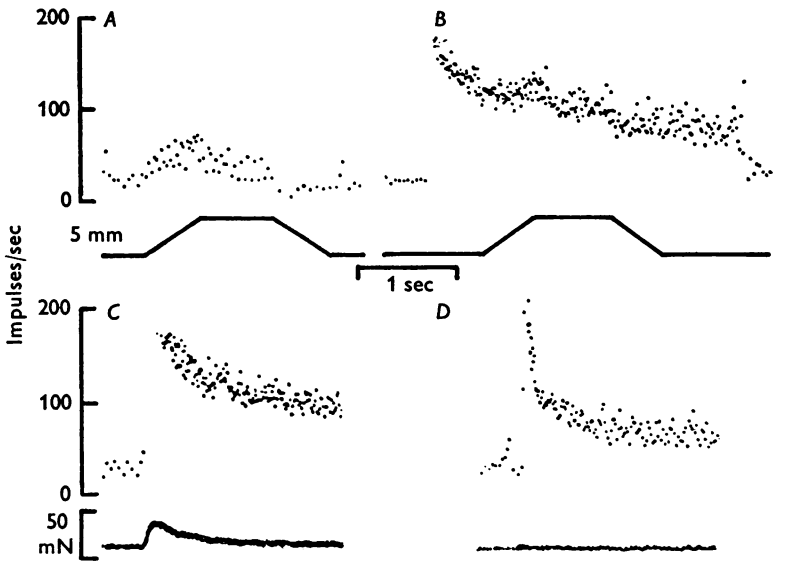

Fig. 6. Example of a static β fibre identified by critical curarization. Tenuissimus, 8 weeks after nerve section. *A*, response of afferent (conduction velocity 78 m.sec^{-1}) to stretch and release alone. *B*, response to same stretch and release during βs (conduction velocity 83 m.sec^{-1}) stimulation at 100/sec. *C*, tension and frequency during 100/sec stimulation at constant length. *D*, as *C*, but with tension blocked by topical application of gallamine.

DISCUSSION

The main question we wish to discuss is whether or not our data provide proof of specificity of different nerves for different sites in the reinnervation process, for apart from the recent experiments of Burgess and his colleagues (Burgess & Horch, 1973; Burgess, English, Horch & Stensaas, 1974) evidence in favour of any notable degree of specificity in mammalian peripheral nerve regeneration has been lacking (Young, 1942; Guth, 1956).

In the case of the afferent fibres our basic observation is that amongst reinnervating afferent fibres particular response patterns characteristic of primary and secondary endings were usually associated with axons of a conduction velocity range close to that found for the same endings in normal cats. This is not a strong argument, however, as the differences in response revealed by ramp stretches might be intrinsic to the afferent terminals themselves and not dependent upon the site of termination. We also cannot be sure in peroneus longus if afferent axons normally intended for Golgi tendon organs might not innervate spindles or even, if branched, supply axons to both types of end organ. Some of the abnormal

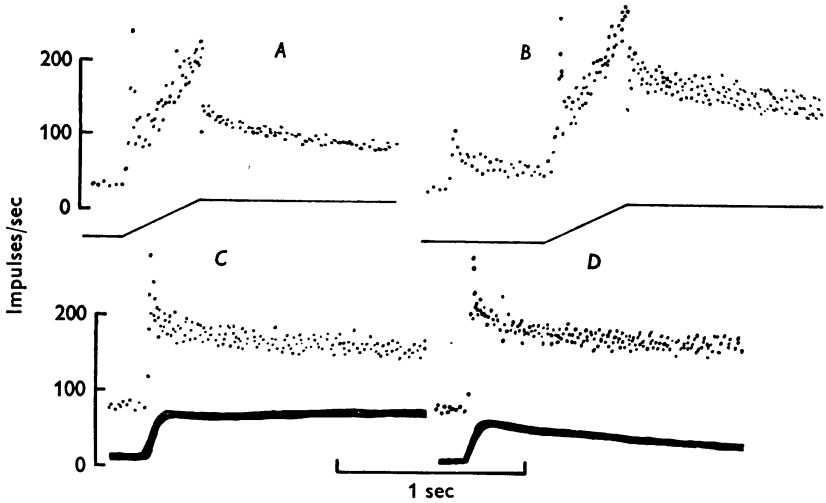

Fig. 7. Example of a static β fibre (conduction velocity 94 m.sec^{-1}) identified by fusion frequency technique. Peroneus longus, 18 weeks after nerve section. *A*, response of afferent (conduction velocity 85 m.sec^{-1}) to stretch alone. *B*, same stretch during β stimulation at 100/sec. *C*, β stimulation at 143/sec with length constant. Tension record underneath: plateau tension = 143 mN. *D*, β stimulation at 200/sec. Tracings of original records.

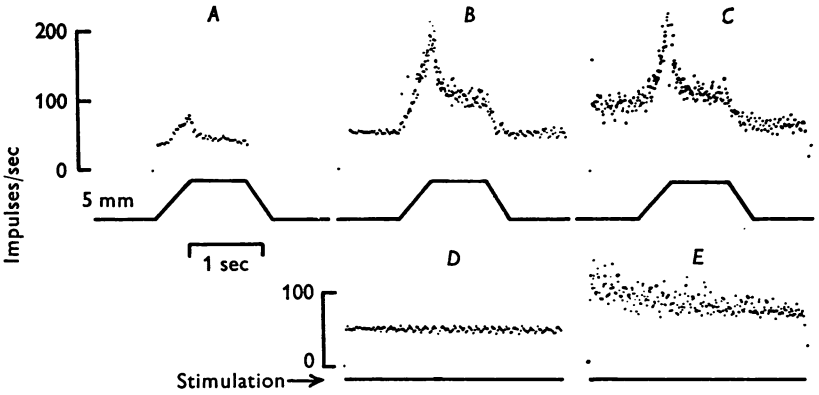

Fig. 8. An example of a β fibre with a mixed excitatory action, increasing the dynamic index during stretching but filling in the firing frequency during release in the manner of a static fibre. Tenuissimus 8 weeks after nerve crush. *A*, response of 69 m.sec^{-1} unit to stretch and release alone. *B*, response to same stretch during β stimulation at 50/sec. *C*, response to same stretch during β stimulation at 100/sec. *D*, *E*, excitatory action of β stimulation at 50 and 100/sec in the absence of stretching. β conduction velocity 69 m.sec^{-1}. This β fibre gave a recordable tension when initially examined, but after some repeated tetanic tension was unrecordable.

responses seen might have been due to this, but it seems more likely that abnormal responses are due to early 'incomplete' innervation for two reasons. First, such abnormal behaviour was commoner in animals examined early after crush, and secondly similar abnormalities were seen in tenuissimus which has no Golgi tendon organs. It would clearly be useful to have histological studies carried out to see if abnormalities in behaviour in anyway correlated with abnormalities in structure. A point in favour of return to specific sites, however, is that many of the endings classified as primary endings were acted on by both static and dynamic motor fibres, whereas thirteen secondary endings whose response was tested to the stimulation of dynamic fibres which had been found to operate primary endings were not excited by them.

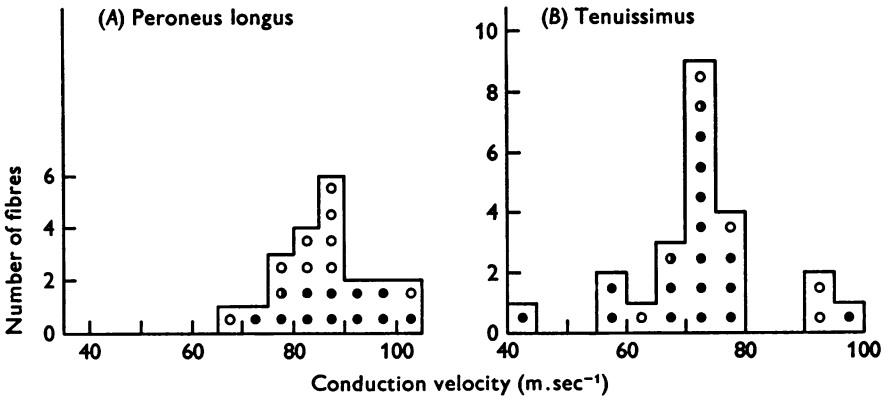

Fig. 9. Conduction velocity histograms of β fibres from peroneus longus (A, 5 cats) and tenuissimus (B, 11 cats). ○, dynamic; ●, static; ◑, mixed.

In agreement with Bessou *et al.* (1966) we did not find any γ motor fibres which generated tension. This evidence in favour of specificity, however, is also not without difficulties. For example, γ fibres might not be able to do more than induce subthreshold depolarization of large extrafusal fibres, or they might innervate so few extrafusal fibres that the tension generated would have been too small for us to record. Further, if α fibres regenerate more swiftly than γ fibres as Thulin's (1960) evidence suggests, then the opportunity for γ fibres to innervate extrafusal muscle might be very limited.

The strongest evidence in favour of specificity is the consistency of action of static and dynamic γ fibres after reinnervation. The large number of observations we have made (set out in Table 1) make it very improbable that this consistency could have arisen by chance. Whether the different effects of these two sorts of fibres are by differential excitation of different

sorts of intrafusal fibre, or by excitation of different sites on the same sorts of intrafusal fibre, it does not seem possible to explain their consistency unless static and dynamic fibres return preferentially to different places. (We would probably not, however, have detected weak innervation of inappropriate sites occurring at the same time.)

The fact that crush injuries are repaired so much more quickly than sectioned nerves is not surprising and argues in favour of some form of conduit or pathway guidance being of importance, but whether this is based on simple mechanical factors alone or on specific chemotactic or other influence it is not possible at present to say.

β fibres

The view that in normal cats β fibres were a sporadic or accidental finding (Bessou *et al.* 1965) has recently changed. Both McWilliam (1975) and Emonet-Dénand, Jami & Laporte (1975) now regularly find dynamic β fibres in various cat hind-limb muscles and they are probably present in all. The question arises as to whether the β fibres we found were simply part of this 'regular' supply or something new arising as a result of denervation. We believe the latter for the following reasons. After crush injuries β fibres were not as commonly found as after nerve section. We found more static β fibres than dynamic β fibres, and we occasionally found β fibres with excitatory effects which were dynamic looking during stretching but static looking during release (Fig. 8).

Although we believe many of the β fibre found in our cats were new (arising as a result of the injury), the presence of β fibres in normal cats shows that there is no absolute bar to α fibres innervating intrafusal muscle fibres, and this provides a ready explanation for their occurrence after injury. Presumably the denervated intrafusal fibres in the absence of possibly more appropriate or preferred γ fibres will accept α motor terminals. There is evidence (e.g. Bessou *et al.* 1965; Brown, Crowe & Matthews, 1965) that γ dynamic fibres and β dynamic fibres can successfully innervate the same spindle. It seems possible then that the extra β motor innervation provided to the spindles as a result of reinnervation will persist even if the γ fibres eventually return to the spindles as well. The alternative would be for the γ fibres to suppress or inactivate the less appropriate β fibres. We have no firm data to support this, and further experiments are needed.

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