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MOTOR INNERVATION, MOTOR UNIT ORGANIZATION AND AFFERENT INNERVATION OF M. EXTENSOR DIGITORUM COMMUNIS OF THE BABOON'S FOREARM

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SUMMARY

1. One hundred and fifty efferent axons innervating m. extensor digitorum communis (EDC) were isolated in filaments of C7 and C8 ventral roots of baboons. Conduction velocities were measured antidromically by stimulating the muscle nerve and recording from the filaments, and fell into two groups: a fast (49–84 m/sec) and a slow (22–41m/sec), presumably fusimotor group. The threshold for these latter axons exceeded the strength needed to elicit the maximal motor twitch.

2. Stimulation of ventral root filaments containing slow axons produced no contractile tension in EDC.

3. Stimulation of ventral root filaments containing fast-group axons elicited all-or-nothing twitches of motor units of EDC. The twitch tensions of 66·3% of the units were < 2·0 g wt.; only 8·7% were > 5·0 g wt. Tetanus-twitch ratios were 1·4–4·7 in a sample of 14 units. Contraction times were between 15 and 35 msec in 97% of the units. There was no correlation between contractile properties and axonal conduction velocity.

4. Afferent volleys from the stimulated EDC nerve were recorded from C6 or C7 dorsal roots. The threshold was below the threshold for a just-detectable motor twitch in ten out of eleven baboons. Conduction velocity of the earliest component of the muscle afferent volley was 67–83 m/sec.

5. The conduction velocities of twenty-eight spindle afferents, identified by their responses to linear stretches of EDC and by their unloading by maximal twitches, were all < 70 m/sec. Higher dynamic sensitivity tended to be associated with higher conduction velocity.

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INTRODUCTION

Details of the innervation of some of the muscles of the cat's hind limb are common knowledge amongst experimental neurophysiologists. These details include the conduction velocities and relative electrical thresholds of the afferent fibres (Groups Ia, Ib, II and III) and efferent fibres (α, skeletomotor and γ, fusimotor), and the contraction-times and tensions of the motor units. This paper reports corresponding data for m. extensor digitorum communis of the baboon's forelimb. These were required in connexion with experiments on the cortical control of the hand (Koeze, Phillips & Sheridan, 1968), but a wider interest attaches to the general comparison between a muscle of a primate's forelimb, which is used by the animal in exploratory and manipulative behaviour, and the postural and locomotor muscles of the cat's hind limb. A preliminary note has already been published (Eccles, Phillips & Wu Chien-ping, 1966).

METHODS

The subjects were young baboons of 4–6 kg. They were anaesthetized with N_2O, O_2, chloroform and pentobarbitone, and fixed by skull, spine and pelvis (Hern, Landgren, Phillips & Porter, 1962).

The nerve to m. extensor digitorum communis (EDC) is a short branch of the deep interosseous nerve. The terminal branches of this nerve in the left forearm were explored under the dissecting microscope and the EDC branch identified by electrical stimulation, the tendons being lifted from their sheath in order to be sure of the response. The other branches of the interosseous nerve were then cut, and the EDC branch enclosed in continuity in a polythene cuff in which the stimulating electrodes were embedded. The ulnar, median and musculocutaneous nerves, the musculospiral branches to triceps, and the medial cutaneous nerves of arm and forearm were also cut. To allow setting of the muscle to its minimum and maximum physiological length during the experiment, a marker suture was placed in the tendons proximal to the wrist. The distance of this suture from the proximal drill holder was measured with the muscle in its extreme positions before cutting the tendons and fixing the bones to the animal holder. The lower end of the humerus and proximal end of the ulna were transfixed by one drill, and the distal ends of ulna and radius were transfixed by another with the forearm fully pronated. These drills were clamped at both ends to the animal frame and electrically isolated by Tufnol bushes. In the later experiments the spine of the scapula was held by fine wood screws driven into it through holes in a Tufnol bar, also clamped to the frame. The tendons of EDC were transfixed with a steel needle at wrist level, and lashed together and to the needle by linen thread; the needle was then nipped off so that it projected only 2 mm on either side of the lashing. The tendons were cut distally and attached to the myograph by a light chain looped round the tendons and needle. The muscle was set to the minimum physiological length, and any applied passive stretches were kept within the natural range. When recording twitches, the muscle was set half-way between minimum and maximum physiological length. Skin flaps formed a paraffin pool out of which the chain rose at an angle of about 10° to the horizontal to join the myograph. The pool was filled with paraffin at about 38° C which flowed at about 30 ml./min through a thermostatically-controlled electrical warmer into the laminectomy wound, cascaded into the muscle pool through a cannula and tubing and was then recirculated. The paraffin was equilibrated with 5 % CO_2 in O_2.

The muscle was attached to the stretcher-myograph apparatus used by Koeze *et al.* (1968). The frequency of discharge of single spindle endings was recorded as a reciprocal impulse-interval display (Matthews, 1963). In one experiment the myograph was a cantilever spring to which two semiconductor strain gauges (Ether Ltd., Type P.) were cemented, one on either side. The output of the bridge network of which they formed part was displayed on one beam of a Tektronix 502A Oscilloscope.

The C4–T1 segments of the spinal cord were exposed by laminectomy. After cutting the left dorsal roots and slightly retracting the spinal cord to the right side the left C7 and C8 ventral roots were exposed. Under a dissecting microscope the ventral root filaments were cut proximally and subdivided into progressively finer filaments until single 0·2 msec rectangular pulses applied to the EDC nerve elicited all-or-none potentials in a filament (Fig. 1*A*). These selected filaments were then stimulated orthodromically with single 0·2 msec pulses. The resulting twitches were recorded myographically. Since these ventral root filaments were very short, great care had to be taken to ensure that the twitches were not due to spread of stimulating current to adjacent filaments containing other motor axons: (1) The rootlets, under the paraffin oil, were kept free of c.s.f. by continuous suction; (2) At threshold stimulus strength the motor twitches had to be all-or-none (Fig. 1*B*); (3) Increase of stimulus strength to several times the threshold strength did not increase the twitch tension. We rejected many filaments which produced graded increases in twitch tension when stimulated with gradually increasing stimulus strengths; (4) Through a dissecting microscope, we carefully watched the surface of the muscle, whose whole length was exposed in the paraffin pool, and in cases in which superficial bundles of fibres could be seen to contract we recorded the motor unit electromyogram by means of fine electrodes applied locally to the surface (Fig. 1*C*, upper trace) (Liddell & Phillips, 1952). Stimulating current was always measured in oscillographic records of the voltage drop across a resistor in series with the stimulating electrodes. In several cases, the tetanic tensions of single motor units were also recorded (Fig. 1*D*, lower record).

In a few experiments the EDC nerve was splinted and fixed in 1 % osmic acid for 72 hr; dehydrated for 12 hr in 50 %, 12 hr in 70 %, ½ hr in 90 % and ½ hr in two changes of 100 % alcohol; and then embedded in paraffin. The fibres were counted and their diameters measured on enlarged photographs of the sections.

RESULTS

Motor innervation and properties of motor units. Figure 1 illustrates the stages in the investigation of a motor unit. The upper record in *A* shows an all-or-none antidromic impulse in a ventral root filament in response to stimulation of the EDC nerve. The conduction velocity was 74 m/sec. The threshold stimulating current was 0·8 times that needed to elicit a maximal twitch of EDC. The ventral root filament was then stimulated orthodromically, eliciting an all-or-none twitch whose contraction time was 28 msec and peak tension 1·4 g wt. (Fig. 1*B*). The twitch was visible in a superficial bundle under the microscope, and Fig. 1*C* shows the muscle spike recorded by fine paired silver wires applied locally, together with the twitch, recorded on a faster sweep than in Fig. 1*B*. In Fig. 1*D* the ventral root filament was stimulated repetitively at 100/sec. The tetanus/twitch tension ratio was 3·5. Figure 2 shows an all-or-none antidromic impulse whose conduction velocity from EDC nerve to ventral

root filament was 25 m/sec. Threshold current strength for this axon was 1·3 times that needed to elicit a maximal twitch of EDC. This slowly-conducting axon should not, therefore, have contributed any tension, and it produced no detectable tension at high myographic sensitivity when the ventral root was stimulated orthodromically. It was presumably a fusi-motor axon.

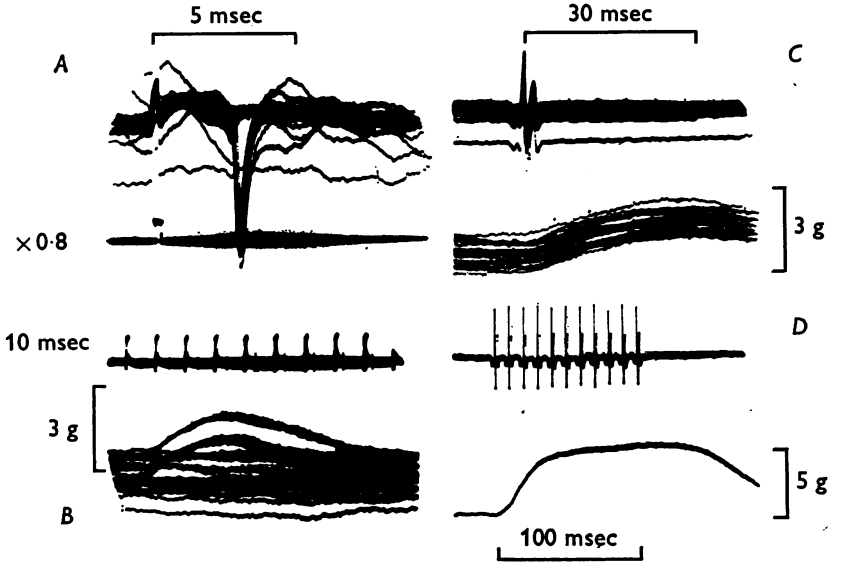

Fig. 1. Electrical and mechanical responses of a motor unit.

A. All-or-none antidromic impulses in motor axon, recorded from ventral root filament while stimulating the muscle nerve. Stimulus strength was 0·8 times the threshold of maximal motor twitches. Conduction velocity 74 m/sec.

B. Mechanical responses to near-threshold stimulation of same ventral root filament, showing all-or-none response.

C. Faster sweeps, stimuli above threshold. Upper traces: action potential of the motor unit.

D. Electrical (upper trace) and mechanical (lower trace) responses to repetitive stimuli, frequency 100/sec. Tetanus-twitch tension ratio = 3·5. Records *A–C* comprised of twenty superimposed sweeps.

In Fig. 3 the conduction velocities of 150 axons are plotted against the numbers of axons. The axons fall into two groups: a fast group with conduction velocities ranging from 49 to 84 m/sec (peak at about 70 m/sec) and a slow group ranging from 22 to 41 m/sec. All fibres of the fast group had thresholds below the strength for maximal motor twitch. On the other hand those of slow-group fibres all exceeded the strength for maximal motor twitch. The inset in the upper part of Fig. 2 shows the distribution of threshold of the forty-one slow-group fibres as multiples of the strength needed for maximal isometrie twitches. They ranged from ×1·27 to

× 5·1. Accordingly, no detectable tension change was produced by stimulating those ventral root filaments which contained EDC fibres with conduction velocities below 41 m/sec. The slow-group fibres were presumably fusimotor fibres.

Stimulation of ventral roots containing EDC fibres which conducted faster than 49 m/sec developed measurable tension in all instances. It is interesting that most of the motor units were rather small in terms of the twitch tensions they produced.

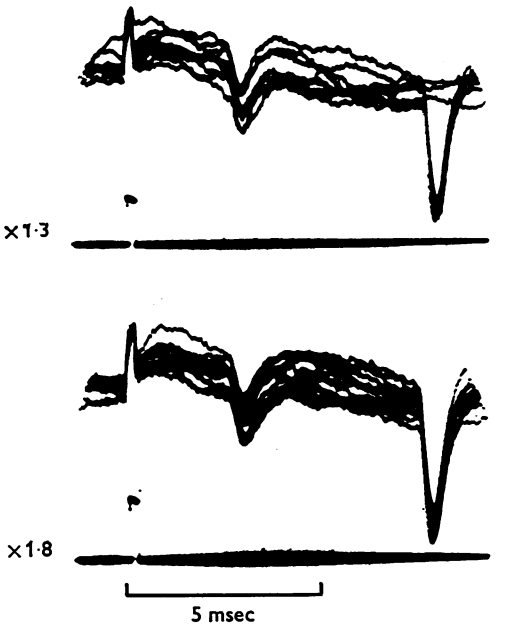

Fig. 2. Antidromic impulses in a presumed fusimotor axon recorded from ventral root filament while stimulating the muscle nerve. Twenty sweeps superimposed. Conduction velocity 25 m/sec. The stimulus strengths of top and bottom records are 1·3 and 1·8 times the threshold of the maximal motor twitch. Top record taken at threshold stimulus strength showing all-or-none responses. The early small potentials in both records are field potentials from large motor axons, spread from neighbouring filaments.

Figure 4 illustrates motor units of different sizes. In Fig. 4*A* the motor axon had a conduction velocity of 73 m/sec and the twitch tension was 5 g wt. Figure 4*B* illustrates a small motor unit: the motor axon had a conduction velocity of 74 m/sec and the twitch tension was 0·37 g wt. Of ninety-two units, sixty-one, i.e. 66·3% had twitch tensions of less than 2 g wt., the highest being 8·5 g wt. The distribution of twitch tensions is plotted in Fig. 5. The maximal twitch tensions of the whole muscle ranged from 510 to 980 g wt. (Table 1). It is unlikely that these low tensions were due to series-elastic losses in the long thin tendons of the muscle, for the

tetanus/twitch tension ratios, which we measured in 14 units, lay between 1·4 and 4·7. These ratios were more or less in the same range as those of whole muscles (Cooper & Eccles, 1930) and single motor units (Devanandan, Eccles & Westerman, 1965) of the cat's hind limb.

Figure 6 shows the distribution of the contraction times of ninety-four motor units. They ranged from 10 to 55 msec, but the majority were between 15 and 35 msec. Obviously the majority of these small motor

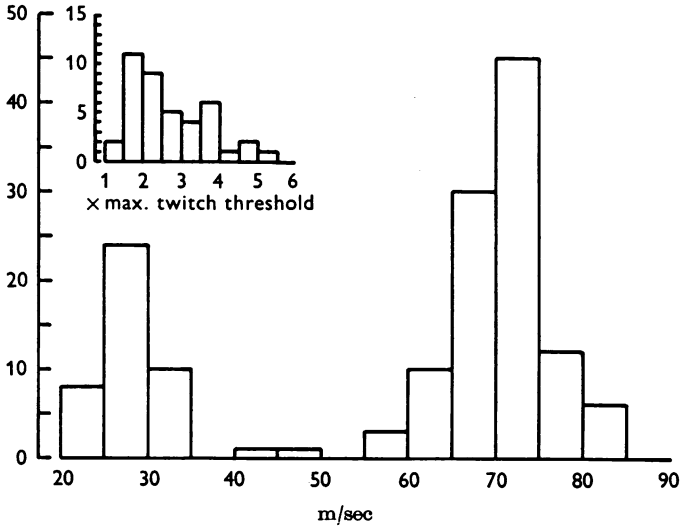

Fig. 3. Conduction velocities of 150 motor axons arranged in 5 m/sec groups. Abscissae: conduction velocities. Ordinates: number of fibres in each group. The inset shows the thresholds of forty-one presumed fusimotor axons. Abscissae: thresholds as multiples of maximal twitch thresholds. Ordinates: number of axons.

units are fast-contracting units. We have plotted both the twitch tensions and the contraction times of all motor units against the conduction velocities of their motor axons. The dots of both figures (not reproduced) were well scattered. There was no relationship between contractile properties and axonal conduction velocity.

Conduction velocities of afferent fibres and relative thresholds of afferent and efferent fibres. In thirteen baboons we recorded simultaneously the spike potential evoked in the cut C6 or C7 dorsal roots and the twitches evoked in EDC by graded single-pulse stimulation of the muscle nerve. We measured and compared the strengths of stimuli needed (1) for a just-detectable dorsal root volley, (2) for a just-detectable motor twitch, (3) for a maximal 'group I' volley, and (4) for a maximal motor twitch. The results are presented in Table 1. The conduction velocity of the earliest component of the muscle afferent volley ranged from 67 to 83 m/sec. If the

threshold for a minimal motor twitch, i.e. for the lowest-threshold motor axons, was taken as 1·0, then in only one animal out of eleven was the threshold for the dorsal root spike 1·0; the others were all below the motor axon threshold, ranging from 0·52 to 0·93. The strengths needed for maximal 'Group I' afferent volleys were about the same as those for maximal twitches, i.e. for maximal motor volleys.

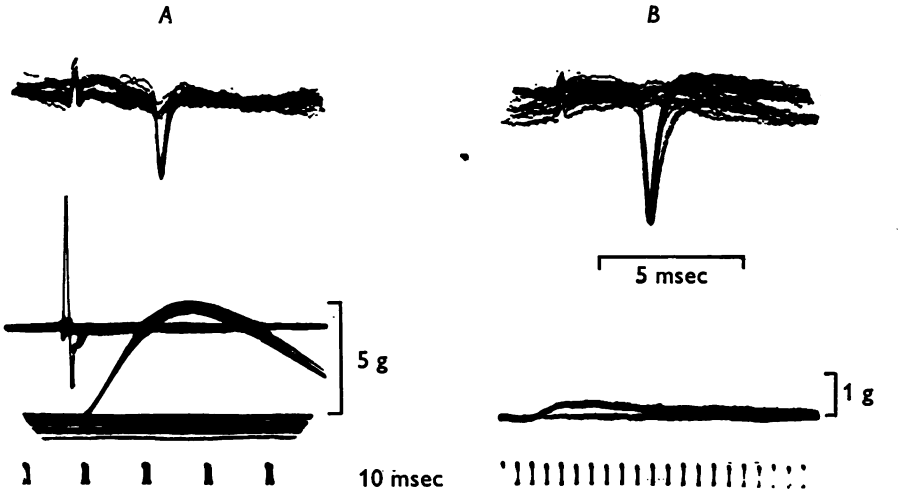

Fig. 4. Electrical and mechanical responses of two motor units. All records comprised of 20 superimposed sweeps.

A. Upper trace: All-or-none antidromic impulses in motor axon, recorded from ventral root filament while stimulating the muscle nerve. Stimulus strength 0·77 times threshold of maximal motor twitch. Conduction velocity 73 m/sec.

Lower traces: All-or-none electrical and mechanical responses to near-threshold stimulation of same ventral root filament.

B. Another unit.

Upper trace: all-or-none antidromic impulses in motor axon, recorded from ventral root filament as in *A*. Stimulus strength 0·75 times threshold for maximal motor twitch; conduction velocity 74 m/sec.

Lower trace: all-or-none mechanical response to near-threshold stimulation of same ventral root filament.

Figure 7 gives the evidence from one experiment. The upper traces of records *A*, *B*, *C* are the dorsal root recordings and the lower traces are the tension recordings. Stimulus strength in Fig. 7*B* was near-threshold for motor axons (relative strength 1·0). In Fig. 7*A* a stimulus of relative strength 0·86 evoked a small afferent volley. The relative strength for just-maximal twitches and just-maximal dorsal root spikes was 1·3 (Fig. 7*C*). Further increase of stimulus (14·3, Fig. 7*D*) did not increase the amplitude of the dorsal root spike.

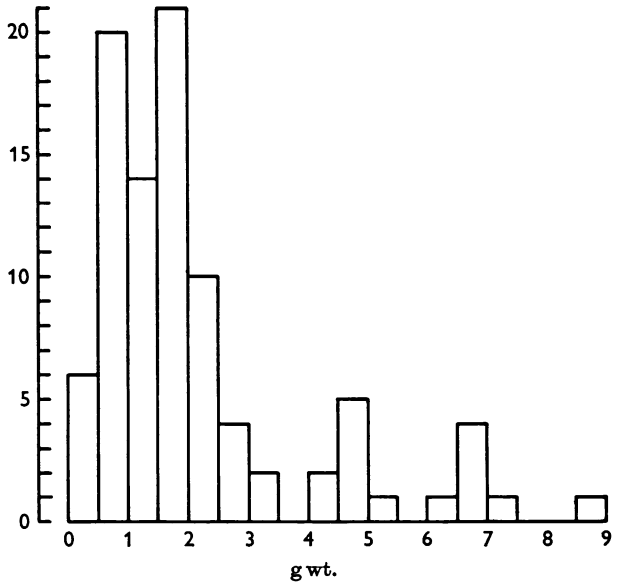

Fig. 5. Twitch tensions of 92 motor units plotted against their numbers, 66·3 % being under 2 g wt., and 8·7 % over 5 g wt.

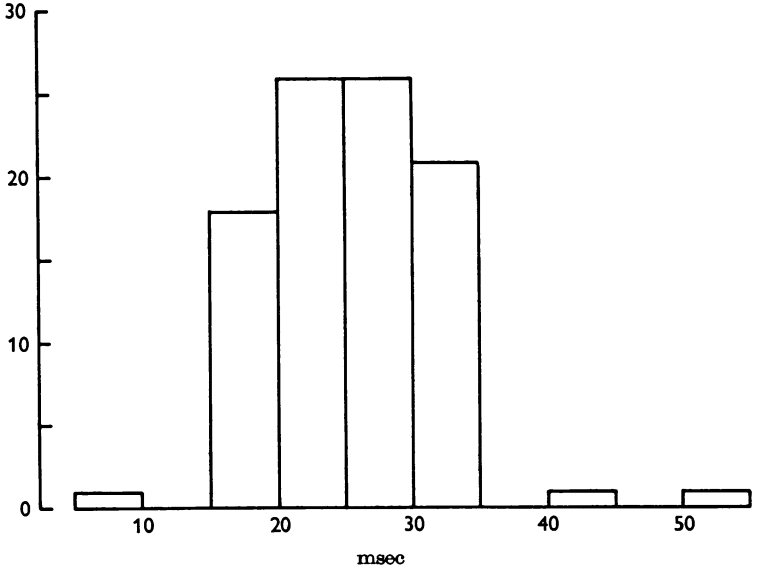

Fig. 6. Contraction times of ninety-four motor units. Abscissae: contraction times. Ordinates: number of motor units.

TABLE 1

Expt.	Weight of animal (kg)	Threshold of motor twitches	Relative strength for maximal motor twitches	Tension of maximal motor twitches (g wt.)	Relative threshold of dorsal root afferent volley	Relative strength for maximal dorsal root afferent volley	Conduction velocity of earliest component of dorsal root afferent volley (m/sec)
1	5·0	1	3	865	0·9	1·5?	70
2	5·4	1	5–6·6	510	1	3·2–3·5	76·2
3	5·5	1	1·3	585	0·93	?	79·3
4	5·3	1	1·5–1·56	420	0·52–88	1·52–1·56	78·3
5	5·5	1	1·9	755	0·83	1·9	67·3
6	5·3	1	3·3	687	< 1?	3·3	70·3
7	5·3	1	1·3	565	< 1?	1·3	79·2
8	5·4	1	1·3	980	0·86	1·3	81·2
9	4·8	1	1·2	690	< 0·9	1·2–2·8?	77
10	4·5	1	1·5	925	< 0·9	1·5	80
11	5·5	1	1·3	941	0·6–0·8	1·3	81·8
12	5·7	1	—	955	—	—	70·6
13	5·2	1	—	590	—	—	83

Since the fastest fibres of the dorsal root volley (Group I) were unexpectedly slow, some conduction velocities were measured from single afferent axons from muscle spindles of EDC, electrically stimulated in the muscle nerve and recorded in dorsal root filaments. The fibres were identified as spindle afferents both by their responses to linear stretches of the muscle and by their unloading in maximal twitches. The dynamic

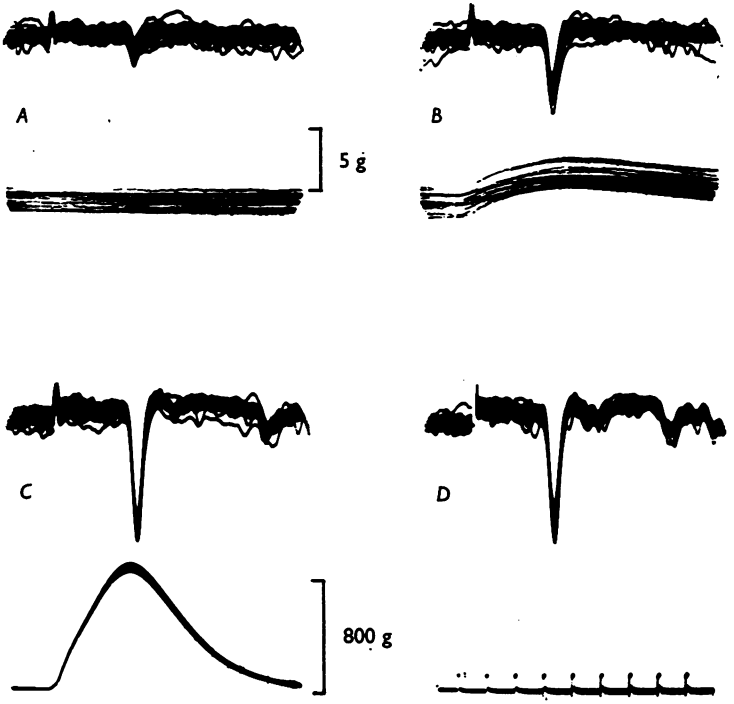

Fig. 7. Relative thresholds of afferent and efferent fibres in nerve to EDC. Single shocks (0·2 m/sec duration) were delivered to the nerve while mechanical responses of the muscle and electrical responses of cut dorsal roots were recorded. All records comprised of twenty superimposed sweeps.

A. Relative strength 0·86. Small dorsal root volley (upper record): no myographic response (lower record).

B. Relative strength 1·0. Larger dorsal root volley: minimal motor twitch.

C. Relative strength 1·3. Maximal Group I dorsal root volley and maximal motor twitch.

D. Relative strength 14·3. Confirms that Group I volley in *C* was maximal.

Time scale: 10 m/sec for myograms, 4 m/sec for dorsal root records. Tension scales: 5 g wt. for *A* and *B*; 800 g wt. for *C*.

indices of twenty-eight spindle receptors (Crowe & Matthews, 1964) were plotted against the conduction velocity of their afferent axons (Fig. 8). Since, in these experiments, the ventral roots were intact, all the spindles were under different degrees of γ bias, which was changing from time to

time. When several different values of dynamic index were measured for one ending, the highest value was chosen for plotting in order to display the largest dynamic response of which the ending had shown itself capable.

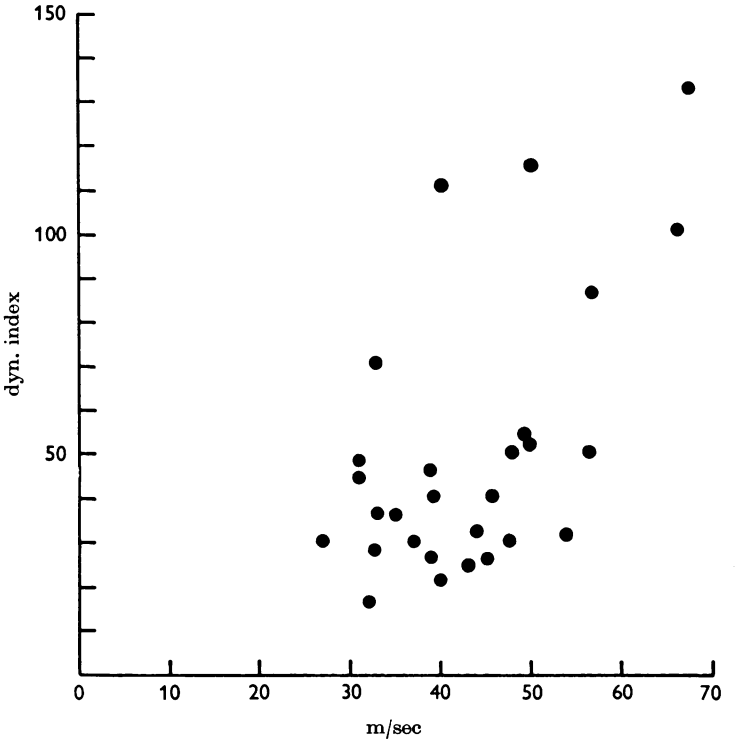

Fig. 8. Scatter diagram relating the dynamic indices of 28 muscles spindle afferents to their conduction velocities. Abscissae: conduction velocities, m/sec. Ordinates: dynamic indices, impulses/sec. The muscles were stretched from minimum to maximum physiological length at a speed of 15 mm/sec.

Figure 8 makes it clear that higher dynamic index tended to be associated with higher conduction velocity. All conduction velocities were < 70 m/sec.

If Hursh's (1939) factor of 6 m/sec per micron of axon diameter applies to EDCs nerve, its largest motor fibres (84 m/sec) should be 14 μ in diameter and its largest afferent fibres (83 m/sec dorsal root volley) about the same. Figure 9 shows that the largest axons, measured near the entry to the muscle, were indeed 14 μ in diameter.

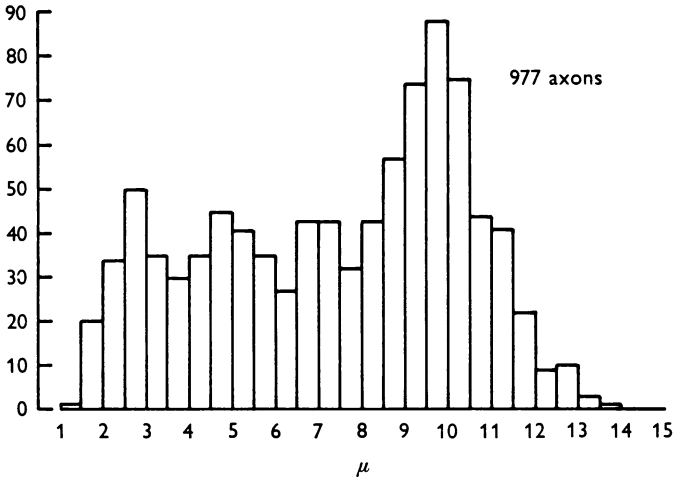

Fig. 9. The calibre spectrum of the nerve to m. extensor digitorum communis, near its entry to the muscle. Abscissae: fibre diameters arranged in 0·5 μ groups. Ordinates: number of fibres in each group.

DISCUSSION

The baboon's m. extensor digitorum communis (EDC) belongs to the category of 'fast' muscles. It is built up of motor units whose individual contributions to the total tension are remarkably small. Of the ninety-two motor units sampled in our experiments, 66% developed individual tensions of less than 2 g wt., and only 9% exceeded 5 g wt. The largest was about 9 g wt. The contrast with some fast muscles of the cat's hind limb is very striking: in plantaris, 6·7–39·0 g wt.; in flexor digitorum longus, 11·0–26·0 g wt.; in flexor hallucis longus, 3·4–9·0 g wt. (Devanandan *et al.* 1965). The feline medial gastrocnemius has had various ranges of unit twitch tensions ascribed to it, e.g. 13·6–59·0 g wt. (averaging 7·4 g wt.) by Wuerker, McPhedran & Henneman (1965); and 2·5–97 g wt. (median = 18 g wt.) by Burke (1967). The smaller, rapidly-contracting motor units of the baboon's EDC would provide for very fine gradation in the strength and velocity of the movements of its fingers.

The afferent innervation of EDC shows a remarkable lack of axons conducting impulses at velocities in excess of 80 m/sec. From cat's soleus, Matthews (1963) found plenty of afferent fibres from the primary endings of muscle spindles conducting to the dorsal roots at 80–120 m/sec. In EDC we have seen spindle endings with decided dynamic behaviour conducting to the dorsal roots at 40–70 m/sec (Fig. 8). Because we have not studied de-efferented spindles, and because our sample is too small, we have not attempted to classify our endings into primaries and secondaries

and to assign an arbitrary dividing-line for their conduction velocities. It seems probable that some of our spindles would fall into a group with properties intermediate between those of primaries and secondaries (cf. Matthews, 1963).

It appears that the fastest afferent fibres in the nerves of primates in general conduct more slowly than the fastest afferent fibres in the cat. T. Hongo, A. Lundberg, C. G. Phillips & R. Thompson (in preparation) found conduction velocities of 66–84 m/sec for volleys travelling from proximal and distal hind limb muscle nerves into the dorsal roots in baboons. In spindle afferents from thenar muscles of the baboon's hand, Sheridan (1965) measured conduction velocities of 40–80 m/sec; one axon only was found to exceed 90 m/sec. In median and ulnar nerves in the same species, McLeod & Wray (1967) found the fastest afferent fibres to conduct at 80–105 m/sec (median) and 81–102 m/sec (ulnar). McLeod & Wray's measurements were made in the forearms of mature baboons weighing 9·5–14·5 kg, and it might be suggested that the smaller and presumably younger specimens used by T. Hongo *et al.* (in preparation), Sheridan (1965) and ourselves had smaller, slower fibres. This seems unlikely, for A. Hopkins (personal communication) found that the fastest afferent conduction velocities in median nerves of baboons weighing 8–15 kg ranged between 75·8 and 98·5 m/sec (adjusted to 37° C); in three animals weighing 2·5–3·3 kg the range was 81·0–88·2 m/sec (adjusted to 37° C), 'within the normal range, although at the lower end of it'. McLeod & Wray (1967) quote evidence that the fastest fibres in human median and ulnar nerves are slower than those in the baboon's.

Clough, Kernell & Phillips (1968*b*) found that conduction in the baboon's brachial plexus is slower than in the peripheral nerves. Thus, the velocities measured from the EDC nerve to the spinal roots in the present experiments would be expected to be less than the velocities measured between electrodes within the forearm by McLeod & Wray (1967).

Although the differences between the fastest afferent and motor conduction velocities are less than in the muscle nerves of the cat, Clough, Kernell & Phillips (1968*a*) have found that the threshold separation was good enough to make it possible to obtain maximal intracellular monosynaptic EPSPs with stimuli below threshold for antidromic excitation of the motor axons of fifty-two out of fifty-seven impaled motoneurones of the forelimb. (In five out of fifty-seven cells the increase in the EPSP was only 0·1–0·7 mV.) Our finding that the strengths of stimuli to the EDC nerve are about equal for maximal motor and maximal dorsal root volleys must therefore mean that those afferent fibres whose threshold exceeds that of the motor axons do not make monosynaptic excitatory connexions with motoneurones. As Fig. 7 shows, there is no obvious notching of the

initial sharp dorsal root spike indicative of Group Ia and Ib components; but this spike needs further analysis by the double-volley technique (Bradley & Eccles, 1953; Eccles, Eccles & Lundberg, 1957).

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REFERENCES

BRADLEY, K. & ECCLES, J. C. (1953). Analysis of the fast afferent impulses from thigh muscles. *J. Physiol.* **122**, 462–473.

BURKE, R. E. (1967). Motor unit types of cat triceps surae muscle. *J. Physiol.* **193**, 141–160.

CLOUGH, J. F. M., KERNELL, D. & PHILLIPS, C. G. (1968*a*). The distribution of monosynaptic excitation from the pyramidal tract and from primary spindle afferents to motoneurones of the baboon's hand and forearm. *J. Physiol.* **198**, 145–166.

CLOUGH, J. F. M., KERNELL, D. & PHILLIPS, C. G. (1968*b*). Conduction velocity in proximal and distal portions of forelimb axons in the baboon. *J. Physiol.* **198**, 167–178

COOPER, S. & ECCLES, J. C. (1930). The isometric responses of mammalian muscles. *J. Physiol.* **69**, 377–385.

CROWE, A. & MATTHEWS, P. B. C. (1964). The effects of stimulation of static and dynamic fusimotor fibres on the response to stretching of the primary endings of muscle spindles. *J. Physiol.* **174**, 109–131.

DEVANANDAN, M. S., ECCLES, R. M. & WESTERMAN, R. A. (1965). Single motor units of mammalian muscle. *J. Physiol.* **178**, 359–367.

ECCLES, J. C., ECCLES, R. M. & LUNDBERG, A. (1957). Synaptic actions on motoneurones in relation to the two components of the group I muscle afferent volley. *J. Physiol.* **136**, 527–546.

ECCLES, R. M., PHILLIPS, C. G. & WU CHIEN-PING (1966). The innervation of m. extensor digitorum communis of the baboon's forearm. *J. Physiol.* **185**, 25–26*P*.

HERN, J. E. C., LANDGREN, S., PHILLIPS, C. G. & PORTER, R. (1962). Selective excitation of corticofugal neurones by surface-anodal stimulation of the baboon's motor cortex. *J. Physiol.* **161**, 73–90.

HURSH, J. B. (1939). Conduction velocity and diameter of nerve fibres. *Am. J. Physiol.* **127**, 131–139.

KOEZE, T. H., PHILLIPS, C. G. & SHERIDAN, J. D. (1968). Thresholds of cortical activation of muscle spindles and α motoneurones of the baboon's hand. *J. Physiol.* **195**, 419–449.

LIDDELL, E. G. T. & PHILLIPS, C. G. (1952). The cortical representation of motor units. *Brain* **75**, 510–525.

MCLEOD, J. G. & WRAY, S. H. (1967). Conduction velocity and fibre diameter of the median and ulnar nerves of the baboon. *J. Neurol. Psychiat., Lond.* **30**, 240–247.

MATTHEWS, P. B. C. (1963). The response of de-efferented muscle spindle receptors to stretching at different velocities. *J. Physiol.* **168**, 660–678.

SHERIDAN, J. D. (1965). Supraspinal control of reflex arcs of primate's forelimb. Ph.D. Thesis, Oxford.

WUERKER, R. B., MCPHEDRAN, A. M. & HENNEMAN, E. (1965). Properties of motor units in a heterogeneous pale muscle (M. gastrocnemius) of the cat. *J. Neurophysiol.* **28**, 85–99.