J. Physiol. (1958) 142, 275–291

THE ACTION POTENTIALS OF THE ALPHA MOTONEURONES SUPPLYING FAST AND SLOW MUSCLES

By J. C. ECCLES, ROSAMOND M. ECCLES and A. LUNDBERG

From the Department of Physiology, Australian National University, Canberra

(*Received* 7 *February* 1958)

Ever since the discovery by Ranvier (1874) and Kronecker & Stirling (1878) that red striated muscle has a slower contraction than pale, and consequently gives a fused tetanus at a lower frequency of stimulation, there has been much speculation in regard to the possibility that the slow-red muscles might be specially concerned in the tonic postural movements of limbs, while the fast-pale muscles would give the quick phasic movements. Cobb and Fulton (cf. Fulton, 1926) were the first to record with an isometric myograph the independent contractions of the slow soleus and the fast gastrocnemius of the cat. It was shown by Denny-Brown (1929*a*, *b*) that with these ankle extensors there is a more striking discrimination into the slow-red and the fast-pale types than with any other synergic groups of muscles. In addition, Denny-Brown systematically investigated the participation of slow and fast muscles in the various types of postural reflexes, including the tonic labyrinthine and neck reflexes of Magnus, as well as in the stretch reflex and the crossed extensor reflex. In all the synergic groups of extensor muscles the slow muscles were activated in the lowest threshold range of the postural reflexes, while the fast muscles were in the middle and upper range of threshold (Denny-Brown, 1929*a*). On the other hand, the fast muscles were at times more readily excitable in brief reflex actions, such as, for example, were evoked on rapidly moving the head.

Recently Granit and his co-workers have approached with new concepts and new techniques the problem of the tonic and phasic activity of the 'alpha' motoneurones which innervate by the alpha motor fibres the extrafusal muscle fibres and which are, of course, clearly distinguishable from the 'gamma' motoneurones that give via the gamma motor axons probably the exclusive motor innervation of the muscle spindles of mammalian muscles (Leksell, 1945; Hunt & Kuffler, 1951). The experimental investigations were restricted to the cat gastrocnemius-soleus group of synergic ankle extensors. It has been shown by Granit, Henatsch & Steg (1956) that about 53% of the

alpha motoneurones are phasic, responding reflexly with only one or two discharges to sustained muscle stretch, even when under the influence of post-activation potentiation, while the remainder are tonic, responding by a relatively prolonged discharge under such conditions. These differences are quite independent of the γ-loop activation of the motoneurones. The phasic motoneurones are also distinguished from the tonic by their large axonal spike potentials, as recorded in the same ventral root filament. It has further been shown (Granit, Phillips, Skoglund & Steg, 1957) that activation by two other reflexes (the crossed-extensor and the pinna-twist reflexes) gives the same discrimination between phasic and tonic motoneurones. During their brief repetitive responses the phasic exhibit a higher frequency of discharge than the tonic, 30–60 as against 10–20/sec being the usual frequencies, though tonic motoneurones could discharge at a frequency as high as 40/sec (cf. Adrian & Bronk, 1929; Adrian & Umrath, 1929; Denny-Brown, 1929*a*). Thus it was concluded that the separation of motoneurones into tonic and phasic types represents a fundamental distinction. However, there was evidence which suggested that this functional separation did not conform with the anatomical separation into the motoneurones supplying the slow-red soleus and those supplying the fast-pale gastrocnemius muscles respectively.

Granit *et al.* (1957) recorded intracellularly from tonic motoneurones in an attempt to discover if there were specially large depolarizations during the repetitive discharge of tonic motoneurones, but failed to find any intracellular response that was suitable for discriminating between tonic and phasic motoneurones. The present paper gives an account of a systematic investigation into the intracellular action potentials of over 260 motoneurones belonging to twenty different species of muscles and also into the thresholds and conduction velocities of their axons and the contraction times of the muscles they innervate. It will emerge that the motoneurones supplying the slow and fast muscles that operate as extensors of three hinge joints are characterized by their after-potentials as well as by the conduction velocities of their axons, and on the basis of this discrimination it will be concluded that in general the tonic and phasic types of motoneurones activate the slow and fast types of muscle respectively. A preliminary account has already been published (Eccles, Eccles & Lundberg, 1957*a*).

METHODS

The experimental technique was similar to that described by Eccles, Eccles & Lundberg (1957*b*). The antidromic impulses that invaded the motoneurones were generated by stimuli applied to the central end of the cut motor nerves. Under such conditions with the dorsal roots intact, as was the case in most experiments, motoneurones were subjected not only to invasion by antidromic impulses, but also to the monosynaptic excitatory action by group Ia afferent impulses and to the inhibitory action which is exerted via the pathway from motor-axon collaterals to Renshaw cells (Eccles, Fatt & Koketsu, 1954). The excitatory and inhibitory post-synaptic potentials (EPSP

and IPSP) so produced would be superimposed on the after-hyperpolarization that follows the neuronal spike potential; however, discrimination between the EPSP and IPSP on the one hand, and the after-hyperpolarization on the other, was readily achieved by stimulating the muscle nerve at just-threshold strength for the axon of the motoneurone under observation. Two series of traces were thus obtained; in one there were the EPSP and IPSP alone, and in the other there was in addition the antidromic spike potential and the subsequent after-hyperpolarization. Furthermore, a record was taken with a stimulus strength just adequate always to excite the motor axon, so as to avoid the overlapping of the two curves which obscured the latter part o the after-hyperpolarization (cf. the records in the second column of Figs. 1–4). Though it has not been possible to allow accurately for the partial occlusion between the two superimposed hyperpolarizations (i.e. the IPSP and the true after-hyperpolarization), it was nevertheless possible to determine from the second type of curve the total duration of the after-hyperpolarization, which has been regarded as the most convenient measurement for the time scale of the after-hyperpolarization. Actually, as indicated in Figs. 1–4, the after-hyperpolarization terminates in a low (0·2–0·4 mV) and prolonged after-depolarization, much as has been reported by Gasser & Grundfest (1936) for the after-hyperpolarization of peripheral nerve and by Lloyd (1951) for the ventral root. The durations recorded and plotted in this paper have been measured to the summit of this terminal after-depolarization, as indicated by the arrows in the inset traces of Fig. 5 *A*, but similar relative durations for the different motoneurones would have been obtained if the measurements had been made to the actual point of crossing the initial potential level. The identification of the species of a motoneurone has been made by determining the muscle nerve from which it can be antidromically activated, as has already been described (cf. Eccles *et al.* 1957*b*).

When investigating the time courses of the muscle twitches, the muscle was isolated as far as was compatible with the preservation of its blood supply and was completely immersed in a warm paraffin pool at 36–38° C. The origin of the muscle was fixed by drills through the appropriate bones and the tendon was firmly attached to the strain gauge, usually by means of its bony insertion. The strain gauge (Statham, Model G 1–80–350) was aligned so that the muscle pull on it was accurately in the line of its normal action and the initial tension was adjusted so that all muscle fibres would be passively stretched in the resting state. Initial tensions of 3–4% of the maximum twitch contraction were usually adequate, but higher tensions (up to 10%) were also employed. The output of the strain gauge was fed into a d.c. amplifier and thence to an optically flat oscilloscope for photography by a Grass camera. The calibration of the myographic system was performed immediately after each experiment. Since the aim of this myographic investigation was to discover if the motor units supplied by small axons had longer contraction times than those supplied by large axons, particular care was taken to preserve the blood supply to the region of the cut distal stump of the motor nerve to which the stimuli were applied, and so to maintain the normal range of threshold between the different motor axons. The successive twitch contractions were evoked at intervals of not less than 2 sec.

RESULTS

The spike potentials of alpha motoneurones

As already described (Eccles *et al.* 1957*b*), spike potentials of the impaled motoneurone were generated when it was invaded by impulses propagating antidromically up its motor axon. The spike potentials of motoneurones belonging to the slow-red muscle components of the extensor synergic groups acting at knee, ankle and elbow joints have been compared with the spikes of the corresponding fast-pale synergists. For example, Fig. 1 *D*, *H*, *L* shows, respectively, the spike potentials of crureus, vastus lateralis and rectis femoris motoneurones, the first supplying a slow muscle, the other two fast muscles.

Similarly, Fig. 3 *D*, *H* are the spike potentials of motoneurones supplying the slow elbow extensor muscles, caput mediale of triceps brachii and anconeus, while *L* and *P* are generated by motoneurones supplying the fast muscles caput laterale and caput longum of triceps brachii. All these spike potentials exhibit the characteristic step on the rising phase which has been shown (cf. Coombs, Curtis & Eccles, 1957) to be generated by the initial segment of the motor axon (the axon hillock plus the non-medullated segment). The origin of the SD (soma-dendrite) spike from the initial IS spike is indicated by

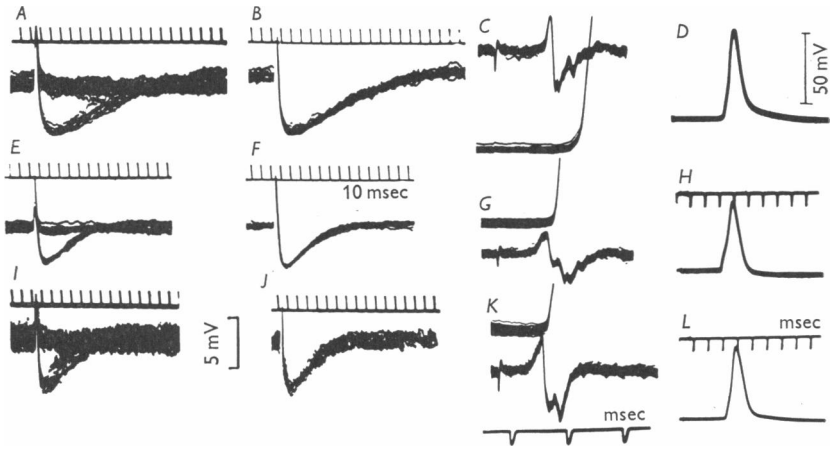

Fig. 1. Intracellular recording of responses set up in quadriceps motoneurones by stimuli applied to the nerves to crureus muscle (*A–D*), to vastus lateralis muscle (*E–H*) and to rectus femoris muscle (*I–L*), the motoneurones for the respective series being thus identified as supplying crureus, vastus lateralis and rectus femoris muscles (cf. Eccles *et al.* 1957*b*). With *A*, *E* and *I* the stimuli were just at threshold for the respective motor axons and just above threshold in *B*, *F* and *J*. With *C*, *G* and *K* the respective stimuli were several times threshold and the upper traces in *C* and the lower in *G*, *K* were recorded from the surface of the spinal cord at the segmental level for quadriceps motoneurones (note stimulus artifacts on the left of the traces). All records were formed by the superposition of about 40 faint traces. *A*, *B*, *E*, *F*, *I*, *J* have the same potential and time scales. Records *D*, *H*, *L* also have the same potential and time scales as indicated.

arrows in the records of Fig. 4 *D*, *H*. It should be noted in passing that both the motoneurones of Fig. 4 *A–H* supplied the nominally slow-red caput mediale of triceps brachii. However, it will be shown later that the duration of the after-hyperpolarization and the fast conduction velocity of the motor axon both indicate that the motoneurone of Fig. 4 *E–H* was of the fast type, and this classification will be adopted when considering the spike potentials of the two types of motoneurones.

Figs. 1–4 show that there were no large differences in the time courses of the spike potentials generated by motoneurones supplying slow and fast

muscles. However, column 5 of Table 1 indicates that with 'slow motoneurones' the declining phase of the spike was more prolonged than in the 'fast motoneurones' of the same synergic group. It should be noted that there was usually a considerable uncertainty in assessing the end of the spike of 'slow motoneurones'. In Figs. 1 *D*; 3 *D*, *H*; 4 *D* the declining phase gradually merged into the after-potential, whereas there was a fairly abrupt termination in Figs. 1 *H*, *L*; 3 *L*, *P*; 4 *H*. It is probable that the spikes of

TABLE 1. Mean durations of the rise and decline of spikes and of the after-hyperpolarizations for fast and slow extensor motoneurones at the knee, ankle and elbow joints. (Standard deviation in parentheses)

1	2	3	4	5	6
Motoneurone type	No. of moto-neurones	Potential of SD spike (mV)	Duration of rise of SD spike (msec)	Duration of decline of SD spike (msec)	Duration of after-hyper-polarizations (msec)
Soleus	5	70 (11)	0·40 (0·12)	1·08 (0·16)	177 (37)
Medial and lateral gastrocnemius	11	68·5 (13)	0·38 (0·08)	0·85 (0·15)	82 (19)
Slow quadriceps mostly crureus*	9	64 (9)	0·45 (0·01)	1·17 (0·19)	152 (19)
Fast rectus femoris, vastus medialis, and lateralis	9	63 (6)	0·43 (0·09)	0·95 (0·19)	88 (13)
Anconeus and slow caput mediale†	11	66 (11)	0·37 (0·06)	1·06 (0·11)	152 (17)
Caput longum, laterale and fast caput mediale of triceps brachii	22	60 (8)	0·33 (0·06)	0·84 (0·14)	77 (10)

Only those motoneurones with SD spike potentials in excess of 50 mV are included in the table.

* Including two vastus motoneurones whose after-hyperpolarizations were 140 and 150 msec in duration.

† All caput mediale with after-hyperpolarizations in excess of 130 msec.

'slow motoneurones' were even more prolonged than is shown in Table 1. Most of the measurements were made on fast records such as those of Fig. 4 *D*, *H*, where the vertical arrows indicate the points of measurement for the rising and declining phases of the SD spikes as given in columns 4 and 5 of Table 1. No significance can be attached to a comparison of the IS spikes or of the IS–SD intervals for the two classes of motoneurones, because these are modified by too many extraneous factors (cf. Coombs *et al.* 1957).

In addition, the spike potentials have been recorded from the motoneurones of flexor muscles at the knee and ankle, and of various muscles operating at the joints of the foot. Almost all these muscles are of the fast type and the spike potentials resembled those of the motoneurones supplying the fast extensor muscles.

The after-potentials of alpha motoneurones

The spike potential of a motoneurone normally declines on to a low after-depolarization that, in a few milliseconds, passes over into the after-hyper-

polarization, which reaches a maximum usually in 10–20 msec after the onset of the spike potential, and then gradually declines (Brock, Coombs & Eccles, 1952; Coombs, Eccles & Fatt, 1955). If the motoneurone is depolarized, e.g. by the injury inflicted by the micro-electrode, the spike potential may decline very rapidly to an after-hyperpolarization (cf. Figs. 1 *H*; 3 *D*) which may appear in two phases, the latter of which corresponds to the true after-hyperpolarization. The diminution of the resting potential of the motoneurone has resulted in a reversal of the after-depolarization (cf. Coombs *et al.* 1955; Eccles, 1957, pp. 82–3). For this reason there is much variability in the after-depolarization during a prolonged investigation on any one motoneurone, and the phase of transition at the end of the spike has provided the only significant difference between the two classes of motoneurones (cf. previous section).

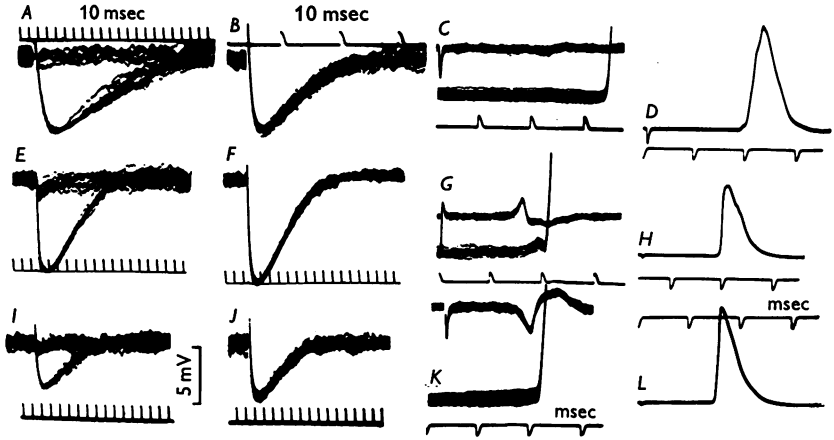

Fig. 2. A series of responses as in Fig. 1 for three ankle extensor motoneurones, soleus, lateral gastrocnemius and medial gastrocnemius respectively; but *D*, *H* and *L* were recorded monophasically from the S1, L7 and S1 ventral roots respectively in response to maximum stimulation of the soleus, lateral gastrocnemius and medial gastrocnemius nerves. Note that *B* is recorded at a slower sweep speed in order to show the full duration of the after-hyperpolarization.

In contrast, the great majority of the motoneurones supplying slow-red muscles have been characterized by the slow time course and long duration of the after-hyperpolarization. For example, in Fig. 1 the after-hyperpolarization of the crureus motoneurone (*A*, *B*) attained its maximum later and declined much more slowly than the after-hyperpolarization of the vastus (*E*, *F*) and rectus femoris (*I*, *J*) motoneurones. Similarly, in Fig. 2, the soleus motoneurone had a much slower after-hyperpolarization (*A*, *B*; note slower time scale in *B*) than the lateral (*E*, *F*) and medial (*I*, *J*) gastrocnemius motoneurones. Finally in the elbow extensor group (Fig. 3) the slow-red muscles, caput mediale of triceps brachii and anconeus, were supplied by moto-

neurones exhibiting long after-hyperpolarizations, *A*, *B* and *E*, *F* respectively, while the fast pale caput laterale and caput longum of triceps brachii were supplied by motoneurones having much briefer after-hyperpolarizations, *I*, *J* and *M*, *N* respectively.

With soleus the after-hyperpolarizations have always had a long duration (>140 msec) and with crureus most were in excess of 130 msec, though a few were as brief as 100 msec and one was only about 70 msec. However, the motoneurones of caput mediale tended to fall into two distinct groups, according to whether the after-hyperpolarization was longer or shorter than 110 msec. Two such motoneurones from one experiment are illustrated in Fig. 4 *A–H*, the duration of the after-hyperpolarization in *A*, *B* being 144 msec, while that in *E*, *F* was only 70 msec. Careful examination of the after-hyperpolarizations of Figs. 1–4 will reveal that other measurements such as time to maximum or to half decay gave the same relative values for the different motoneurones. The measurement of the total duration has been chosen because it was almost always beyond the range of complication by the Renshaw inhibition and also was always beyond the synaptic excitatory or inhibitory actions which would be exerted by the afferent volleys from the muscle nerves, for in most experiments the dorsal roots were intact (cf. Eccles *et al.* 1957*b*, *c*).

Since Lorente de Nó & Graham (1938) found that the depression of oculomotor neurones following antidromic activation was much briefer (30–40 msec) than that which occurred after antidromic activation of limb motoneurones (Eccles & Pritchard, 1937; Gasser, 1939; Brooks, Downman & Eccles, 1950; Lloyd, 1951) it would be expected that the causally related after-hyperpolarization would also be shorter in duration. Movements of the brain stem due to respiratory action made intracellular recording from oculomotor neurones much more difficult than from motoneurones in the spinal cord. Nevertheless, it was possible to record intracellular action potentials from a few oculomotor neurones. As shown in Fig. 4 *I*, *J*, the after-hyperpolarization had the expected brief duration of about 40 msec.

Conduction velocity of motor axons

The interval between the stimulation of the muscle nerve and the antidromic invasion of the motoneurone under examination can be measured for each of the limb motoneurones illustrated in Figs. 1–4. The stimulus was made sufficiently strong so that no significant error would be introduced by assuming that there was no delay in initiating the antidromic impulse; hence the measured interval gives the antidromic conduction time in the axon of that motoneurone. Measurement of the conduction distance enables the conduction velocity to be calculated. For example it was 61, 92 and 98 m/sec for the records illustrated in Fig. 1 *C*, *G* and *K* respectively, and 51, 80 and 83 m/sec for the records of Fig. 2 *C*, *G* and *K* respectively. The slower conduction

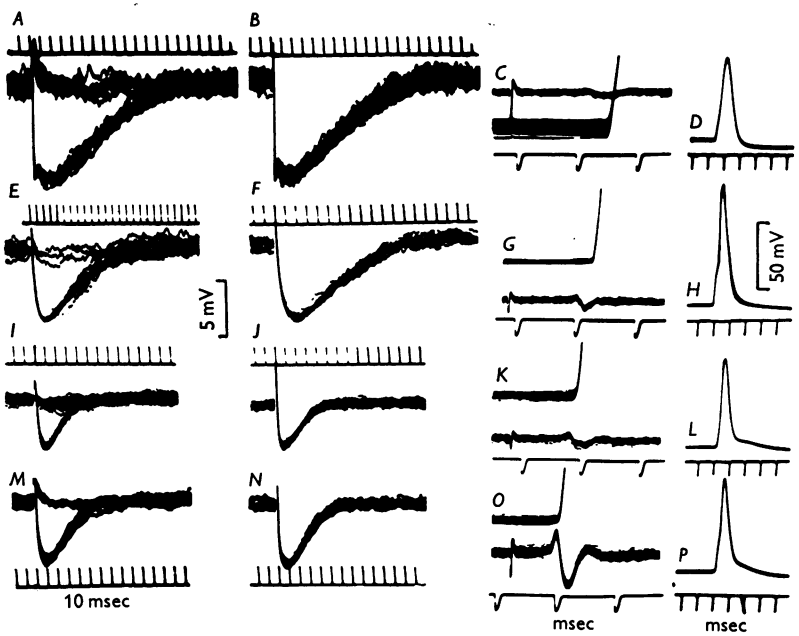

Fig. 3. A series of responses as in Fig. 1, but for four elbow extensor motoneurones; *E–H* supplies anconeus muscle, *A–D*, *I–L* and *M–P* supply respectively the caput mediale, the caput laterale and the caput longum of triceps brachii.

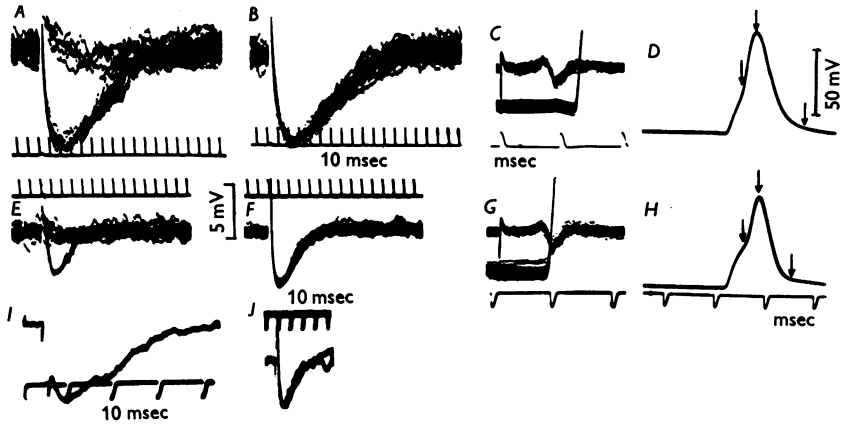

Fig. 4. As in Fig. 1, but *A–D* and *E–H* are both for motoneurones supplying caput mediale of triceps brachii, the former showing a much longer after-hyperpolarization than the latter. *I* and *J* show after-hyperpolarization produced when an oculomotor neurone supplying rectus superior muscle was invaded by an antidromic impulse, *I* being taken at much faster speed than *J*. Amplification for *I*, *J* as for *A*, *B*; single trace in *I* and three superimposed traces in *J*.

velocity for the whole population of soleus motor nerve fibres is evident when the combined spike potential of Fig. 2 *D* is compared with Fig. 2 *H* and *L*.

There has in general been a significant correlation between the duration of the after-hyperpolarization of a motoneurone and the conduction velocity along its axon. For example, in Fig. 5 *A* the long durations of after-hyperpolarizations of soleus motoneurones could be correlated with the long durations calculated for the conduction time along 1 m of axon (cf. inset traces). On the whole both these durations were briefer for the gastrocnemius motoneurones. A straight line may be drawn as in Fig. 5 *A* to express this correlation. It should, however, be pointed out that a direct proportionality

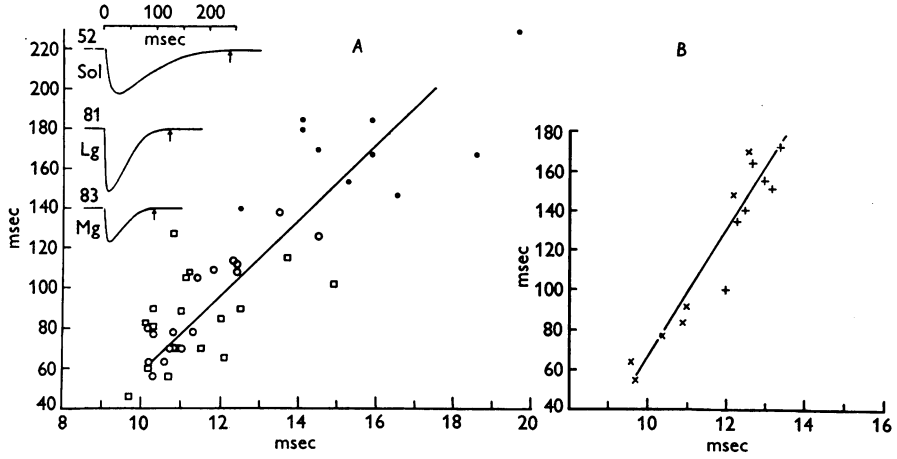

Fig. 5. (*A*) Plotting for the whole series of ankle extensor motoneurones the durations of the after-hyperpolarization (ordinates) against the times required for conduction along 1 m of the corresponding motor axons (abscissae). The inset curves are traces from Fig. 2 *B*, *F* and *J* respectively and the arrows mark the points to which measurements were made in assessing the durations of the after-hyperpolarizations. The numbers above the beginnings of each trace give the respective conduction velocities of the motor axons in metres per second. The points belonging to the three types of motoneurones are indicated by the symbols: Sol, ● = soleus; Lg, ○ = lateral gastrocnemius; Mg, □ = medial gastrocnemius. (*B*) As *A*, but for +, plantaris and × flexor digitorum longus motoneurones.

was not thereby demonstrated, because the line did not pass through the zero co-ordinates. Similar graphical representation for the extensors of the knee (Fig. 6 *A*) and the elbow (Fig. 6 *B*) revealed that the points lay about straight lines having co-ordinates almost identical with those of Fig. 5 *A*. Both durations tended to be long for the motoneurones of the slow-red muscle, crureus, but there was more overlap between crureus on the one hand and the vasti and rectus femoris on the other than occurred with soleus and gastrocnemius. With the motoneurones of the elbow extensors (Fig. 6 *B*) about one third of those supplying the slow-red caput mediale were interspersed with the

motoneurones of capita laterale and longum. Otherwise there was a separation almost as complete as with the ankle extensors (Fig. 5 *A*). The four motoneurones belonging to the slow-red anconeus muscle lay with the main group of caput mediale. Fig. 4 gives examples of the slow (*A–D*) and the fast (*E–H*) types of caput mediale motoneurones from the same preparation. Usually the caput mediale muscle is supplied by two nerves. Each of these nerves contains an admixture of axons from fast and slow motoneurones.

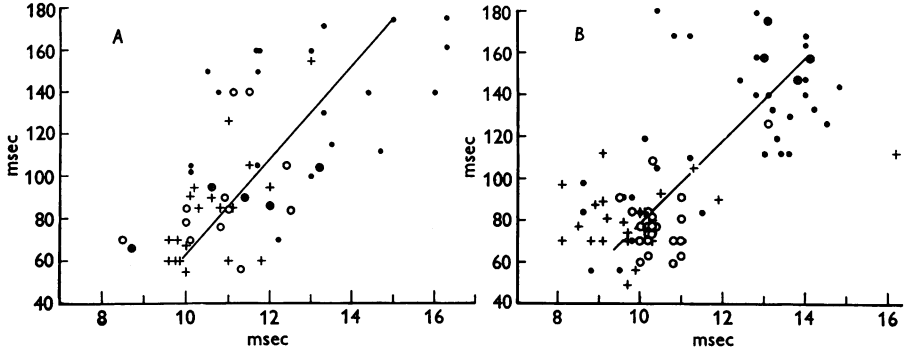

Fig. 6. (*A*) Plotting as in Fig. 5 for the whole series of three extensor motoneurones. ● = crureus; + = rectus femoris; ○ = vasti lateralis and medialis; ⊕ = rectus and vastus, which were not separated in one experiment. (*B*) Elbow extensor motoneurones: ● = caput mediale; ○ = caput laterale and + caput longum of triceps brachii; ⊕ = anconeus.

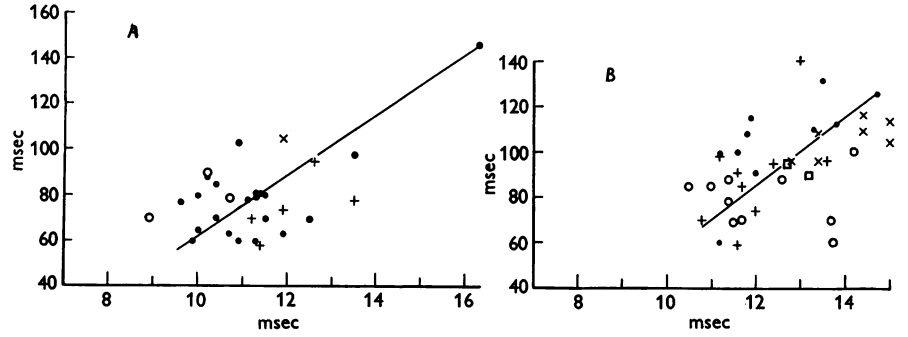

Fig. 7. (*A*) Knee flexor motoneurones and other components of the hamstring group. ● = biceps posterior and semitendinosus; ○ = biceps anterior; + = gracilis; × = semimembranosus. (*B*) Pretibial flexors. ● = extensor digitorum longus; ○ = tibialis anticus; + = peroneus longus; × = extensor digitorum brevis; □ = peroneus brevis.

In general, the motoneurones supplying flexor muscles exhibited durations of after-hyperpolarization and conduction time which were comparable with those of motoneurones belonging to fast-pale extensor muscles. However, there was a considerable range in the population plotted in Fig. 7 *A*, *B*, and some of these flexor motoneurones had co-ordinates comparable with those of

the slow extensor motoneurones. Again the correlation between the two durations can be approximately expressed by straight lines (Fig. 7 *A*, *B*), which, however, had less steep slopes than the lines drawn for extensor motoneurones.

Finally, in Fig. 5 *B* are plotted the durations for motoneurones supplying muscles importantly concerned in plantar flexion of the toes. Functionally these muscles are extensors and the line expressing the correlation between the two durations had a slope even steeper than for the other extensors. It is of interest that plantaris motoneurones tended to be slow while those supplying flexor digitorum longus tended to be fast.

The slow conduction velocity for the motor nerve fibres to soleus can be correlated with their smaller diameter. The soleus alpha motor fibres have a mean diameter that is about 78% of that obtaining for gastrocnemius alpha motor fibres (Eccles & Sherrington, 1930); a relationship which is also approximately indicated by the measurements of Hagbarth & Wohlfart (1952). The ratio of the respective mean conduction velocities (calculated as reciprocals of the conduction times for the points plotted in Fig. 5 *A*) was about 72% for soleus with respect to gastrocnemius. Thus these observations are in approximate agreement with the direct proportionality that has been established between axon diameter and conduction velocity of myelinated nerve fibres (Hursh, 1939; Tasaki, Ishii & Ito, 1943; Rushton, 1951; Tasaki, 1953). The diameters of the motor axons supplying the slow-red and the fast-pale components of other extensor groups of muscles have not been measured, but the conduction times shown in Fig. 6 *A*, *B* indicate that the slow-red muscles tend to be supplied by smaller axons than the fast-pale muscles.

Contraction times of motor units of fast and slow muscles

In this investigation it is essential to adopt the rigorous precautions described under Methods in order to ensure that the contractions of all the fibres of a muscle are being observed under virtually uniform isometric conditions. As an additional check of this prescribed uniformity the whole range of contractions of a muscle, from a few motor units to maximum, has often been recorded at two initial tensions, one about 3–4% of the maximum twitch tension, and one at about 10%. Characteristically the twitches were considerably slower at the high initial tension (cf. Fig. 8 *B*, *C*).

With fast-pale muscles such as lateral and medial gastrocnemius and caput laterale of triceps brachii, small submaximal twitches usually had time courses that either did not differ significantly from maximal twitches, or were a little slower (Fig. 8 *A*, *D*). The small submaximal twitches would be impeded by the frictional resistance of the inactive muscle mass, and hence an explanation is provided for the slower time course. It thus seems likely that the alpha motor axons from the lowest to the highest threshold innervate a population of fast-

pale muscle fibres that is not selectively distributed, at least in so far as contraction time is concerned. The recorded values for the contraction times (onset to summit of the twitch contraction) of the medial and lateral gastrocnemius and of the caput laterale of triceps brachii have been within the range 21–30 msec.

With twitch contractions of soleus muscle there was also virtually the same time course for all sizes of twitches (Fig. 8 *E*), but the contraction times were characteristically much longer (68–74 msec in our three experiments) for this slow-red muscle, which is in good agreement with the value of about 73 msec given by Gordon & Phillips (1953).

In the preceding section it was concluded that slow muscles are supplied by smaller alpha motor fibres than are fast muscles, and, furthermore, that the small motor fibres innervating slowly contracting motor units arise from motoneurones characterized by long after-hyperpolarizations (cf. Figs. 5 *A*, 6). Since the caput mediale of triceps brachii is innervated by slow and fast types of motoneurones (cf. Figs. 4, 6 *B*), it is of interest to see whether, correspondingly, this muscle is composed of an admixture of slow and fast contracting motor units. As shown in Figs. 8 *B*, 9 *A*, very weak submaximal contractions were relatively fast, and with strengthening stimulation much slower contracting motor units were added, the contraction time lengthening from 30·5 to 59 msec and the time from onset to half decay from 85 to 120 msec. The general time courses of the stronger contractions in Fig. 8 *B* indicate an admixture of slow and fast contracting units, closely resembling in this respect the isometric twitches of tibialis anterior (Gordon & Phillips, 1953). With the higher initial tension of Fig. 8 *C* there was the same lengthening of contraction times as motor units with higher threshold axons were brought into contraction. This lengthening is further illustrated by the × points in Fig. 9 *A*, where the time to half decay is seen not to be further lengthened with twitches above one third of maximum. In contrast with the caput laterale component of this same triceps brachii the smaller twitches were a little slower than the larger (Figs. 8 *A*, 9 *B*), an effect that may be due to mechanical distortion as suggested above. One of the four experiments with caput mediale was exceptional in that all sizes of twitches had virtually the same slow time course, just as occurred with soleus and crureus (Fig. 8 *E*, *F*). Unfortunately intracellular recording from the motoneurones was not attempted in the same experiment as the mechanical recording, so it is not known if in this case the caput mediale was supplied in part by fast motoneurones which would be innervating slowly contracting muscle fibres. As shown in Fig. 6 *A*, some crureus motoneurones were of the fast type, and correspondingly there was evidence in one experiment, but not in Fig. 8 *F*, that the lowest threshold motor axons innervated fast contracting motor units.

A partial exception to the correlation of motoneurone type with contraction

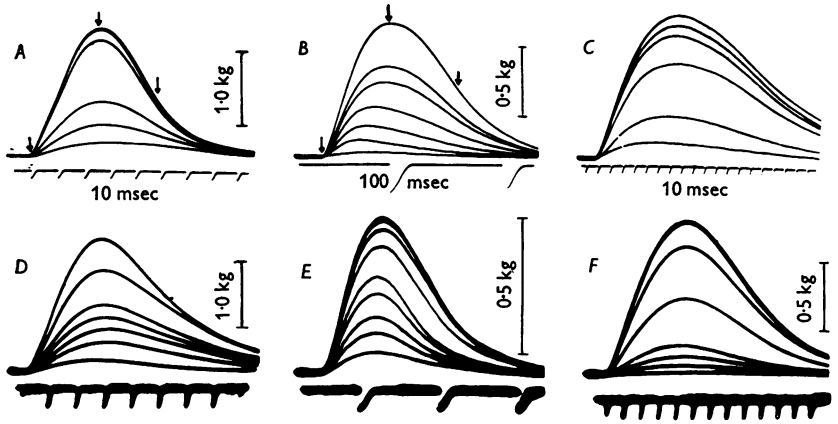

Fig. 8. Isometric twitch contractions produced by varying degrees of submaximal stimulation as well as by maximal stimulation of the motor nerve. *A* is for caput laterale and *B*, *C* for the caput mediale of the same triceps brachii; the initial tensions of *A*, *B* and *C* are 63, 33 and 246 g respectively. *D*, *E* and *F* show similar series for medial gastrocnemius, soleus and crureus muscles in another experiment. The temperature of the paraffin pool surrounding the muscle was 36° C for *A* and *C* and 37·3° C for *B*. Tension and time scales are shown for each series.

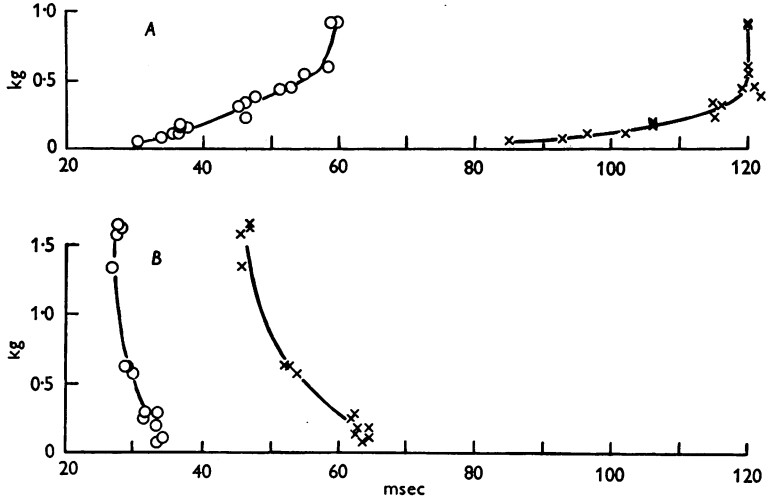

Fig. 9. (*A*) Plotting of contraction tension against the contraction time and the time from onset to half decay for the muscle twitches illustrated by the superimposed contractions in Fig. 8*B*. (*B*) Similar plotting for muscle twitches of Fig. 8*A*. However, the plotted measurements are for individually recorded contractions, not the superimposed series of Fig. 8. The arrows in Fig. 8 show the points for measurement of maximum twitches, the contraction line being measured between the first two arrows and the line to half decay between the first and third arrows.

time of its motor unit was provided by plantaris, a muscle which is innervated by motoneurones that usually had an after-hyperpolarization about 160 msec in duration (Fig. 5 *B*), yet it had a contraction time which was as brief as 24–27 msec in two experiments. In another it was longer (27–38 msec) though still much faster than the contractions of other muscles such as soleus and crureus, that are innervated by motoneurones with comparably long after-hyperpolarizations.

In summary it can be stated that there is good evidence that motoneurones of the 'fast' type innervate motor units having a fast contraction time, and correspondingly for motoneurones of the 'slow' type. This correspondence between motoneurone type and motor unit type seems to occur even with muscles such as the caput mediale which is supplied by an admixture of 'fast' and 'slow' motoneurones. However, such a detailed correspondence could be established only by recording the contractions of the individual motor units (cf. Gordon & Phillips, 1953) supplied by the motoneurones whose after-hyperpolarizations were also recorded intracellularly.

DISCUSSION

The criterion of axon diameter allows the results of our experiments to be correlated with those of Granit *et al.* (1956, 1957), who have shown that alpha motoneurones with small axons (as revealed by the relatively small size of the spike potential recorded monophasically in a ventral root filament) belong to the tonically responding class, whereas those with large axons are specialized to give phasic responses. Thus it may be concluded that the tonic motoneurones have long after-hyperpolarizations and supply as a rule the slow-red type of muscle, and that the phasic motoneurones have brief after-hyperpolarizations and supply usually the fast-pale type of muscle. Some slow-red muscles such as crureus and especially caput mediale of triceps brachii often contain a significant proportion of motor units which are innervated by relatively large nerve fibres and which have fast contraction times (cf. Figs. 8 *B*, *C*; 9 *A*). The motoneurones belonging to these large motor nerve fibres have relatively brief after-hyperpolarizations (cf. Figs. 4 *E–G*, 6).

Granit *et al.* (1957) found that the application of a stretch to gastrocnemius muscle alone was able to cause a discharge of tonic motoneurones, and hence concluded that tonic motoneurones did not exclusively innervate the slow-red soleus muscle. Since it has now been found that impulses from the stretch afferents of the gastrocnemius muscle exert a strong monosynaptic excitatory action on soleus motoneurones (Eccles *et al.* 1957*b*), the motoneurones tonically responding to stretch of the gastrocnemius might well be innervating the soleus muscle. However, in Fig. 5 *A* some gastrocnemius motoneurones are lying transitionally between the main soleus and gastrocnemius groups, and

could be examples of the tonically responding gastrocnemius motoneurones postulated by Granit *et al.* (1957).

It has been postulated that the after-hyperpolarization of a motoneurone is responsible for determining the frequency at which it discharges when subjected to a continuous synaptic bombardment (cf. Eccles, 1936, 1953, pp. 174–8; Pitts, 1943). This postulate is supported by the present evidence that the slowly discharging tonic motoneurones (usually 10–20 and never above 40/sec) have a much longer after-hyperpolarization than the rapidly discharging (usually 30–60/sec) phasic motoneurones. The tonic motoneurones innervate slowly contracting motor units which would give a fused tetanus of almost maximum size at the relatively slow frequency of discharge of these motoneurones. On the other hand, the phasic motoneurones with their relatively high frequencies of discharge are matched to the relatively fast frequency required to give optimal tetanic fusion in the contractions of the fast-pale muscles which they innervate. Finally, the extremely fast-contracting extrinsic eye muscles require very high frequency (up to 200/sec) for optimal tetanic fusion (Denny-Brown, 1929*b*; Cooper & Eccles, 1930), and correspondingly the frequency discharge of the motoneurones is as high as 170/sec (Reid, 1949) and the after-hyperpolarization (Fig. 4 *I*, *J*) and associated depression (Lorente de Nó & Graham, 1938) of these motoneurones are as brief as 40 msec.

It may now be asked: How does it come about that there is such an appropriate matching of the frequency characteristic of motoneurones with the contraction times of their motor units? Any serious mismatching would result in inefficiency, particularly in relationship to the frequency-modulation of reflex contraction tension (Adrian & Bronk, 1929). For example, a high frequency discharge to slow motor units would merely serve to fatigue the muscle for no effective return in a higher contraction tension, while the low frequency discharge from a tonic motoneurone to a fast motor unit would be inefficient in fusing the individual twitch responses to give an effective tetanic contraction. All limb muscles are equally slow in the new-born kitten (Denny-Brown, 1929*b*; cf. Meyer, 1875), and differentiation into slow and fast types of muscle occurs during the third to sixth weeks. In this connexion it would be of interest to discover the time of the differentiation of the corresponding motoneurones into slow and fast types.

SUMMARY

1. Over 260 alpha motoneurones belonging to twenty-one different muscles have been stimulated antidromically by exciting impulses in their motor axons and have been recorded from intracellularly. Special investigation has been made of three synergic groups of motoneurones that innervate slow-red and fast-pale extensor muscles.

2. The antidromic spike potentials of the 'slow' motoneurones have differed significantly from those of the 'fast' only in having a slower decline, which merges more gradually into the after-depolarization.

3. The great majority of motoneurones supplying slow muscles have been characterized by a much more prolonged after-hyperpolarization. All the motoneurones to soleus and anconeus, and most of those to the crureus and the caput mediale of the triceps brachii, had after-hyperpolarizations in excess of 130 msec, whereas almost all the motoneurones supplying the fast extensor muscles and the flexor muscles had after-hyperpolarizations in the range of 50–110 msec. With oculomotor neurones the after-hyperpolarization was only about 40 msec in duration.

4. The isometric twitch contractions of caput mediale gave evidence that the low threshold motor axons from motoneurones with brief after-hyperpolarizations supplied motor units of the fast-contracting type.

5. In all synergic groups of motoneurones the after-hyperpolarizations were found to bear an inverse relationship to the conduction velocity of the motor axons. Thus it is inferred that slow motoneurones have axons of small diameter.

6. This relationship indicates that the motoneurones supplying slow-red muscles are the tonic alpha motoneurones defined by Granit, while those supplying fast-pale muscles form the phasic alpha group.

7. It is suggested that, since it seems likely that the frequency of repetitive discharge from motoneurones is controlled by the after-hyperpolarization, durations of the after-hyperpolarizations are matched to the twitch durations of muscles, so that the individual motoneurones discharge at frequencies appropriate to the contraction responses of their own motor units.

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