MOTOR INNERVATION OF SKELETAL MUSCLE: MULTIPLE INNERVATION OF INDIVIDUAL MUSCLE FIBRES AND MOTOR UNIT FUNCTION*

BY CARLTON C. HUNT† AND STEPHEN W. KUFFLER

From the Wilmer Institute, The Johns Hopkins Hospital and University, Baltimore, Maryland, U.S.A.

(Received 7 May 1954)

Large diameter efferent nerve fibres to skeletal muscle in the cat and frog are concerned with a similar function, namely the excitation of muscle fibres which produce rapid tension development. Such a 'twitch' system, which appears to be the only mechanism for the production of tension in mammalian limb muscles, does not normally operate on a graded basis at the unit level. Each muscle fibre contracts in an all-or-none fashion. The sequence of events in excitation is the following: the motor nerve impulse evokes a local potential change at the nerve muscle junction, the end-plate potential, which does not activate the contractile mechanism itself but initiates a propagated muscle impulse. The latter spreads by conduction over the length of the fibre and causes, in a manner yet unknown, activation of the contractile mechanism. Each large motor nerve fibre and the muscle fibres it innervates comprise a motor unit. There seems, at first sight, little merit in the innervation of 'twitch' muscle fibres by more than one motor nerve terminal, for a muscle impulse initiated at one site would spread by conduction to excite the whole fibre. However, studies have shown that muscle fibres in the frog's sartorius are innervated in two major zones and most of the fibres receive motor endings at at least two regions along their length (Katz & Kuffler, 1941). In this case a multiply-innervated muscle fibre may derive its several end-plates from the same motor nerve fibre. The possibility also exists that a muscle fibre may receive end-plates from more than one nerve fibre, i.e. polyneuronal innervation. Indeed, this is suggested by certain studies on plurisegmental innervation in mammals (Agduhr, 1919) and in the frog (Cattell, 1928) in which,

judging from histological studies and tension responses, some muscle fibres may be activated by nerve fibres emerging in different ventral roots. Recently, Jarcho, Eyzaguirre, Berman & Lilienthal (1952) concluded that some muscle fibres of the gracilis muscle in the rat were multiply innervated.

In contrast to the physiological evidence mentioned above, most histological studies have failed to demonstrate polyneuronal innervation of muscle fibres (see reviews of Hinsey, 1934 and Tiegs, 1953). The difficulties of viewing the entire length of muscle fibres make this negative evidence inconclusive. The case for plurisegmental innervation based on tension measurement has also been questioned (Fulton, 1926).

Multiple motor innervation of other types of muscle, not under consideration in this study, has been clearly demonstrated. For example, the 'slow' skeletal muscle fibres in the frog, which possess properties distinct from the 'twitch' fibres and are innervated by small diameter efferent fibres, give evidence of extensive polyneuronal innervation (Kuffler & Vaughan Williams, 1953). Here the multiple endings are of obvious utility since the muscle fibres concerned show only local non-propagated contractions about the nerve endings. Variation in number of nerve endings activated along the length of an individual muscle fibre results in gradation of contraction. A similar multiple innervation and physiological use of local contraction occurs in crustacean muscle (van Harreveld, 1939; Wiersma, 1941; Fatt & Katz, 1953). Another example of multiple innervation may be found in the mammalian muscle spindle where more than one efferent nerve fibre of small diameter may terminate on the same intrafusal muscle fibre (Barker, 1948; Hunt & Kuffler, 1951).

The present study re-examines the question of multiple innervation in 'twitch' muscle fibres in the cat and frog. It will be shown that muscle fibres of this type, in both species, frequently receive multiple motor endings derived from one or several nerve fibres. The functional significance of multiple innervation in 'twitch' systems will be discussed.

METHOD

The muscles studied in the cat were soleus, gastrocnemius, flexor digitorum longus and cricothyroideus. In the case of limb muscles the leg was fixed by steel pins to a rigid base which also afforded support for a movable strain gauge (Statham). The signal from the latter, after suitable DC amplification, was displayed on a cathode-ray tube. Roots and muscle nerves were freed for stimulation and kept under pools of paraffin oil maintained at 37–39° C. Tension was recorded in a rigidly isometric system, initial tensions being selected which gave optimal tension responses on nerve stimulation.

Tension in frog muscles was recorded by a myograph employing a transducer tube (R.C.A. 5734). In the frog the sartorius, adductor longus and iliofibularis were studied.

Intracellular potentials from individual muscle fibres were recorded by glass microelectrodes filled with 3 M-KCl and connected by Ag-AgCl electrodes to an input circuit similar to that described by Nastuk & Hodgkin (1950).

<div align="center">RESULTS</div>

<div align="center">*Multiple motor innervation in the cat*</div>

Tension overlap. When two portions of the ventral root outflow to a muscle are stimulated separately the sum of the tensions developed in the separate contractions may be considerably in excess of the tension produced when both portions are stimulated simultaneously. Such tension overlap may be demonstrated most readily in a preparation in which the ventral root outflow is divided approximately equally between two adjacent roots. Fig. 1 illustrates such tension overlap in the flexor digitorum longus. A single stimulus to root *a* evoked a tension response of 232 g while stimulation of root *b* caused a twitch of 312 g. Thus, the sum of the separate contractions was 544 g. However, when the two roots were stimulated simultaneously (*a*+*b*) the tension developed was only 352 g. The deficit of 192 g could be explained if a certain proportion of the muscle fibres received innervation from both roots.
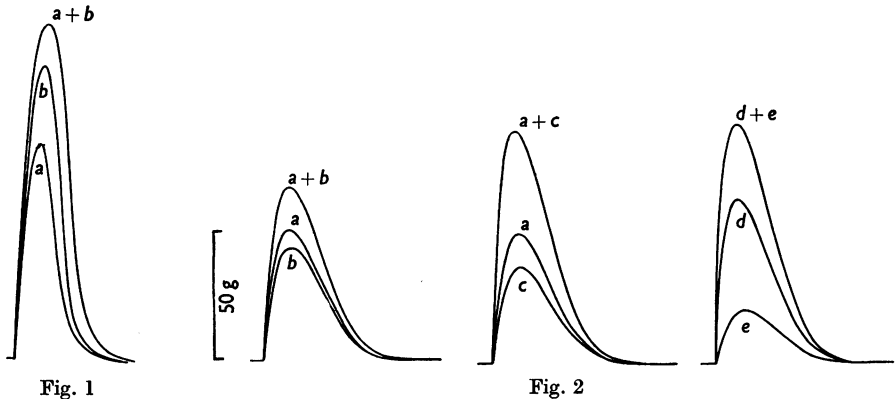

Fig. 1   Fig. 2

Fig. 1. Isometric twitch tension responses of flexor digitorum longus (cat) to stimulation of two ventral roots, *a* and *b*, separately and together. Time to peak tension, 20 msec.

Fig. 2. Isometric twitch tension responses of soleus (cat) to stimulation of five subdivisions (*a* to *e*) of a ventral root. Note tension overlap in *a*+*b* but not in *a*+*c* and *d*+*e*. Time to peak tension, 40 msec.

In some preparations most of the motor fibres to a muscle may emerge in one ventral root. Tension overlap may still be demonstrated in these circumstances as is shown in Fig. 2, taken from an experiment on soleus. The root was separated into five subdivisions (*a* to *e*) which could be stimulated alone or in various combinations. Subdivisions *a* and *b* revealed considerable tension overlap while certain other pairs showed none (*a* and *c*, *d* and *e*). Again, the most likely explanation is that *a* and *b* contained nerve fibres which innervated some muscle fibres in common while the other combinations did not.

The extent of tension overlap varied in different preparations depending in part on the particular distribution of nerve fibres to the muscle in different

roots. Table 1 summarizes the results on soleus and flexor digitorum longus. Overlap has been estimated in the following manner: twitch tensions following separate stimulation of two roots, *a* and *b*, were determined. Subsequently the tension developed by a stimulus to both roots simultaneously (*a b* together) was measured. When the root giving the smaller tension (*a*) was stimulated, together with root *b*, *a* sometimes failed to add the amount of tension it produced alone. This deficit, expressed as a percentage of the tension developed by *a* alone, provides a measure of overlap in muscle fibres innervated by *a*. By this measure overlap as great as 60–90 % was often observed. It will be shown below that overlap of this magnitude does not result from a lack of tension addition due to mechanical factors but indicates that a large proportion of muscle fibres receive polyneuronal innervation.

TABLE 1. Tension overlap on ventral root stimulation (cat)

Muscle	Twitch tension (g)			% of fibres innervated by root *a* which are overlapped by root *b*
	Root *a*	Root *b*	Roots *a b* together	
Soleus	70	190	220	57
	70	210	300	—
	105	410	450	62
	67	121	147	61
	39	60	78	54
	43	52	77	42
	95	105	185	16
	6	54	55	—
	13	100	110	—
	58	70	90	66
	62	83	102	69
	0	95	—	—
	1	76	—	—
Flex. dig. longus	232	312	352	82
	230	310	335	89
	165	270	325	67
	250	300	360	76

In the past, tension overlap has been attributed by some authors to the following mechanical factors: (i) shortening of one portion of a muscle causes a reduction of the tension produced by the remainder, or (ii) the angle at which two muscle fractions are inserted into a common tendon prevents the full development of tension during combined excitation of the two portions. The extent to which such mechanical factors enter into the production of tension overlap in the present experiments was tested in the following manner: electrodes were fitted to the separate nerves to the two heads of the gastrocnemius and tension was recorded in the common tendon with a minimum of external shortening. Twitch tensions were recorded following stimulation of the nerves to the two heads separately and then together. Since muscle fibres of one head are inserted into the tendon at a different angle from those of the other head, and since the efferent innervation to the two heads is completely

separate, this experiment should display to a maximal extent the overlap which may result from mechanical cause. Fig. 3 shows that no appreciable overlap need occur in these circumstances (see also Fig. 2, $a+c, d+e$). The sum of the tensions produced by the two heads in separate contraction was equal to the tension developed by simultaneous contraction of the whole muscle. The results of studies on tension overlap in a muscle when two separate roots are stimulated provide adequate evidence for polyneuronal innervation. Corroborative evidence obtained by other methods will be presented below.
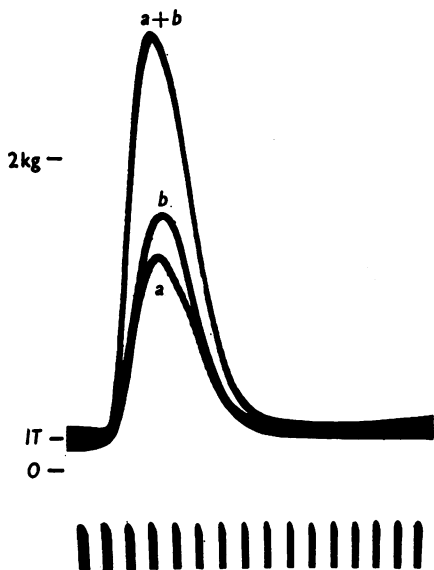

Fig. 3   Fig. 4

Fig. 3. Isometric twitch tension responses of triceps surae (cat). a: stimulation of medial gastrocnemius nerve; b: stimulation of lateral gastrocnemius and soleus nerve; $a+b$ simultaneous stimulation of both nerves. Note practically complete summation of twitch tensions. Inclusion of slower soleus delays twitch peak in b. Time, 10 msec.
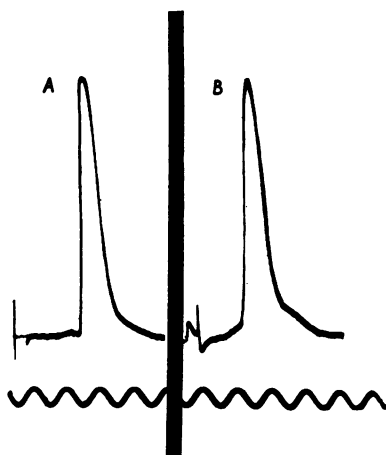
Fig. 4. Intracellular recording in an individual muscle fibre of cricothyroideus (cat). Separate stimulations of nerve supply from superior laryngeal nerve (A) and from pharyngeal plexus (B) set up impulses in the same muscle fibre. Resting potential about 80 mV, total action potential 110 mV. Time, 1000 c/s.

Intracellular recording. Polyneuronal innervation could be clearly shown in single muscle fibres of cricothyroideus. This muscle receives motor innervation from two distinct nerves, arising from the superior laryngeal nerve and from the pharyngeal plexus. After impalement of a single muscle fibre the two nerve supplies were stimulated in succession. The majority of muscle fibres examined showed a propagated response following a volley in each nerve. Fig. 4 displays responses of a representative fibre to stimulation of first one

and then the other of the two nerves. This provides conclusive evidence of polyneuronal innervation.

The end-plates from separate axons appear to lie in close proximity on the muscle fibres of cricothyroideus as shown by the following experiments. When external leads were used for recording from the curarized muscle, two stimuli to the *combined* nerve supply at appropriate intervals caused the well-known facilitation of the second response (Bremer, 1927). This facilitation is known to be due to summation of end-plate potentials (Eccles, Katz & Kuffler, 1941), the second stimulus firing those muscle fibres already subject to subthreshold depolarization by the first. A similar facilitation was observed with stimulation to the *separate* nerve branches, i.e. first one and several msec later the other of the two nerves to cricothyroideus were excited. Many end-plates from the two nerve branches must therefore lie in close proximity to effect spatial and temporal summation of end-plate potentials.

Multiple motor innervation in the frog

Tension overlap. Tension overlap may be easily demonstrated in twitch fibres of the sartorius. The nerve to this parallel-fibred muscle usually divides, several mm before entering the muscle, into a pelvic and tibial branch. These branches can be cut and placed on electrodes for stimulation together or separately. In the experiment illustrated by Fig. 5 stimulation of the tibial branch (*a*) caused a twitch tension of 10·4 g while excitation of the pelvic branch (*b*) produced 12·2 g. Usually the ratio of tensions is more in favour of the pelvic branch. When both branches were excited together (*a* + *b*) the resultant twitch tension was 12·75 g., i.e. only 5 % greater than after stimulation of the pelvic branch alone. In accord with the previous demonstration of potential 'occlusion' in frog sartorius (Katz & Kuffler, 1941), the observed tension overlap indicates that practically all the muscle fibres innervated by the smaller tibial branch are also innervated by the pelvic nerve branch. Such multiple innervation could result from innervation of individual muscle fibres by branches of the same axons. However, tension overlap in sartorius was also observed with stimulation, separately and together, of ventral roots 8 and 9 indicating, as in the cat, that polyneuronal innervation is an important factor (see also Cattell, 1928).

The nerve supply to adductor longus can also be separated into a pelvic and tibial portion but the conditions of branching make this a more difficult procedure than in sartorius. As judged by tension overlap, the pelvic nerve branch has been found, on occasion, to innervate virtually all the fibres in the muscle, including those also innervated by the tibial branch. Stimulation of the latter branch may produce a twitch which is 50–80 % of that developed following excitation of the entire nerve supply.

In the iliofibularis about a third to a half of the twitch muscle fibres,

principally those located near the site of nerve entry, are supplied by ventral root 10 while VR 9 may innervate nearly all the twitch fibres in the muscle. As a consequence VR 10 frequently adds little tension when stimulated together with the larger outflow from VR 9. This overlap is illustrated in Fig. 6 and is exclusively due to polyneuronal innervation.
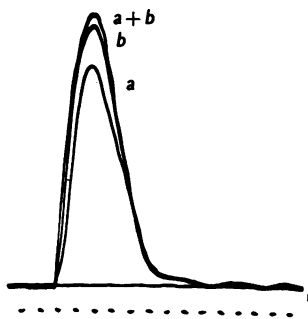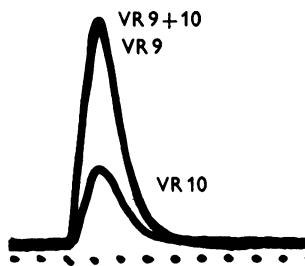

Fig. 5.

Fig. 6.

Fig. 5. Tension records from sartorius (frog) at an initial tension of 2 g at 26° C. Single stimulus to cut tibial nerve branch (*a*) caused 10·4 g. twitch tension, while pelvic branch (*b*) excitation resulted in 12·2 g. twitch. *a* + *b* was 12·75 g, i.e. about 95 % tension overlap occurred. Time, 10 msec.

Fig. 6. Iliofibularis (frog), at initial tension of 2 g at 25° C. Stimulation of VR 10 caused a 7·65 g and VR 9 a 21 g twitch. When VR 10 was stimulated with VR 9 it caused no appreciable tension increment over VR 9 alone. Note that in the larger tension record two sweeps are superimposed. Time, 20 msec.

Axon branching and axon 'reflex'. One of the corollaries of multiple innervation is the well-known extensive branching of motor axons. Nerve fibres reaching sartorius and adductor longus divide to innervate widely separate portions of the muscle. One of the nerve branches to a muscle may be cut and its central end stimulated, initiating impulses which spread antidromically to the nearest bifurcation and thence peripherally into the muscle. In this manner an 'axon reflex' is set up.

In Fig. 7 the nerve branch to the tibial portion of adductor longus was cut and electrodes were placed on the muscle nerve central to the bifurcation (*a*), on the central end of the cut tibial branch (*b*) and on the peripheral end of the cut tibial branch (*c*). A stimulus at *a* evoked a twitch of 10 g, while at *b* it caused one of 4 g. It may be inferred that about 40 % of the nerve fibres which innervate the pelvic portion also send branches into the tibial end of the muscle. Stimulation of *c* caused a twitch of 7·5 g and when stimulated together with *a* evoked a response of 10·8 g, thus demonstrating extensive innervation overlap between the pelvic and tibial branches (not illustrated). Similar experiments on sartorius also proved axon division into the pelvic and tibial nerve branches. Cross excitation between nerve fibres at cut ends (Hering's

phenomenon) seems excluded since (1) the effect of antidromic volleys in the cut branch was quite constant even during tetanic stimulation, and (2) crushing at different points of the main nerve trunk did not introduce fluctuations in response until the injury was placed within 1–2 mm of the place of branching. The latter also indicates that the division of motor axons to these frog muscles occurs near the macroscopically visible site of nerve bifurcation. Excitation by stimulus spread to nerve regions at some distance from the stimulating electrodes was carefully avoided when axon 'reflexes' were tested. The central portions of cut nerves (e.g. *b* in Fig. 7) were lifted into paraffin oil while the rest of the preparation, including the nerve bifurcation, remained in Ringer solution, thus limiting exciting current flow by shunting the submerged tissues.
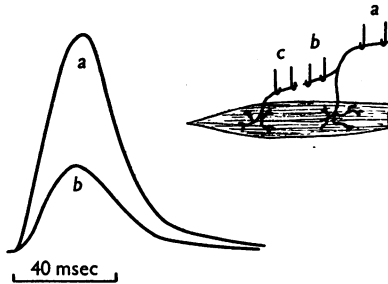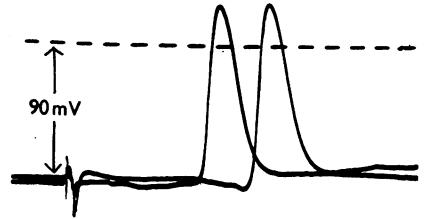

Fig. 7   Fig. 8

Fig. 7. Axon 'reflex'. Tension recorded from adductor longus (frog), at initial tension of 2·0 g at 25° C. Tibial branch of nerve cut as indicated in scheme. Stimulation of central end of cut nerve (*b*) set up a twitch of 4 g, while (*a*) caused one of 10 g. Stimulation of branch *c* set up a tension of 7·5 g (not illustrated).

Fig. 8. Intracellular recording from one muscle fibre of the sartorius (frog). Separate stimulation of pelvic and tibial nerve branch set up a propagated muscle impulse in the same fibre. Note different latent periods. Two sweep exposures superimposed. Excitation of both branches together caused only the impulse with the shorter latency. Resting potential, 90 mV. Time, 1 msec.

Intracellular recording. Capillary electrodes were inserted into individual muscle fibres of various muscles and portions of the nerve supply were stimulated. Multiple innervation as indicated by tension overlap experiments was easily confirmed. An example is shown in Fig. 8 in which muscle impulses in one fibre of the sartorius were obtained by separate excitation of the pelvic and tibial nerve branches. The latent periods were characteristically different since the junctions on the muscle fibre are widely separated and therefore conduction distance to the recording electrode differs. If both nerve branches were excited simultaneously only the impulse of shorter latency, starting at the nearest end-plate, was recorded. The impulse from the more distal end-plates was apparently 'extinguished' by collision.

DISCUSSION

Muscle fibres in which the contractile mechanism is activated by propagated muscle impulses are frequently innervated by multiple motor endings. Such 'twitch' muscle fibres, in the frog and cat, may derive multiple endings from one or from several nerve fibres. The extent of multiple innervation is known only approximately. In some muscles the majority of fibres are multiply innervated, e.g. sartorius of frog and cricothyroideus of cat. The amount of polyneuronal innervation in hindlimb muscles of the cat must be considerable for the large tension overlap observed reveals only the amount of occlusion between two samples of root outflow. Within each sample additional overlap must be present. For example, in Fig. 1 about 82% of the muscle fibres innervated by root *a* received additional innervation from root *b*. This provides a minimal estimate of polyneuronal innervation.

Multiple motor endings may influence the rate at which tension is developed by the muscle fibre. If nerve impulses reach terminations synchronously at several points along the muscle fibre, impulses will be initiated and will spread over the length of the fibre in less time than if activity began at only one focus. Since muscle conduction is relatively slow (2–3 m/sec) excitation at multiple points may provide a means for more rapid activation of the contractile system. The very brief latency of contractile activation found by Hill (1951) supports this view.

The number of mammalian muscle fibres innervated by one motoneurone in the cat has been estimated by dividing the total number of muscle fibres by the number of efferent nerve fibres reaching the muscle (Clark, 1931). The tension developed by individual motor units has been calculated in a similar manner from the ratio of the maximal tetanic tension developed by the muscle to the number of efferent fibres (Eccles & Sherrington, 1930; van Harreveld, 1947). These values must be revised on several counts. (1) It has been shown that only two-thirds of the efferent fibres to hindlimb muscles of the cat innervate ordinary muscle fibres; the remaining third, small medullated fibres provide the motor innervation to muscle spindles (Kuffler, Hunt & Quilliam, 1951). (2) A large number of muscle fibres are innervated by more than one nerve fibre. Both these factors indicate that the previous estimates of motor unit size and tension were too small.

The present experiments show that many muscle fibres may receive terminations from several efferent axons. If there is a background of muscle contraction, a motoneurone discharge will excite only those muscle fibres which are not already activated by other efferent neurones. Thus, an increment in contractile response, when a muscle is partly contracted, may involve less than a whole motor unit. Such a gradation would only be operative when motoneurones innervating some muscle fibres in common discharged almost

synchronously; its importance is conjectural and gradation of contraction on this basis is unlikely to play a significant functional role.

The distribution of motor innervation within a number of mammalian muscles was recently studied by Feindel, Hinshaw & Weddell (1952). They found that individual motor axons do not often terminate on contiguous muscle fibres but are distributed more widely. They also noted multiple endplates on single muscle fibres but were unable to trace them to different axons. Although excitation of an individual motor nerve fibre usually causes contraction visible in a strip of muscle it is unlikely that the motor axon innervates exclusively any anatomically distinct group of muscle fibres such as a fasciculus (Feindel *et al.* 1952). Indeed, in certain muscles it can be shown that a motor axon divides to innervate quite separate parts of the muscle. For example, in tenuissimus a motor axon may innervate muscle fibres which may be many centimetres apart (Adrian, 1925; Kuffler *et al.* 1951).

Some observations made on regenerating nerves may have a bearing on the present study of multiple innervation. It was reported by Stookey (1924) that a cut ulnar nerve implanted into a normally innervated biceps of the rabbit may make functional connexion with the muscle. More recently, Sunderland (1952) observed that in man an injured ulnar nerve may regenerate into an intact triceps muscle. These findings then provide instances of 'excessive' innervation of muscle fibres, by adding neuromuscular connexions. It is not known, however, whether entirely new junctions are being formed or whether regenerating nerve fibres grow into existing end-plates.

SUMMARY

1. Large motor nerve fibres in the cat and frog may innervate individual skeletal muscle fibres at two or more places. Such a multiple nerve supply may be derived from one branching nerve fibre or from several (polyneuronal innervation).

2. The evidence for the multiple innervation of single muscle fibres rests on the following observations:

(*a*) Ventral roots in the lumbosacral region of the cat were stimulated individually and together or sometimes the subdivisions of a single root were used. Tension overlap, up to 90 % in the cat and nearly complete in the frog, was frequently obtained indicating that a large number of muscle fibres were multiply innervated.

(*b*) More direct proof of multiple innervation was obtained by the use of intracellular electrodes. Action potentials in a single muscle fibre could be set up by stimulation of separate efferent axons.

(*c*) Axon 'reflexes' have shown that in the frog many motor nerve fibres divide and innervate widely separated regions of a muscle.

3. The relation of multiple innervation to motor unit function is discussed.

REFERENCES

ADRIAN, E. D. (1925). The spread of activity in the tenuissimus muscle of the cat and in other complex muscles. *J. Physiol.* **60**, 301–315.

AGDUHR, E. (1919). Über die plurisegmentelle Innervation der einzelnen quergestreiften Muskelfasern. *Anat. Anz.* **52**, 273–291.

BARKER, D. (1948). The innervation of the muscle-spindle. *Quart. J. micr. Sci.* **89**, 143–186.

BREMER, F. (1927). Sur le mécanisme de la sommation d'influx. *C.R. Soc. Biol., Paris,* **97**, 1179–1184.

CATTELL, McK. (1928). Plurisegmental innervation in the frog. *J. Physiol.* **66**, 431–442.

CLARK, A. D. (1931). Muscle counts of motor units: a study in innervation ratios. *Amer. J. Physiol.* **96**, 296–304.

ECCLES, J. C., KATZ, B. & KUFFLER, S. W. (1941). Nature of the 'end-plate potential' in curarized muscle. *J. Neurophysiol.* **4**, 362–387.

ECCLES, J. C. & SHERRINGTON, C. S. (1930). Numbers and contraction-values of individual motor-units examined in some muscles of the limb. *Proc. Roy. Soc.* B, **106**, 326–357.

FATT, P. & KATZ, B. (1953). Distributed 'end-plate potentials' of crustacean muscle fibres. *J. exp. Biol.* **30**, 433–439.

FEINDEL, W., HINSHAW, J. R. & WEDDELL, G. (1952). The pattern of motor innervation in mammalian striated muscle. *J. Anat., Lond.,* **86**, 35–48.

FULTON, J. F. (1926). *Muscular contraction and the reflex control of movement.* London: Baillière, Tindall and Cox.

VAN HARREVELD, A. (1939). The nerve supply of doubly and triply innervated crayfish muscles related to their function. *J. comp. Neurol.* **70**, 267–284.

VAN HARREVELD, A. (1947). On the force and size of motor units in the rabbit's sartorius muscle. *Amer. J. Physiol.* **151**, 96–106.

HILL, A. V. (1951). The earliest manifestation of the mechanical response of striated muscle. *Proc. Roy. Soc.* B, **138**, 339–348.

HINSEY, J. C. (1934). The innervation of skeletal muscle. *Physiol. Rev.* **14**, 514–585.

HUNT, C. C. & KUFFLER, S. W. (1951). Further study of efferent small-nerve fibres to mammalian muscle spindles. Multiple spindle innervation and activity during contraction. *J. Physiol.* **113**, 283–297.

JARCHO, L. W., EYZAGUIRRE, C., BERMAN, B. & LILIENTHAL, J. L., Jr. (1952). Spread of excitation in skeletal muscle: some factors contributing to the form of the electromyogram. *Amer. J. Physiol.* **168**, 446–457.

KATZ, B. & KUFFLER, S. W. (1941). Multiple motor innervation of the frog's sartorius muscle. *J. Neurophysiol.* **4**, 209–223.

KUFFLER, S. W., HUNT, C. C. & QUILLIAM, J. P. (1951). Function of medullated small-nerve fibres in mammalian ventral roots: efferent muscle spindle innervation. *J. Neurophysiol.* **14**, 29–54.

KUFFLER, S. W. & VAUGHAN WILLIAMS, E. M. (1953). Small-nerve junctional potentials. The distribution of small motor nerves to frog skeletal muscle, and the membrane characteristics of the fibres they innervate. *J. Physiol.* **121**, 289–317.

NASTUK, W. L. & HODGKIN, A. L. (1950). The electrical activity of single muscle fibers. *J. cell. comp. Physiol.* **35**, 39–73.

STOOKEY, B. (1924). An experimental study of hyperneurotization. *Arch. Neurol. Psychiat., Chicago,* **11**, 113–120.

SUNDERLAND, S. (1952). The multiple motor innervation of individual muscle fibres in man. *Acta anat.* **16**, 167–168.

TIEGS, O. W. (1953). Innervation of voluntary muscle. *Physiol. Rev.* **33**, 90–144.

WIERSMA, C. A. G. (1941). The efferent innervation of muscle. *Biol. Symp.* **3**, 259–289.