THE EFFECTS OF
LENGTH AND STIMULUS RATE ON TENSION IN THE
ISOMETRIC CAT SOLEUS MUSCLE

BY P. M. H. RACK AND D. R. WESTBURY

From the Department of Physiology, University of Birmingham,
Birmingham 15

SUMMARY

1. By subdividing ventral roots and supplying stimulating pulses to different groups of motor units in rotation, smooth contractions of soleus could be obtained with low rates of stimulation.

2. Isometric tension was recorded with different rates of stimulation, and at different muscle lengths.

3. Longitudinal histological sections were cut from muscles fixed at different lengths, and sarcomeres were measured. Mean sarcomere lengths in soleus could then be related to the angle at the ankle.

4. At high rates of stimulation the maximum active tension was obtained at a length corresponding to an angle of about 60° at the ankle, and a mean sarcomere length of about 2·8 μ. The isometric tension fell only slightly on shortening the muscle to a length equivalent to 100°, and a mean sarcomere length about 2·3 μ. Further shortening caused a marked fall in tension.

5. There was a reciprocal relationship between stimulus rate and muscle length; when the muscle was long low rates of stimulation gave near maximal tension, whereas at short lengths the maximum tension was reached only when the stimulus rate was very high. It is suggested that stimulating pulses activate the contractile machinery of the muscle more effectively at long than at short muscle lengths.

6. When at low rates of stimulation pulses were distributed among the motor units in rotation to give a smooth contraction, the tension rose higher than during the unfused tetanus that accompanied synchronous stimulation of the same motor units at the same rate. It is suggested that in an unfused tetanus internal movement of the muscle reduces the tension below that developed in a truly isometric state.

7. The rate of rise of tension in an isometric tetanus varied with both muscle length and rate of stimulation. At each stimulus rate there was a

range of lengths in which the isometric tension developed slowly, this was the same length range in which, at that stimulus rate, the length tension curve was steep.

INTRODUCTION

Attempts to study the control of posture and movement in animals have often been impeded by a lack of knowledge of the behaviour of skeletal muscles under physiological conditions. There exists a wealth of information about muscle twitches, and muscle tetani obtained at high rates of stimulation, but in ordinary use muscles are activated in neither of these ways. Muscles take up different lengths, and move through these lengths at varying speeds and with varying levels of activation. Length, velocity and stimulus rate each affect the muscle tension, and these different variables interact in ways that are seldom simple.

In the hope of gaining a better understanding of the mechanics of mammalian muscles, we chose to study a single muscle, the cat soleus, under a wide variety of conditions. In particular, we have developed a method of stimulating different groups of motor units in rotation to obtain a smooth contraction of the whole muscle with stimulus rates that would otherwise have given an unfused tetanus. This method has led to some new findings.

This paper describes the tension during isometric contractions at various muscle lengths and stimulus rates. Lengthening and shortening movements will be described in later papers. The effect of length on soleus tension has been studied previously by Granit (1958), Matthews (1959) and Buller & Lewis (1963). The effects of different stimulus rates have been studied by Cooper & Eccles (1930) and Matthews (1959).

METHODS

Physiological studies

Sixteen cats were used, weighing between 1·7 and 3·8 kg. The animals were anaesthetized with intraperitoneal pentobarbitone sodium (Nembutal, Abbott Laboratories), and anaesthesia was maintained with further intravenous pentobarbitone as necessary.

Dissection. Soleus was exposed by the removal of gastrocnemius and plantaris, it was then dissected free from the surrounding structures, leaving it attached by only its origin, blood supply and nerve supply. Other muscles of the leg and hip were denervated. A lumbar laminectomy was performed and the sacral and lower lumbar nerve roots were detached from the spinal cord.

Before detaching the tendon of soleus from its insertion, a thread was tied round the tendon to serve as a marker and a drill was driven into the lower end of the tibia. The relation of the marker to this drill was measured in nine different positions of the foot, the angle between the plantar surface of the foot and the anterior border of the tibia being measured in each position. The tendon was then detached from the calcaneum along with a flake of that bone.

Fixation. The animal was fixed on a rigid metal frame by steel pins driven into the spine and pelvis, and two pairs of steel pins in the tibia of the dissected side. The skin was drawn up to contain a pool of fluid (either Krebs–Henseleit solution, or liquid paraffin) around the muscle. The fluid was agitated by a flow of 95 % O_2 and 5 % CO_2 and maintained at body temperature by an immersion heater. Soleus tendon was split longitudinally where it joined the remaining fragment of bone; the vertical limb of a T-shaped bar was pushed through this split until the cross-bar engaged behind the tendon, the foot of the T bar was then coupled to a force transducer. The muscle length was adjusted by a calibrated lead screw that moved the whole cat frame in relation to the force transducer. A muscle length corresponding to an angle of 30° at the ankle was regarded as the maximum physiological length, and the muscle was never extended more than 2·5 mm beyond that length.

Recording system. The force transducer consisted of a pair of semi-conductor strain gauges mounted on a beryllium copper link which was so shaped that tension applied to the ends of the link caused distortion of the gauges. The strain gauges formed part of a Wheatstone bridge circuit the output of which was displayed on a cathode ray oscilloscope, and either photographed direct, or stored on magnetic tape for later analysis. The transducer had an unloaded natural frequency of 5,000 c/s; its output was linear to within 2 % of its maximum output.

Stimulation and root splitting. The muscle was stimulated through its nerve supply. In some experiments the muscle nerve was drawn up over silver wire electrodes in a liquid paraffin pool. In other experiments the stimulating pulses were delivered to the appropriate ventral roots as follows. The seventh lumbar and first sacral ventral roots were subdivided until all filaments that supplied soleus could be recombined into a number of groups each of which, on stimulation, caused an approximately equal muscle twitch (Fig. 6a). In most of the experiments five such groups of filaments were obtained. Each group of filaments was then arranged on a separate stimulating electrode (Fig. 1). Trigger pulses were supplied to the stimulators through an electronic distributor, which could be set to function in two different ways. During distributed stimulation trigger pulses were supplied to each of the stimulators in turn as indicated by the circular arrow in Fig. 1a. During synchronous stimulation only the first pulse of each distributor cycle was used, and this triggered all the stimulators together. When, therefore, the distributor was switched from synchronous stimulation (Fig. 1b) to distributed stimulation (Fig. 1c) stimuli reached each filament at the same rate, but instead of being synchronized they were distributed in time.

The undivided peripheral parts of the nerve roots were surrounded by physiological saline, and lay on a silver plate which served as a common cathode for the stimulators. The divided filaments were drawn up out of the saline into an overlying layer of liquid paraffin, and arranged on separate silver wire electrodes connected to the stimulator anodes. The stimulators delivered rectangular pulses of 0·1 msec duration, which were independently adjusted to be supramaximal for the filaments.

It was important to be sure that no part of the muscle received impulses from more than one electrode. On a number of occasions tests for cross-stimulation were carried out as described by Brown & Matthews (1960b), two of the root filaments were stimulated together, and then the same pair were stimulated with pulses separated by an interval of 10 msec. As long as the root filaments were separate from each other as they passed through the saline–paraffin interface the two methods of stimulation gave identical twitches, and cross-stimulation was presumed not to occur.

The twitch obtained by combined stimulation of all the root filaments was compared with the twitch from motor nerve stimulation. The combined filaments

usually gave a slightly smaller twitch than the muscle nerve (presumably some fibres had been destroyed during splitting), but the loss of tension was rarely as much as 10 % of the total.
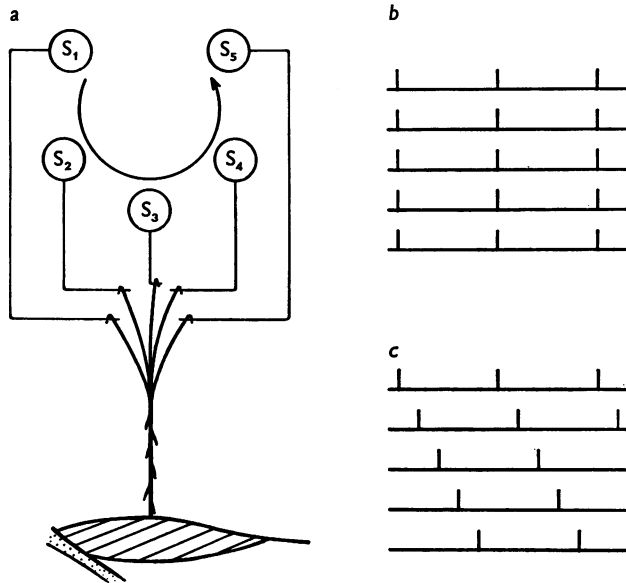

Fig. 1. The method of stimulation. (*a*) Five subdivisions of the ventral roots were mounted on electrodes each connected to a separate stimulator (S₁ to S₅). Stimulating pulses in the five channels could either be synchronized (*b*), or distributed (*c*).

Experimental procedure. In order to avoid the complicating effects of post-tetanic potentiation (Brown & Euler, 1938), a rigid experimental procedure was adopted. Tetanic stimulation was always carried out at 2 min intervals and the results of the first two such contractions were discarded. Twitch tests consisted of trains of five or six twitches with half-minute intervals between each train. Measurements were always made on the fifth twitch of each train.

No special precautions were taken to exclude the possibility of ephaptic stimulation (Brown & Matthews, 1960*a*), but since all the results to be described could be seen in small (less than 2·5 kg) as well as large cats, it is unlikely that this was a serious source of error (Buller & Lewis, 1965).

Anatomical studies

Fibre measurements. Cats that had been used for other experiments were killed with their ankle joints fixed in a position of plantar flexion so that the calf muscles stiffened at a short length. The following day soleus was exposed by removal of the other posterior leg muscles, its, origin and insertion being left intact. Under a dissecting microscope the muscle was split into two halves in an approximately antero–posterior direction along the line of its fibres, and the lateral half was removed. The surface thus exposed was made up of bundles of muscle fibres that could be followed throughout their length. These were then measured and photographed with the ankle held at various different angles.

Sarcomere measurements. Both soleus muscles from each of five cats weighing 1·7–2·5 kg were prepared for histological examination. These animals were dissected immediately after death; in each case soleus was exposed and split along the line of its fibres as described above. The legs were then fastened to splints that held one ankle at 90°, and the other dorsiflexed at 45°. (In each case the angle was measured between the anterior border of the tibia and the under surface of the foot.) Both legs were then immersed in 10 % formol saline to fix the muscles at those lengths. After fixation for 48 hr or more, the muscle lengths were measured; each muscle was then detached from the leg, and clamped in a metal scaffold which held it at that same length. The muscle remained in this scaffold through the processes of dehydration, clearing and embedding in Celloidin and paraffin wax. When the wax had cooled the scaffold was cut away together with surplus wax leaving the muscle in the block at the same length that it had been in the animal.

Sections 7–10 μ thick were cut from the surface that had been exposed when the fresh muscle was split, there was then no difficulty in obtaining accurate longitudinal sections of muscle fibres. During cutting the microtome knife always travelled across the line of the muscle fibres. Sections were stained with phosphotungstic acid haematoxylin, and sarcomere lengths were estimated by counting the number of striations that fell between two lines on a calibrated eyepiece. With our optical system (a 40 × objective) this distance represented 84 μ at the plane of the section.

Eighteen sarcomere counts were made on each muscle, six at different positions across each end of the section, and six across the middle. The actual fibres to be counted were selected at random.

Soleus structure   RESULTS

The structure of rat soleus has been described in detail by Close (1964), and the structure of the same muscle was very similar in kittens (Close & Hoh, 1967). The muscle fibres are approximately uniform in length; they arise from the head of the fibula and the adjoining part of the tibia, and from a tendon attached to those bones they pass downward and backward to an expanded tendon that covers the posterior surface of the lower part of the muscle. Each bundle of fibres extends the whole distance between the tendons, and each fibre probably extends for virtually the whole length of the fibre bundle.

Figure 2*a* shows that arrangement of fibres in soleus. The dashed lines indicate the positions of three bundles of muscle fibres that were selected for measurement. Figure 2*b* shows the lengths of these fibre bundles when the muscle was extended different amounts by dorsiflexion of the ankle. Measurements were made only at muscle lengths which rendered the fibres taut, but the dotted line in Fig. 2*b* indicates the lengths that the fibres could be expected to take up if they had continued to shorten. The measurements showed that muscle fibres in soleus shorten to about three quarters of their initial length when the angle at the ankle changes from 45 to 90°.

Measurements made on dead muscle will give fibre lengths slightly longer than during active contractions since during active contraction the tendon will yield a

small amount under the greater tension. It is unlikely that this yielding of the tendon could alter the total length of the fibre bundles by more than about 2 mm.

The oblique arrangement of the muscle fibres implies that only a component of the tension they generate acts in the direction of the tendon of insertion. This obliquity increases as the muscle shortens, but even at the shortest muscle lengths it is unlikely to account for more than about 5 % of the tension generated.
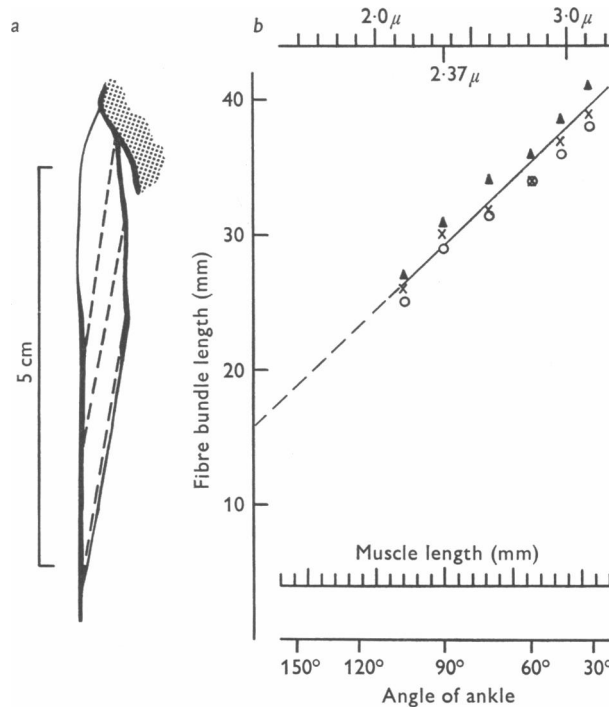

Fig. 2. (a) Tracing from a photograph of the muscle surface exposed by splitting in the direction of the fibres. The ankle was held at an angle of 110°. The dashed lines show the positions of three bundles of fibres that were marked and measured.

(b) The lengths of the fibre bundles shown in (a) have been plotted against muscle length; the corresponding ankle positions are shown below. Note that the angle at the ankle is related to muscle length in a non-linear manner. Mean sarcomere lengths equivalent to the 90 and 45° positions (taken from Table 1) are shown above, and the sarcomere lengths that would be expected for other muscle lengths are added.

The relation between muscle length and sarcomere length. Table 1 shows the mean sarcomere lengths of muscles from five cats fixed with the ankle joints held at 90 and 45°. Each of these mean values was derived from eighteen measurements made as described under Methods. There was no consistent difference between sarcomere lengths in different parts of the muscle.

The muscles in which sarcomere lengths had been measured were not those in which the fibre lengths had been measured or the mechanical properties examined, but there was fair agreement between the different muscles shown in Table 1, so we have assumed that those measurements approximately indicate the relationship between mean sarcomere length and angle at the ankle in all cat soleus muscles. The mean sarcomere lengths at 45 and 90° have been indicated on Fig. 2b, and the sarcomere lengths that might be expected at other muscle lengths are also shown.

TABLE 1. Mean sarcomere lengths in five cats at two different angles of the ankle

90°		45°	
length (μ)	S.D.	length (μ)	S.D.
2·41	0·115	2·97	0·084
2·31	0·177	3·15	0·106
2·32	0·079	2·96	0·057
2·34	0·090	2·89	0·109
2·49	0·137	3·04	0·084
Mean: 2·37	—	3·00	—

Mechanical properties of soleus

The cat soleus is a robust muscle, it remains in good condition for many hours, so that it is often possible to obtain consistent results from the same preparation at many different muscle lengths and stimulus rates.

The effect of length on tetanus tension. Isometric tension was recorded during tetanic stimulation of the soleus nerve with the muscle at various lengths. Stimulation at 50 impulses/sec gave a near maximum contraction at all but the shortest muscle lengths; this stimulus rate was therefore often used. The muscle then developed its highest tension at a length corresponding to about 60° flexion at the ankle (Fig. 3), and active tension declined if the muscle was stretched beyond that point. If the muscle was shortened from this optimum length to a length equivalent to an angle 90–110° at the ankle, the fall in isometric tension was quite slight; when, however, the muscle was shortened further the isometric tension fell steeply to become very small at a length corresponding to about 150° at the ankle. This length–tension plot is consistent with the findings of Buller & Lewis (1963), and similar in many respects to the curves obtained for frog muscle fibres (Ramsey & Street, 1940; Edman, 1966; Gordon, Huxley & Julian, 1966). The mean sarcomere lengths at the 90 and 45° positions of the ankle were approximately known (Table 1). Using these two values and assuming a linear relationship between mean sarcomere

length and muscle length it was possible to estimate the mean sarcomere length that would correspond to each muscle length. These values have been added at the top of Fig. 3.
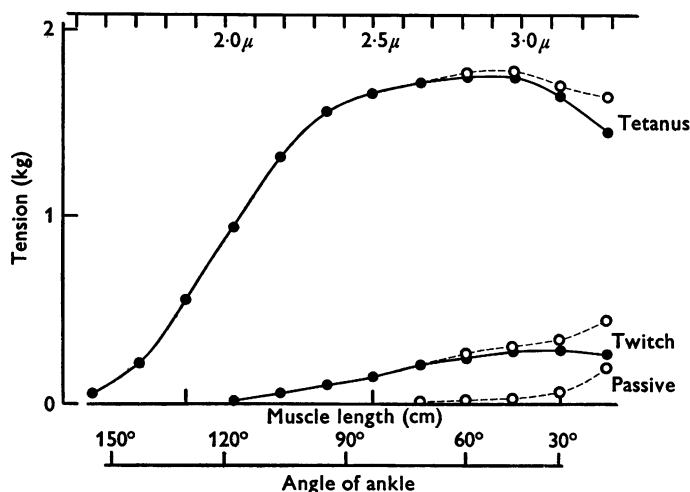

Fig. 3. The effect of length on tension. The upper continuous line shows active tension measured after 1·5 sec synchronous stimulation at 50 impulses/ sec. The lower continuous line shows the peak active twitch tensions in the same muscle. The lowest dashed line is the passive tension, the upper dashed lines show total tensions during tetani and twitches. Positions of the ankle corresponding to the muscle lengths are shown below.

Mean sarcomere lengths equivalent to the ankle positions (obtained from Table 1) have been added above the Figure.

Prolonged tetani of frog muscle at short lengths lead to a 'delta state' (Ramsey & Street, 1940), in which the muscle shows irreversible changes. We have seen a similar occurrence in cat gastrocnemius, but no such changes were seen in soleus, the whole range of these length–tension plots could readily be repeated.

The plot of passive tension against length was similar in general shape to that of Matthews (1959); the actual tensions recorded here were relatively low, presumably because surrounding structures had been removed.

Twitches. The peak active tension in an isometric twitch increased with increasing muscle length, but the length–tension plots for twitches and tetani differed in various respects. At the shortest lengths no twitch tension could be recorded, but when the muscle was stretched beyond a length equivalent to about 120° at the ankle the tension rose relatively more steeply than in the tetani. In Fig. 3, for example, extension from the 90 to the 60° length more than doubled the twitch tension, whereas the tetanus tension increased by only 8 %. Unlike the tetani, the length–tension curves for twitches varied a good deal from cat to cat, sometimes

both twitch and tetanus gave their maximum tensions at about the same length, but in other animals the active twitch tension continued to rise with progressive extension even beyond the maximum physiological length.
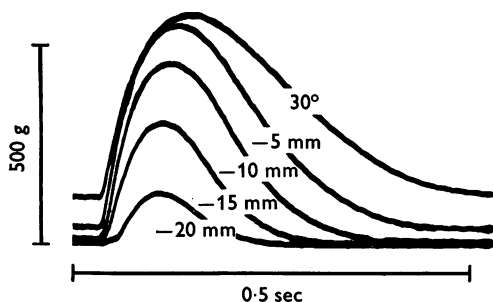

Fig. 4. Oscilloscope photographs of tension records during isometric twitches at different muscle lengths. The longest twitch was at a muscle length equivalent to an angle of 30° at the ankle. The others were recorded after shortening the muscle by successive 5 mm steps.

Measurements of peak tension do not, however, give a complete picture of the variations in the muscle twitch that occur at different lengths. With increasing muscle length the time course of the twitch also changed (Buller, Eccles & Eccles, 1960; Buller & Lewis, 1963; Close 1964); the tension took longer to rise to a peak, and the decay was even more protracted (Fig. 4). Increasing the muscle length prolonged the twitch even though the muscle was extended into a range in which the peak tension declined. Similar differences in twitch duration at different muscle lengths are seen in frog sartorius muscle (Hartree & Hill, 1921; Jewell & Wilkie, 1960).

The effect of stimulus rate on muscle tension. The preceding paragraphs describe some properties of muscle during synchronized stimulation of the whole of its motor nerve supply. This method of stimulation was satisfactory for a study of twitches or of fused tetani. When, however, a muscle is stimulated repetitively at lower rates such as the intact animal more often uses (Denny-Brown, 1929), synchronous stimulation gives an unfused tetanus that is obviously very different from the normal activity of muscle in an intact animal. By subdividing the nerve supply and distributing stimuli to different groups of motor units in rotation it was possible to go some way towards achieving the smooth contraction of an intact muscle in normal use (Fig. 5).

Figure 6*b* shows the course of isometric tetani during such distributed stimulation of soleus at four different rates. When each filament received 4 impulses/sec, the tension record showed a ripple amounting to less than

5 % of the tension, and at 7 impulses/sec this ripple was only about 1 %. In another experiment in which eight equal subdivisions were used, the tension at 2 impulses/sec fluctuated by only about 5 %.
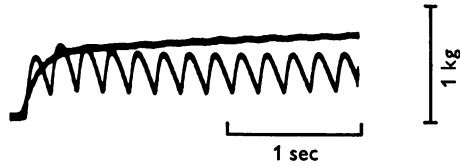

Fig. 5. Tension during stimulation at 5 impulses/sec. The grossly unfused contraction was recorded during synchronized stimulation of all the roots, the smoother contraction during distributed stimulation at the same rate. Five stimulating channels were used.
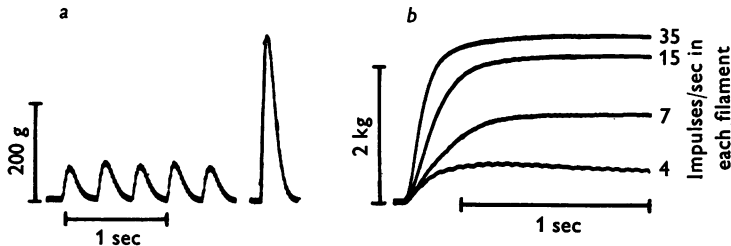

Fig. 6. (*a*) Twitches from five subdivisions of the ventral roots, followed by the twitch obtained when all five were stimulated together.
(*b*) Tensions recorded during distributed stimulation of the five divisions at various rates ((*a*) and (*b*) from different experiments).

Muscle tension increased with increasing stimulus rate in a characteristic way (Cooper & Eccles, 1930; Matthews, 1959). The stimulus rate–tension plot had a sigmoid form, and this was true whether stimulation was distributed (continuous line in Fig. 7), or synchronous. There was always a middle range within which tension rose steeply with each increment in stimulus rate; but further increases in stimulation beyond that range had diminishing effects on the tension, and at all but the shortest lengths 50 impulses/sec gave an almost maximal contraction.

At the lowest stimulus rates tension fluctuated even during distributed stimulation, the double line in Fig. 7 indicates the limits of the tension fluctuation in that preparation.

Comparison of synchronous and distributed stimulation. Synchronous stimulation of the muscle at a low rate (5–10 impulses/sec) gave an irregular contraction that was made up of a series of partially fused twitches (Fig. 5), and a corresponding movement of the muscle fibres could be seen. When, however, during stimulation at the same rate the impulses were

distributed among different parts of the muscle in rotation, the movement was quite slight once the final tension had been reached.

Whenever the change from synchronous to distributed stimulation led to a smoother contraction with less internal movement of the muscle, the tension increased (Fig. 5), and often became higher than even the peak tension during synchronous stimulation. The vertical lines in Fig. 7 show the tension during synchronous stimulation, and the length of each line indicates the extent of the tension fluctuation; at high rates of stimulation the contraction was smooth whichever method of stimulation was used, but as the stimulus rate was reduced below 20 impulses/sec synchronous stimulation caused increasingly irregular contractions, and the tension fell below that obtained during distributed stimulation.
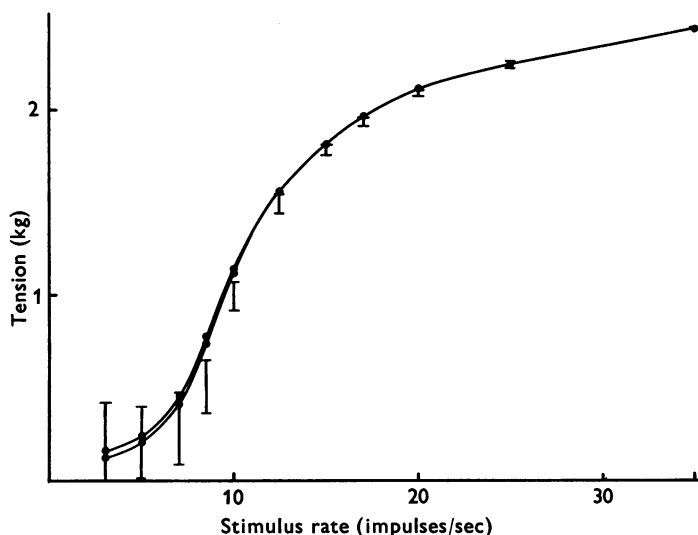

Fig. 7. The effect of stimulus rate on tension. The continuous line shows tension when the stimulating pulses were distributed among five channels. At the lowest rates this tension fluctuated; the double line indicates the maxima and minima of these fluctuations.

The vertical lines show tension during synchronous stimulation, the upper and lower ends of the lines being the peak and trough of the fluctuations. In each case measurements were made 1·5 sec after the onset of stimulation.

At the lowest stimulus rates, such as 3 impulses/sec in Fig. 7, synchronous stimulation gave a series of more or less separate twitches, the tension falling to zero after each contraction; under these circumstances the mean tension was a good deal less than half the peak tension. During distributed stimulation the tension still remained above this mean though this is not obvious in Fig. 7.

The stimulus rate–tension plot, and the fusion frequency for synchronous stimulation differed at different muscle lengths, but whenever in these experiments a change from synchronous to distributed stimulation was associated with a large decrease in the tension fluctuation, this smoothing was accompanied by an increase in the mean tension.

The interrelation of length, stimulus rate and tension. In previous paragraphs the effects on tension of muscle length, and of stimulus rate have been considered separately, but changes in muscle length have a different effect on tension at different stimulus rates (Fig. 8), and the stimulus rate affects tension differently at different lengths (Fig. 9). Muscle length and stimulus rate are to some extent complementary, a low stimulus rate gave a near maximal tension when the muscle was long, whereas at very short lengths only high rates of stimulation gave a significant contraction.

The effect of length on tension at low stimulus rates can conveniently be described in relation to the 5 impulses/sec record of Fig. 8. The continuous lines indicate tension during distributed stimulation, the vertical lines the tension during synchronized stimulation and the extent of its fluctuation. At short lengths synchronous stimuli gave quite separate twitches, and the tension fell to zero after each one. Increasing the muscle length increased the twitch duration (see Fig. 4), so that at a slightly greater length the twitches at 5 impulses/sec began to coalesce, and the tension no longer returned to zero. With further increments in muscle length the fusion between twitches became more complete so that the tension fluctuation became a smaller proportion of the total tension. As the contraction became more fused, the tension rose above the value obtained by a graphical summation of the separate twitches, and if the tension fluctuations were then diminished further by changing from synchronous to distributed stimulation of the filaments, the tension rose to a higher level still.

When length was increased it seemed that three factors acted together to increase the muscle tension. Each stimulating pulse caused a more forcible contraction, this contractile activity lasted for longer, and its longer duration in turn led to a smoother contraction in which a higher tension could develop. At the greatest lengths, the tension at low stimulus rates decreased in the same way it did during stimulation at high rates in Fig. 3.

The length–tension plots at different rates of stimulation (Fig. 7) are similar in general shape but they have their steep sections in different places. Conversely at any one length the curves differ a good deal in their slope. At a length corresponding to 90°, for example, the tension at 5 impulses/sec would be doubled by extending the muscle 3 mm. Such an extension increased the tension at 10 impulses/sec by 25 %, and at 35 impulses/sec by only 5 %.
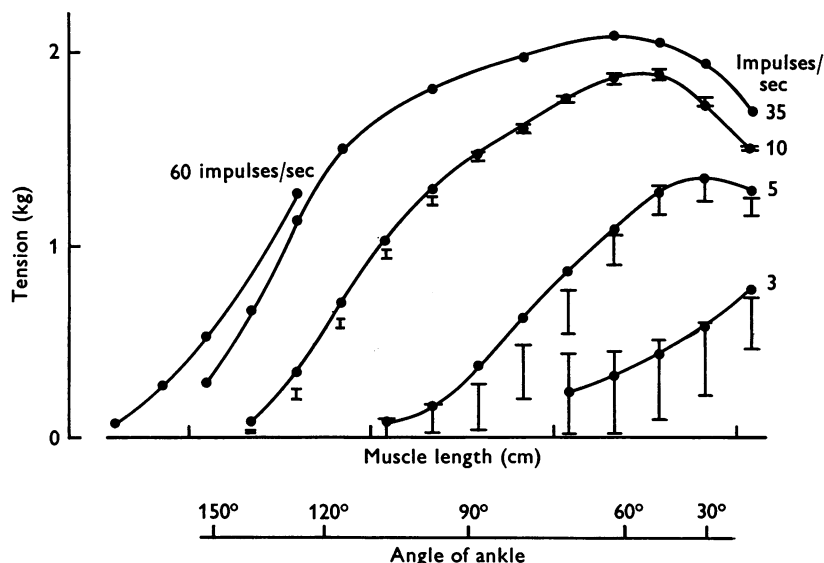
Fig. 8. The effect of length on active tension at different stimulus rates. Continuous lines show the tension during distributed stimulation at the rates indicated (five stimulating channels were used). The vertical lines show the limits of tension fluctuations during synchronous stimulation.
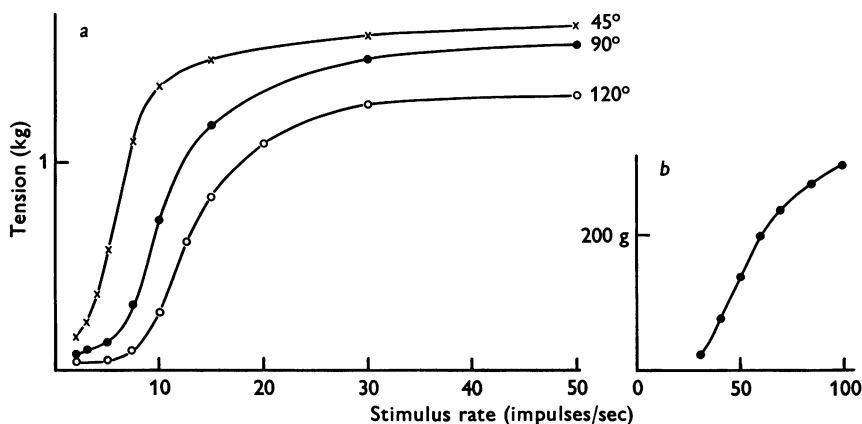

Fig. 9. The effect of stimulus rate on active tension.

(a) Stimulus rate–tension plots at three different muscle lengths. The equivalent angles of the ankle are shown on the Figure. Stimuli were distributed among five channels. Tension was measured 1·2 sec after the onset of stimulation.

(b) Tension at a very short length (equivalent to 140° at the ankle). The muscle nerve was stimulated directly. Tension was measured 2 sec after the onset of stimulation, at which time it had risen to more than 90 % of its maximum.

(a) and (b) were taken from different experiments.

In Fig. 9 stimulus rate–tension curves have been plotted at different muscle lengths. These are all similar in general shape, and in each case there is a range within which a small increase in stimulus rate yields a relatively large increment in tension, though this range was different at different muscle lengths (Matthews, 1959). At the 45° length the muscle achieved almost its maximum tension with 10 impulses/sec though at the 120° length the muscle needed double that stimulus rate to exert the same fraction of its maximum force.

At all but the shortest lengths stimulation at 35 impulses/sec led to an isometric tension that approached the maximum for that length. At very short lengths, however, the tension continued to rise with increases in stimulus rate up to about 100 impulses/sec (Fig. 9b). The effect of high rates of stimulation at short lengths is also seen in Fig. 8 where at a length corresponding to 150° the tension at 60 impulses/sec was double the tension at 35 impulses/sec.

The onset of contraction. During isometric contraction Cooper & Eccles (1930), and Buller & Lewis (1965) found that tension rose to its plateau more rapidly with high than with low rates of stimulation. In the present experiments different muscle lengths were used, and very low rates of stimulation were also included; the relationship between the rate of rise of tension, and the stimulus rate was then found to be more complicated.
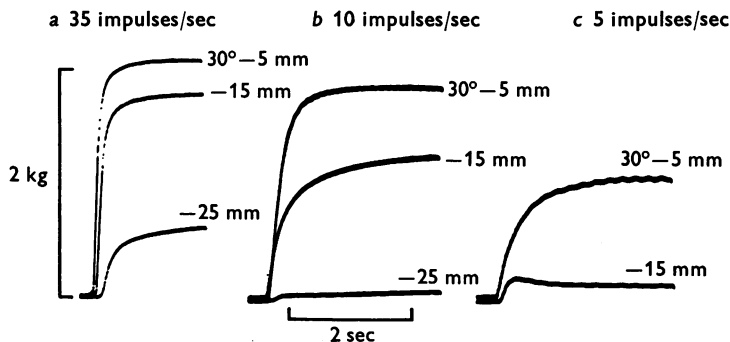

Fig. 10. Records of isometric tetani at different muscle lengths and different stimulus rates. In all cases the stimulating pulses were distributed among five channels.

During stimulation at very low rates the tension often rose quite rapidly to a maximum value from which it then declined toward a steady level (Fig. 6, 4 impulses/sec). A similar decline is seen in the first few of a series of repeated soleus twitches.

The rate of rise of isometric tension depended on the muscle length as well as on the rate of stimulation. Figure 10 shows some of the tetani that

were used in constructing Fig. 8; these records were all made during distributed stimulation, the rates being 35, 10 and 5 impulses/sec. At each of these stimulus rates there was a length range in which the isometric tension developed rather slowly, at 35 impulses/sec (Fig. 10a) the tension developed slowly at very short lengths whereas at 5 impulses/sec (Fig. 10c) tension developed slowly at long lengths, and at 10 impulses/sec (Fig. 10b) the slowest rise was at an intermediate length. Comparing Figs. 8 and 10 it will be seen that the tension develops slowly at the same length at which the length–tension plot is steep, or, when the isometric tension rises steeply with increasing length, that tension can only be slowly achieved. A possible explanation for these findings will be offered in a later paper.

DISCUSSION

Gordon *et al.* (1966) have shown that many features of the isometric length–tension diagram for tetanized frog muscle fibres may be explained in terms of the relative positions of thick and thin filaments within the myofibrils. The tension fell steeply when the fibre was shortened to sarcomere lengths less than $1\cdot6\,\mu$, at which lengths the ends of the thick filaments could be expected to be compressed against the Z lines.

In cat soleus, however, the isometric tension falls steeply when the muscle is shortened to sarcomere lengths less than about $2\cdot2\,\mu$ (Fig. 3), though the thick filaments in this muscle are $1\cdot5$–$1\cdot6\,\mu$ in length (Sally G. Page, personal communication). The fall in tension with shortening was more gradual when very high rates of stimulation were used, but this fall still occurred at lengths a good deal longer than could be expected from the findings of Gordon *et al.* (1966) on frog muscle fibres.

The estimates of sarcomere length in this paper take no account of the possibility that irregularities may develop during contraction so that some parts of the muscle fibres shorten at the expense of others. This is an important source of error when muscles are extended into regions where increasing length is associated with decreasing tension (Huxley & Peachey, 1961) but at shorter lengths where force declines along with length the errors are unlikely to be large. It is anyway difficult to see how irregularities of this sort could explain the unexpectedly low tensions at short muscle lengths.

It is likely that at short lengths the tension in cat soleus is limited by something other than end-to-end apposition of the thick filaments within the muscle fibres. There are a number of possibilities, but the present results suggest that at short lengths the process of activation may function less effectively, so that each action potential gives a smaller, and perhaps briefer activation of the contractile machinery. This would explain the reciprocal relationship between muscle length and stimulus rate seen in Figs. 8 and 9, where at short muscle lengths a high stimulus rate was

needed to obtain a maximum tension, whereas at the longer lengths relatively low stimulus rates gave high tensions.

A decline in activation with decreasing muscle length would also explain the very striking reduction of twitch tension that accompanied shortening (Fig. 4), and the accompanying changes in twitch duration suggest to us that the duration as well as the intensity of activation depend on muscle length. An alternative explanation for the correlation between twitch duration and tension appears in the work of Hill (1964) who, in describing twitches of toad sartorius muscle, noted that 'a kind of weak positive feed-back occurs, tension prolonging activity, and activity prolonging tension.'

The process of activation of a muscle fibre spreads inward from its surface, probably along the system of transverse tubules (Huxley & Taylor, 1958). Alterations in the muscle length might well alter the geometry of these tubules: if they became flattened as the fibres shortened, they would offer a higher resistance to the inward spread of depolarizing current, which could perhaps account for a decline in activation of the muscle fibre.

As a muscle shortens the passive tension decreases; it could be argued that at lower initial tensions the series elastic elements of the muscle were more compliant (Hill, 1950), and that this compliance accounts for the fall in twitch tension. A more compliant series elastic element would, however, delay the peak tension (Hill, 1951), whereas in fact the peak tension occurred earlier at shorter muscle lengths.

The differences between synchronous and distributed stimulation. During an isometric contraction muscle fibres are not necessarily stationary; any increase in tension stretches the tendon allowing the muscle fibres to shorten. The tension fluctuations in an unfused tetanus were accompanied by visible movement within the muscle, but this became less when the stimuli were distributed among different parts of the muscle in rotation, this was to be expected since the tension fluctuations were then much smaller. Furthermore, the fibres in mammalian muscles are bound together by connective tissue in a way that must limit free movement between them, so that each fibre probably moves freely only when it is contracting in synchrony with its near neighbours.

We believe that at low stimulus rates this muscle is best able to generate tension when the fibres are quite still. (We shall advance further evidence for this suggestion in the succeeding paper.) This property of muscle fibres would explain the gain in tension that occurred whenever, at low stimulus rates, the muscle contraction was made smoother by distribution of the stimulating pulses.

Length–tension plots at low stimulus rates. At low rates of stimulation such as an animal often uses, the isometric muscle tension may change quite considerably with small alterations of muscle length, a fact that is no

doubt important in the control of posture (Granit, 1958; Matthews, 1959). We wish to emphasize, however, that the length–tension plots in this paper were obtained during isometric contractions and cannot be used to describe the tension during movements.

REFERENCES

BROWN, G. L. & EULER, U. S. v. (1938). The after effects of a tetanus on mammalian muscle. *J. Physiol.* **93**, 39–60.

BROWN, M. C. & MATTHEWS, P. B. C. (1960*a*). The effect on a muscle twitch of the back response of its motor nerve fibres. *J. Physiol.* **150**, 332–346.

BROWN, M. C. & MATTHEWS, P. B. C. (1960*b*). An investigation into the possible existence of polyneuronal innervation of individual skeletal muscle fibres in certain hind-limb muscles of the cat. *J. Physiol.* **151**, 436–457.

BULLER, A. J., ECCLES, J. C. & ECCLES, R. M. (1960). Differentiation of fast and slow muscles in the cat hind limb. *J. Physiol.* **150**, 399–416.

BULLER, A. J. & LEWIS, D. M. (1963). Factors affecting the differentiation of mammalian fast and slow muscle fibres. In *Proceedings of Symposium on 'The effect of use and disuse on neuromuscular functions'*, ed. GUTMANN, E. & HNÍK, P. Prague: Czechoslovak Academy of Science.

BULLER, A. J. & LEWIS, D. M. (1965). The rate of tension development in isometric tetanic contractions of mammalian fast and slow skeletal muscle. *J. Physiol.* **176**, 337–354.

CLOSE, R. (1964). Dynamic properties of fast and slow skeletal muscles of the rat during development. *J. Physiol.* **173**, 74–95.

CLOSE, R. & HOH, J. F. Y. (1967). Force:velocity properties of kitten muscles. *J. Physiol.* **192**, 815–822.

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

DENNY-BROWN, D. (1929). Nature of postural reflexes. *Proc. R. Soc.* B **104**, 252–301.

EDMAN, K. A. P. (1966). The relation between sarcomere length and active tension in isolated semitendinosus fibres of the frog. *J. Physiol.* **183**, 407–417.

GORDON, A. M., HUXLEY, A. F. & JULIAN, F. J. (1966). The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *J. Physiol.* **184**, 170–192.

GRANIT, R. (1958). Neuromuscular interaction in postural tone of the cat's isometric soleus muscle. *J. Physiol.* **143**, 387–402.

HARTREE,, W. & HILL, A. V. (1921). The nature of the isometric twitch. *J. Physiol.* **55**, 389–411.

HILL, A. V. (1950). The series elastic component of muscle. *Proc. R. Soc.* B **137**, 273–280.

HILL, A. V. (1951). The effect of series compliance on the tension developed in a muscle twitch. *Proc. R. Soc.* B **138**, 325–329.

HILL, A. V. (1964). The effect of tension in prolonging the active state in a twitch. *Proc. R. Soc.* B **159**, 589–595.

HUXLEY, A. F. & PEACHEY, L. D. (1961). The maximum length for contraction in vertebrate striated muscle. *J. Physiol.* **156**, 150–165.

HUXLEY, A. F. & TAYLOR, R. E. (1958). Local activation of striated muscle fibres. *J. Physiol.* **144**, 426–441.

JEWELL, B. R. & WILKIE, D. R. (1960). The mechanical properties of relaxing muscle. *J. Physiol.* **152**, 30–47.

MATTHEWS, P. B. C. (1959). The dependence of tension upon the tension in the stretch reflex of the soleus muscle of the decerebrate cat. *J. Physiol.* **147**, 521–546.

RAMSEY, R. W. & STREET, S. F. (1940). The isometric length–tension diagram or isolated skeletal muscle fibres of the frog. *J. cell. comp. Physiol.* **15**, 11–34.