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THE SHORT RANGE STIFFNESS OF ACTIVE MAMMALIAN MUSCLE AND ITS EFFECT ON MECHANICAL PROPERTIES

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SUMMARY

1. The tension in tetanized cat soleus and lateral gastrocnemius muscles was measured during alternating lengthening and shortening movements. Sinusoidal movements were sometimes used; on other occasions the movement was at a constant velocity but with periodic reversal of direction.

2. With constant velocity movements of small amplitude the tension rose steeply during lengthening and fell during shortening in a relatively simple way. With longer movements the tension at first changed steeply as it had done with the smaller movement, but later in the movement the resistance of the muscles decreased so that the tension change became more gradual. The muscles resisted a small movement or the first part of a larger movement with a 'short range stiffness' which did not persist as the movement continued.

3. So long as the constant velocity movement was not too slow the short range stiffness was independent of velocity though it lasted for more of a fast movement than of a slow one.

4. In small movements the muscle was never extended beyond its short range stiffness, and the over-all peak-to-peak tension change was therefore large compared with the amplitude of movement. When, with larger movements, the muscle was stretched into a range in which it became more compliant, the peak-to-peak force fluctuation did not increase by an equivalent amount, and over the whole course of the movement the force change per unit extension was smaller.

5. When the movement was confined to a short range, little work was expended in driving the muscle through a cycle of movement; its properties were essentially elastic. With larger amplitudes the muscle met the movement with a frictional resistance, the tension during lengthening then being greater than during shortening. A considerable amount of work had then to be done on the muscle to maintain the movement.

6. The short range stiffness was also apparent in the response to sinusoidal movements.
7. The short range stiffness was attributed to elastic properties of crossbridges between thick and thin filaments in the myofibrils.

8. The effect of the short range stiffness on the mechanical properties of the limb is discussed.

INTRODUCTION

When, after a period of isometric contraction, a cat soleus muscle is forcibly lengthened, the first part of the lengthening movement is opposed by a steep rise in tension. In the later part of the movement, however, the resisting force increases much more slowly and may actually decrease (Joyce, Rack & Westbury, 1969). A converse effect is seen during shortening, the tension falls steeply at first but much more gradually during the later part of the movement. The large force changes at the beginning of the movement have been attributed to distortion but not breakage of crossbridges that link thick and thin filaments within the myofibrils.

In this paper we describe the forces generated by muscles during alternating lengthening and shortening movements. Again, there was a large change in force during the first part of the movement which we attribute to distortion of cross-bridges; this we shall refer to as the 'short range stiffness'. This stiffness has hitherto been described as a 'series elastic resistance' within the muscle, but more recently this terminology has seemed less helpful. In some respects the short range stiffness is similar to the short range elasticity described by Hill (1968), though it persists for longer movements.

When a muscle was alternately lengthened and shortened with a constant velocity, the results could be compared with those that were obtained when the movement followed an isometric contraction, and this was of some help in interpreting them. The response to sinusoidal movements was less easy to understand, but it is of particular interest since sinusoidal movements have often been used in studies of normally innervated muscles under reflex control (Partridge & Glaser, 1960; Roberts, 1963; Jansen & Rack, 1966; Poppele & Terzulo, 1968) and in studies of the properties of human limbs (Robson, 1962; Neilson, 1972; Joyce, Rack & Ross, 1974); the results of these experiments cannot be interpreted without a knowledge of the response of a continuously activated muscle to sinusoidal stretching. Sinusoidal movements have been used in previous investigations of muscle properties, and the results have been described in terms of work absorption, phase shifts, and viscous and elastic stiffness (Buchtal & Kaiser, 1951; Rack, 1966). Unfortunately it is often difficult to relate these quantities to the results obtained by physiologists who used constant velocity movements or isotonic movements.

In this investigation, therefore, we have attempted to reconcile these
two different approaches to the subject by examining the properties of muscle during constant velocity lengthening and shortening movements, and then going on to examine the response of the same muscle to sinusoidal movements of similar amplitudes and frequencies.

Some results of these experiments have already been briefly reported (Rack & Westbury, 1973).

METHODS

Experiments were done on fourteen cats weighing between 2.2 and 3.5 kg; the animals were anaesthetized with intraperitoneal pentobarbitone sodium (Nembutal, Abbott Laboratories), further quantities being given i.v. as necessary; rectal temperature was maintained at 36–38°C. Soleus muscle was studied in eleven of the experiments, the lateral head of gastrocnemius in the remaining three.

The methods of dissection, fixation, and stimulation of soleus have already been described in detail (Rack & Westbury, 1969); the muscle was exposed and dissected free from surrounding structures, other muscles in the limb being denervated. The skin of the limb was drawn up to form a trough which was filled with either Krebs–Henseleit solution or liquid paraffin. The fluid was maintained at body temperature and agitated by a flow of gas (95% O₂ and 5% CO₂). The muscle tendon was coupled through a strain gauge to an electromagnetic movement generator. The nerve roots supplying the hind limb were detached from the spinal cord. Stimulation was either by electrodes on the muscle nerve, or by an array of electrodes on filaments of ventral roots through which different groups of motor units could be stimulated in rotation. When the lateral head of gastrocnemius was used, the dissection was essentially similar, the medial head of gastrocnemius and the plantaris were removed and soleus was denervated; additional steel pins were used to fix the femur, with the knee joint flexed to 90°. In some experiments only part of the nerve supply to the lateral head of gastrocnemius was stimulated since the tension produced by contraction of the whole muscle was usually too large for the equipment used.

Generation of movements. An electromagnetic vibrator (Pye Ling, model 406) was fitted with a linear position transducer, the output from which was, after suitable amplification, mixed with the input to the vibrator to give a servo-control of position similar to that described by Matthews (1962). The shaft of the vibrator then followed the output of a waveform generator (Servomex model LF141). This muscle stretcher resisted deflexions from its set position with a stiffness of 80 N/mm. Noise in the servocontrol system caused movements of the vibrator through less than 10 μm, the principal component of the movement being at 100 Hz. Such small amplitude vibrations are unlikely to have affected the muscle tension (Matthews, 1966; Joyce et al. 1969).

Length and tension recording. During the dissection a thread was sewn to the tendon and a drill was driven into the tibia, the relation between the thread and the drill was noted for various positions of the ankle joint, and later used for setting the muscle length (Rack & Westbury, 1969). Movements were recorded from a variable inductance linear position transducer (Cybernetics Ltd) which had negligible phase error at frequencies up to 25 Hz. The tension transducer consisted of a pair of semiconductor strain gauges bonded on either side of a beryllium copper beam, the distortion of which was proportional to the muscle tension. The strain gauges formed two arms of a Wheatstone bridge, the signal across which gave a measure of the muscle tension. The transducer had an unloaded natural frequency of 1700 Hz.

During the experiments the muscle length and tension signals were recorded on
magnetic tape by frequency modulation. The results were later displayed on an oscilloscope for photography, and these photographic records were projected and measured. The areas of length–tension figures were measured by planimetry.

Experimental procedure. In order to avoid the complicating effects of post-tetanic potentiation (Brown & Euler, 1938) a rigid experimental procedure was followed, tetanic stimulation of the muscle being carried out at 2 min intervals. Results from the first two such contractions were discarded.

RESULTS

The effect of alternating movements on mean force

When a contracting muscle was subjected to repeated lengthening and shortening movements the tension increased during lengthening and decreased during shortening. One aim of this investigation was to compare the tension changes that occurred when these lengthening and shortening movements were made through different amplitudes and with different velocities. This comparison was, however, complicated by the fact that during the first few cycles of movements there was often also a gradual decrease in mean tension (Joyce et al. 1969).

This fall in mean tension was seen when high frequencies and large amplitudes of movement were used, and it was greater when the rate of stimulation of the muscle was low. Fig. 1a shows the slight fall in mean tension that occurred when a soleus muscle stimulated at 40 impulses/sec was stretched sinusoidally through 1.1 mm (peak-to-peak) at 11 Hz. When the muscle was stimulated at only 10 impulses/sec the same movements led to a much more striking reduction in tension (Fig. 1b), the mean tension falling to a value that was little more than a quarter of the preceding isometric value. A similar effect was seen with gastrocnemius (Fig. 1c), but only with high frequencies and large amplitudes of movement.

Once the initial fall in tension was over, the response to succeeding cycles of movement remained fairly constant and it was this later part of each sequence of movements that was studied in detail.

The fall in mean tension during the course of an alternating movement was accompanied by a reduction in the extent of the tension fluctuation even though the amplitude of movement remained the same (Fig. 1b, c); the resistance to movement decreased as the tension decreased. The mean tension and the resistance to movement were depressed by different amounts when different amplitudes and velocities of movement were used, and this led to difficulties when one attempted to compare the resistance of a muscle to different movements. If the stimulus rate was kept constant, the different movements depressed the mean tension by different amounts, and the muscle resistance to the movements could be expected to be different for that reason alone.
In these experiments we often wished to compare the resistance of muscles to different alternating movements, but with the same mean muscle tension. Experiments were therefore either carried out with high rates of stimulation when the fall in mean tension during movement was small, or, lower more physiological rates of stimulation were used, the rate being adjusted by trial and error to obtain approximately the same mean tension (within 10%) in a variety of different movements. This second method was closer to the way that an animal might be expected to use the muscle, and it had the additional advantage that longer series of tetani were possible without unduly fatiguing the muscle. The two methods of stimulation gave essentially similar results.

**Constant velocity movements**

The muscle tension always rose during lengthening and fell during shortening; this was true for both gastrocnemius and soleus and at all the rates of stimulation used. The fall in tension during lengthening that had sometimes been seen when the movement followed an isometric contrac-
tion (Joyce et al. 1969) did not occur when alternating lengthening and shortening movements were used.

Fig. 2a and b shows typical records of the tension developed during constant velocity movements; in each of them there was an abrupt change in direction of the tension record when the direction of movement reversed, in other respects however the records obtained with different amplitudes of movement were very different.

![Graph](image_url)

**Fig. 2.** Alternating constant velocity movements of soleus. The muscle was lengthened and shortened at 10 mm/sec, (a) through 0-8 mm, (b) through 2-8 mm (oscilloscope photographs). Length–tension figures from a number of such movements of different amplitudes are shown in c (tracings from oscilloscope photographs).

The stimulus rate was chosen by trial and error to obtain the same mean tension in each contraction. For the smallest movement, 7 impulses/sec were supplied to each ventral root filament, for the largest movement 25 impulses/sec. The mean muscle length was equivalent to an 80° position of the ankle joint.

The effect of amplitude. When small movements were used, the tension increased during lengthening and decreased during shortening in a simple way (Fig. 2a). With larger movements, however, the tension increase during lengthening occurred in two phases (Fig. 2b); during the first part of the movement the tension rose steeply as it did in the smaller movements, but during the later part the increase in tension was more gradual. When the muscle shortened the converse changes were seen, the tension falling steeply at the beginning of shortening but more slowly during
the later part of a prolonged movement. During lengthening the initial steep rise in the tension record was separated from the later more gradual increase by a definite corner, but during shortening the steep fall in tension often merged into the later gradual fall and the corner was then less distinct.

This relationship between muscle length and tension is more clearly seen in Fig. 2c where tension is displayed as a function of length. So long as the muscle properties did not change, the length–tension figure remained the same from cycle to cycle; these length–tension figures form loops traced in a clockwise direction, the tension during lengthening always exceeding the tension during shortening through the same range. The slope of the line in any part of such a length–tension figure indicates the increase in tension per unit extension, which is the stiffness of the muscle in that part of the movement. The area circumscribed gives the amount of work that had to be done on the muscle to lengthen and shorten it through the complete cycle.

The tension changes that accompanied the first part of either a lengthening or shortening movement appear as steep parts of the length–tension figure. The steep slope that in Fig. 2c persisted for the first millimetre of the lengthening movement gives a measure of the short range stiffness of the muscle, which in that experiment was 9 N/mm. If the movement were confined to a short distance so that the muscle was never pulled beyond the range in which it exhibited its short range stiffness it resisted the whole of the extension with a steeply rising force and on reversing the movement the force (as displayed in a length–tension figure) returned by a path that was fairly close to the path traced out during lengthening, giving a thin length–tension figure. If the muscle had been a perfectly elastic material, the lengthening and shortening paths would have been superimposed, tension being independent of direction of movement, and the length–tension figure would have been a line. The separation between the two directions of movement in our length–tension figures shows that although with small movements the muscle behaved in a way that was essentially elastic, it was never perfectly elastic, since there was always some discrepancy between the forces during lengthening and during shortening.

Longer movements began in the same way as short ones. There was at first a steep rise or fall in tension, but the muscle only maintained this high level of resistance for a part of the movement and thereafter the length–tension record levelled off as the muscle became more compliant. This change from the initial short-range stiffness to the later compliance gave the length–tension figures of the larger movements a trapezoidal shape (Fig. 2, 3 and 4); the force during shortening was then much less
than during lengthening, and although the increase in tension during the
first part of the movement was the same as in the shorter movements, the
overall response to these larger movements was far from being that of a
simple elasticity.

The results shown in Fig. 2 were obtained during stimulation of soleus
at rates varying between 7 and 25 impulses/sec, the stimulus rate being
adjusted to keep the mean force approximately constant. Similar results
were obtained from muscles stimulated at higher rates (Fig. 3a).

![Diagram](https://example.com/diagram.png)

Fig. 3. Alternating constant velocity movements, the effects of amplitude
of movement. a, soleus was lengthened and shortened through different
distances at 8.6 mm/sec; stimulation of the muscle nerve at 40 impulses/sec.
The mean muscle length was equivalent to a 65° position of the ankle joint.
The line drawn across the figure is part of the static length–tension curve
for the muscle. b, the lateral head of gastrocnemius was lengthened and
shortened at 10 mm/sec; stimulation of a part of the nerve supply at
200 impulses/sec. The muscle length was equivalent to a 90° position of the
knee joint with a 60° position of the ankle.

The line drawn across Fig. 3a shows the tension generated in successive isometric
contractions in that length range and at that stimulus rate. The muscle responded
to the movement with a larger tension change than could be expected from this
static length–tension relation, all parts of the length–tension figure being steeper
in slope than the isometric length–tension plot. At shorter muscle lengths where the
isometric length–tension plot had a steeper slope this difference was smaller.

Fig. 3b was obtained during similar constant velocity movement of the
lateral head of gastrocnemius while part of the ventral roots supplying the
muscle was stimulated at 200 pps. In this muscle the tension did not re-
main at a steady level in a prolonged tetanus, and in Fig. 3b a fall occurred
in successive cycles of the longer movements so that the length–tension
figures did not form closed loops. In other respects the length–tension
figures from gastrocnemius were similar to those from soleus.

The effect of velocity. Repeated lengthening and shortening movements
were made with velocities 5–40 mm/sec. The tension changes accompani-
ing these movements were similar to those described above, but at different velocities the transition from the initial short range stiffness to the later compliance occurred after different distances. When the movement was relatively slow (Fig. 4, interrupted lines) the short range stiffness lasted only for a short distance (0-6 mm in Fig. 4) and the muscle was relatively compliant for most of the course of a long movement (Fig. 4d.). When, however, the movements were faster (continuous lines) the short range stiffness lasted for longer (more than a millimetre in Fig. 4c and d).

Fig. 4. The response of soleus to movements through four different amplitudes at two different velocities. Continuous line, 20 mm/sec; interrupted line, 5 mm/sec.

Distributed stimulation of ventral root filaments at a rate that was adjusted between 11 and 22 impulses/sec to keep the mean tension constant. Mean muscle length equivalent to 65° position of the ankle joint.

Since the muscle offered a high resistance to more of a rapid movement than of a slow one, the over-all tension changes in fast alternating movements were always greater than in slow ones. The effect on the area enclosed by the length–tension figure was, however, less straightforward. The area of the figure was greatest when the transition from the short range elasticity to the later compliance occurred about half way through the lengthening and shortening movement; the trapezoid was then most open in shape. When the distance moved was long (Fig. 4d) the area was largest with a rapid movement (continuous line) in which the short range stiffness also lasted for a relatively long distance, but when the movement was shorter (Fig. 4b) the area was largest with a slower movement (interrupted line) in which the short range stiffness lasted for a shorter distance.

With the slower movements a clear corner could usually be seen during lengthening where the short range stiffness gave place to the later compliance; in the faster movements this sharp corner became rounded and indistinct.
The short range stiffness. Velocity of movement affected the range over which the short range stiffness operated, but within this range the actual stiffness was independent of velocity so long as the movement was not too slow. With all movements of soleus faster than about 8 mm/sec the increase in force per unit length (in this short range) was approximately the same, though with movements slower than about 8 mm/sec the stiffness was less. The short range stiffness of gastrocnemius was also approximately constant at velocities greater than about 10 mm/sec (slower movements were not used).

The resistance of the muscle to movements did, however, depend on the intensity with which it was activated, the short range stiffness varying approximately in proportion to the mean muscle tension. In soleus, during lengthening movements at 10 mm/sec or more, and with a variety of different mean muscle tensions, this short range stiffness had a value of 0.6–1.0 N/mm per Newton mean tension, and in lateral gastrocnemius 0.5–0.9 N/mm per N. The stiffness during the early part of shortening was greater than that, but since it merged rather more smoothly into the later more compliant part of the movement it was difficult to measure. These figures are comparable to those obtained for the stiffness of the 'series elastic element' of soleus by the quick stretch and quick release methods at various tensions (Joyce & Rack, 1969), and there is little doubt that the same facet of the muscle's behaviour was being measured in either case.

In many of these experiments a rather abrupt change in force was seen during the first 20–30 μm of the lengthening movement (Figs. 2, 3 and 4). This was more than could be attributed to defects in the movement generator or the transducers, but it was too small an effect to be further investigated with the present equipment.

Tension changes and work absorption. The relationship between the amplitude of movement and the peak-to-peak tension change can be used as a measure of the effectiveness of the muscle at resisting the whole movement. Similarly, the amount of work required to drive the muscle through a complete cycle of movement gives a measure of the ability of the muscles to absorb and dissipate mechanical energy. In Fig. 5a and b the peak-to-peak tension changes and the work absorbed per cycle are plotted for a soleus muscle stretched at four different velocities. Length–tension figures for some of these have been shown in Fig. 4.

With very small movements the tension changes were largely determined by the short range stiffness of the muscle since it was never stretched beyond this range and with small increases in the movement the resulting tension increased in an approximately linear manner (Fig. 5a). As the amplitude of movement increased further, the associated tension changes did not continue to increase at the same rate; the muscle was then being

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Fig. 5. The resistance of soleus to alternating constant velocity movements of different amplitude. The four different velocities used are indicated on the right of the figure. The same experiment as for Fig. 4.

a, the peak-to-peak tension variation. The interrupted line indicates the tension that would occur with a 10 N/mm spring.

b, the work absorption per cycle of movement. The broken lines are sections of parabolae which indicate the way that the work absorption would increase with increasing amplitude in a linear system.

c, the work absorption has been divided by the amplitude² to give an index of the ability of the muscle to absorb external work; this index is plotted against amplitude.
stretched into a range in which it was more compliant and with larger movements the over-all resistance fell further and further below the level measured for small movements, this fall being greatest when the movement was slow.

The work absorbed during each cycle of movement was determined by measuring the area of the length–tension figure. This area always increased with increasing amplitude of movement, but, since the length–tension figures did not remain the same shape as their size increased, the work absorbed in a cycle did not increase simply as the square of the distance moved. Fig. 5b shows the way that the work increased with increasing amplitude of movement; the parabolic dotted lines drawn on the figure show the sort of work absorption records that would have been expected if tension had changed in such a way that the length–tension figures remained similar in shape.

By dividing the work absorption by the square of the distance one can obtain an index of the effectiveness of the muscle at absorbing work in each cycle (Fig. 5c). This index, which has the dimension force/length, gives a measure of the openness of the length–tension figure; it is analogous to the 'viscous stiffness' used in the analysis of sinusoids. Records like the broken line of Fig. 4b, or the continuous line of Fig. 4d give large values, whereas the continuous line record of Fig. 4b or the broken line record of Fig. 4d give smaller values.

For any velocity of movement there was some amplitude at which this index had a maximum value and this was the amplitude at which the short range stiffness occupied about a half of the movement. In Fig. 5c with a velocity of 5 mm/sec this maximum was reached when the movement was through about 0.9 mm; with 10 mm/sec the maximum was with a 1.5–2 mm movement, and with the more rapid movements it was higher still.

When the movement was through a small amplitude and at any but the lowest velocities, the muscle behaviour was like that of a stiff spring which resisted extension with a steeply rising force, but during shortening yielded up most of the energy that was expended on it during lengthening. With larger movements the behaviour (over the whole course of the movement) was that of a more compliant spring which was heavily damped, there was a relatively smaller rise in force during lengthening and an appreciable part of the work that went into the lengthening movement was dissipated by the muscle and did not re-emerge during shortening.

Sinusoidal movement

The results obtained during sinusoidal movements were similar to the results of constant velocity alternating movements and will not, therefore,
be described in the same detail. In a sinusoidal movement, however, muscle length and velocity of movement both change continuously and any increase in the amplitude of movement also involves an increase in the speed with which the muscle lengthens and shortens through the midpoint. This interdependence of length and velocity makes the response to sinusoidal movement more difficult to follow than the response to constant velocity movements.

The smooth change in direction of the sinusoidal movement was associated with a smooth change in the muscle tension, quite different from the sharp corner in the tension record that occurred when the movement suddenly reversed; the length–tension figures obtained during sinusoidal stretching were correspondingly rounded (Fig. 6). During lengthening the transition from the initial short range stiffness to the later compliance could still be seen (Fig. 6b–d), and again, the area of the length–tension figure was usually greatest when this transition occurred in the middle of the movement (Fig. 6b, c).

The effect of amplitude. The muscles responded to small sinusoidal movements with the same relatively steep changes in tension that had been seen with the constant velocity movements, and again the length–tension figure was narrow, only a small amount of work being absorbed by the muscle in a cycle.

Increasing the amplitude of a sinusoid involves an increase in the velocity

Fig. 6. Length–tension figures recorded during sinusoidal movements of soleus through different amplitudes at four different frequencies. a, 11 Hz; b, 4.5 Hz; c, 2.1 Hz; d, 0.9 Hz. The motor nerve was stimulated at 35 impulses/sec. Mean muscle length equivalent to 75° position of the ankle joint.
as well as the amplitude of movement, so it was hardly surprising that with increasing amplitude the short range stiffness lasted for a longer distance (Fig. 6c, d), and the peak to peak tension fluctuation became wider. Fig. 7 shows the response to sinusoidal stretching of a soleus muscle stimulated at 35 impulses/sec (the same preparation as in Fig. 6). The peak-to-peak
tensions plotted in Fig. 7a may be compared with those plotted for constant velocity movements in Fig. 5a, but since in a sinusoid velocity increases with amplitude the lines in Fig. 7a must be thought of as progressively moving across those in Fig. 5a as the amplitude increases.

In a sinusoidal movement the length for which the short-range stiffness operated increased as the amplitude (and therefore the velocity) increased, and the length–tension figure changed in shape less than it had done when the movements were at a constant velocity (Figs. 6b, c).

Fig. 7c, like Fig. 5c, shows the work absorbed per cycle of movement divided by the square of the distance moved; as before, this gives a measure of the effectiveness of the muscle at absorbing work done on it. With small

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**Fig. 8.** The resistance of the lateral head of gastrocnemius to sinusoidal movements of different amplitudes at two different frequencies. Stimulus rate 80 impulses/sec. Mean muscle length equivalent to 90° positions of knee and ankle joints. The results are displayed as in Figs. 5 and 7.
amplitudes of movement in which the length–tension figures were narrow the value obtained was low, but with increasing amplitude it passed through a maximum to diminish slightly at the largest amplitudes used.

Gastrocnemius responded to sinusoidal stretching with tension changes that were similar to those seen in soleus. The records that make up Fig. 8 were obtained during stimulation of a part of the nerve supply to the lateral head of gastrocnemius at 80 impulses/sec. The muscle met small amplitude sinusoidal movements with the sort of resistance one would expect from a stiff spring, and with only a small energy absorption. Movements of larger amplitude were met, however, by a relatively smaller force change, but more work was absorbed in each cycle of movement.

When the energy absorption per cycle of a sinusoidal movement is divided by the square of the amplitude (Figs. 7 and 8) the quantity obtained may be described as the 'viscous stiffness'; this quantity gives a measure of that component of the muscle force that alternates 90° out of phase with the movement (Rack, 1966) and it is a useful measure of the frictional resistance of the muscle to the movement (Joyce et al. 1974).

DISCUSSION

Muscle tension is thought to arise from the coupling together of thick and thin filaments by cross-bridges with spring-like properties (Huxley & Niedergerke, 1954; Huxley & Hansen, 1954; Hansen & Huxley, 1955; Huxley, 1957). The short range stiffness that occurs in the early part of a movement could reflect the combined stiffness of a large number of such links acting in parallel in each sarcomere. Cross-bridges within the myofilaments could not, however, be stretched indefinitely, and after the first short distance they must be continuously broken and re-made. The resistance of the muscle to a long movement must therefore be determined by things other than the stiffness of the cross-bridges.

The short range stiffness. For movements faster than about 8 mm/sec the short range stiffness of soleus was the same as the component of muscle stiffness that has usually been attributed to a 'series elastic element'. We now prefer to avoid the term 'series elastic element'; it suggests a passive element in series with the contractile machinery, and there is mounting evidence (Hansen & Huxley, 1955; Huxley, 1960; Joyce & Rack, 1969; Huxley & Simmons, 1971a,b; Blangé, Karemaker & Kramer, 1972) that the change in tension in response to a quick stretch or quick release cannot all be attributed to such a passive element.

In the experiments reported here the soleus muscle was coupled to the movement generator through a tendon which yields by about 0.05 mm/N force (Joyce & Rack, 1969). Part of the movement would therefore be taken up in the tendon and this part has to be subtracted before one can
arrive at an estimate of the short range stiffness of the active part of the muscle tissue.

The short range stiffness was different at different muscle tensions, as one would expect if it were due to the stiffness of the number of cross-bridges acting in parallel. After making a correction for the tendon compliance, the short range stiffness of the active part of the muscle can be expressed as a function of the mean tension; the values obtained were 1·1–1·5 N/mm per N mean tension. Assuming the muscle fibre lengths in these experiments to be 33 mm and the sarcomere lengths 2·6 μm (see Rack & Westbury, 1969, Fig. 2) this result may be stated as a 35–50% increase in force per 1% extension of the soleus fibres or, if the extension is equally distributed through the muscle, a 2·7–3·8% increase in force for each nm/half-sarcomere movement.

Having expressed the short range stiffness (which we believe to be largely due to the properties of the cross-bridges) in a way that is independent of muscle length or force, we are able to compare it with values obtained from other muscles. When Huxley & Simmons (1971a, b) carried out quick stretch and quick release experiments on single fibres of frog semitendinosus muscles the force changed in two distinct phases, but the immediate force change that accompanied the movement lasted for only a few msec, and our short range stiffness must be compared with their second slower phase. Their force changes varied with the amplitude of the length step in a non-linear way, but with the 0·5–1·0% movements such as we generally used, their force decreased by 2·5–5·5% per nanometre/half sarcomere shortening. So far as it goes, this agreement is good, but the records of Huxley & Simmons suggest that their muscles were considerably less stiff in their resistance to lengthening.

One can also express the short range stiffness in terms of the range of movement possible for the muscle in the living animal; such a measurement is useful in comparing the results of animal experiments with those obtained in human subjects (Joyce et al. 1974). Taking the physiological range for cat soleus as 22 mm the short range stiffness would amount to a 25–35% force increase for a length change that was 1% of the muscle range.

We cannot express the short range stiffness of lateral gastrocnemius in terms of either fibre length, or range of movement, since we lack precise information about either of these.

In constant velocity alternating movements the short range stiffness persisted for about twice the distance that was seen when the movement started from an isometric contraction (Joyce et al. 1969). The actual distance for which the muscle was stiff depended on the speed of the movement; this was to be expected since the average cross-bridge would in a rapid movement probably move further before being broken down than it would in a slow movement. In a rapid alternating
movement the short range stiffness lasted for up to 1.4 mm of a lengthening movement, though at least 0.6 mm of this would be taken up in stretching the tendon. The 0.8 mm movement of the muscle fibre, however, still amounts to a 2–3% elongation (or a movement through 3–4% of the physiological range). If this movement were equally distributed along the fibres there would be 25–35 nm of movement in each half sarcomere, which is a larger cross-bridge movement than one would expect from electron micrographs (Huxley, 1969); on the other hand, the results of Huxley & Simmons (1971a, b) suggest that frog muscle fibres could shorten from an isometric contraction by at least 13 nm/half-sarcomere without breakage of cross-bridges. The lengthening movements in the present experiments began immediately after shortening; when many of the cross-bridges would have been in a shortened state, these could presumably be re-extended through their ‘initial’ lengths and then lengthened further giving a longer range of movement than would be seen in a previously isometric muscle.

If the short range stiffness is to be explained in terms of extension of cross-bridges, then many of them must be extended further than the 25–35 nm mentioned above; the cross-bridges could not all break down together at the end of the first steep tension rise, or the tension would then fall as it often did when an extension followed isometric contraction. Presumably many of the cross-bridges persisted for longer distances.

**Work absorption.** If during a cycle of movement the same elastic cross-bridges were sequentially lengthened and shortened, then any work done on them during lengthening would re-emerge during the subsequent shortening. The muscle would behave as a spring and in each cycle of movement there would be no nett work absorption. If, however, cross-bridges that had gained in tension during lengthening were then broken down and re-formed at a lower tension, some of the work that was done on them during lengthening would be lost. The new cross-bridges would certainly exert some tension during the subsequent shortening movement, but at their shorter lengths this tension would be smaller than during the preceding lengthening movement. One would therefore expect to find, as we did, that the work absorption was small in a small movement, but with increasing amplitude of movement there was a more than proportional increase in the work absorption, until the movement was so large that each cross-bridge must have been broken down at least once during lengthening and shortening.

**The physiological significance of the results.** The mechanical properties of muscles modify the way that animal limbs meet external forces. In particular, the response to the first part of an unexpected movement must largely be determined by the muscle properties since some time is re-
quired before any form of reflex response can develop (Rack, 1970; Grillner, 1972). The short range muscle stiffness could well limit the displacement caused by an unexpected force until the nervous system initiated an appropriate response. The response to small displacements was, however, essentially elastic and much of the energy that went into a rapid short extension re-emerged if shortening followed at once. One can imagine both advantages and disadvantages in having limbs operated by relatively undamped elastic muscles; springs may be used for the storage of mechanical energy, and muscles are no doubt sometimes used in this way (Hill, 1950). During such movements as running and hopping, extensor muscles are stretched on landing, and it would clearly be an advantage to have some of the energy from the descent stored in spring-like components of the muscle for the subsequent take off. On the other hand, a mass, such as a limb, held in position by springs would, when disturbed, tend to oscillate and in the presence of any random disturbance it would be difficult to accurately maintain its position. Such an oscillation would, however, be limited to the small amplitude in which the muscles absorb little energy in each cycle of movement.

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