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THE MECHANICAL PROPERTIES OF CAT SOLEUS MUSCLE DURING CONTROLLED LENGTHENING AND SHORTENING MOVEMENTS

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SUMMARY

1. By supplying pulses to different subdivisions of the ventral nerve roots in rotation, it was possible to obtain smooth contractions of cat soleus with low rates of stimulation.

2. After contracting isometrically the muscle was subjected to constant velocity lengthening or shortening movements.

3. During shortening the tension always fell below the isometric value. The fall in tension was usually greatest when low rates of stimulation were used.

4. The effect of lengthening on tension depended on the rate of stimulation. At high rates of stimulation the tension during lengthening always rose above the isometric tension. At lower rates of stimulation (5–15 pulses/sec) the tension rose at the beginning of an extension, but decreased later in the movement to a level that was often less than the isometric tension corresponding to that muscle length. At these stimulus rates the tension during isometric contraction was usually higher than during a sustained movement in either direction.

5. At low rates of stimulation longitudinal vibratory movements of more than 0.1 mm also reduced the tension far below the isometric value, whereas the reduction was quite slight when the rate of stimulation was high.

6. The isometric tension during smooth contractions at low stimulus rates was remarkable in the following respects: it developed rather slowly, it was higher than the tension during or immediately after movements, and it was only slowly regained after movement had ceased.

7. The results are discussed in relation to the sliding filament theory of muscle contraction, which, with certain assumptions, provides an explanation for many of the findings.

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INTRODUCTION

In normal life the lengths of muscles, the extent to which they are activated, and the tension they exert change continually. The relationships between muscle length, velocity of lengthening or shortening, and tension have been studied in detail during twitch contractions, and during stimulation at rates high enough to give a smooth tetanic contraction. The behaviour of muscles stimulated at lower, more normal rates has received less attention.

Hill (1938) and Abbott & Wilkie (1953) found that the tension in frog muscles stimulated at high rates could be expressed as a function of their length and velocity of shortening, though it was necessary to make measurements during isotonic movements in order to avoid the complicating effects of series elastic elements. This relatively simple force–velocity relationship did not however cover lengthening movements, nor did it hold for shortening movements in some mammalian muscles (Rosenblueth & Rubio, 1959).

In the present investigation it became clear that the tension developed by cat soleus during lengthening or shortening was modified by the length changes that had preceded that situation. This effect of preceding movements could be seen during either isotonic movements, or movements that were directly imposed on the muscle; in each case the effect was most striking with rather low rates of stimulation such as the animal might normally use.

The behaviour of the muscle was generally easier to understand when the whole course of a movement was controlled; we shall therefore deal with that situation first. This paper describes the tension changes in cat soleus that accompanied constant velocity movements (Levin & Wyman, 1927; Abbott & Aubert, 1952), and imposed longitudinal vibrations (Buchthal & Kaiser, 1951; Matthews, 1966), but using a variety of different rates of stimulation. Isotonic movements will be described in a later paper (Joyce & Rack, 1969).

METHODS

The anaesthesia, dissection, fixation, and the force transducer have been described in the previous paper (Rack & Westbury, 1969) which also explains the method of stimulating by distributing pulses sequentially to subdivisions of the ventral roots. Thirteen cats were used weighing between 1·7 and 4·5 kg; some of these also contributed results to the preceding paper.

Constant velocity movements. The tendon and force transducer were connected to a lever arm mounted on ball bearings. The position of this lever was controlled by a lead screw, rotation of which caused lengthening or shortening movements of the muscle. Constant velocity movements were obtained by coupling a velodyne to the lead screw through an electro-magnetic clutch. With this arrangement it was
possible to lengthen or shorten the muscle at velocities up to 50 mm/sec (Figs. 1 and 2). This movement was always associated with some vibration, but its amplitude was usually less than 30 \( \mu \) (peak to peak) and always less than 50 \( \mu \); vibration of this magnitude has in itself a negligible effect on the muscle tension.

Length transducer. The rod that coupled the force transducer to the lever carried a diaphragm which passed between a light source and photo-electric cell. Lateral movements were prevented by two steel balls mounted on the coupling rod, one on each side of the diaphragm, these ran in channels cut in Nylatron (Polypenco Ltd., Welwyn Garden City, Herts.). The light source was a bulb ground on its surface, supplied by a circuit designed to provide a constant current flow. This transducer operated over a range of 14 mm; it was linear to within 1% of the full scale signal.

Imposed vibration. When longitudinal vibration was required the tendon and strain gauge were attached to another lighter lever which was held against an eccentrically rotating cam. This mechanism provided longitudinal sinusoidal oscillations through distances up to 1 mm (peak to peak) at frequencies up to 100 c/s.

Experimental procedure. As in the previous paper (Rack & Westbury, 1969), stimulation of the muscles was carried out at 2 min intervals, the results of the first two such contractions being discarded.

RESULTS

When, after contracting isometrically, the muscle was allowed to shorten or obliged to lengthen, the onset of movement was usually accompanied by an abrupt change in tension; this was then followed by more gradual changes which continued throughout the movement (Figs. 1 and 2). This paper is mainly concerned with the behaviour of the muscle during the later part of the movement, when it had already moved through a number of millimetres at a constant velocity.

The tension during shortening. When the muscle was allowed to shorten at constant velocity (Fig. 1), the tension at first fell rapidly below the isometric value, and then more slowly; through the whole course of shortening it was always less than the muscle would have generated during isometric contraction at the lengths it was passing through (dashed line in Fig. 1).

This fall in tension during shortening was more striking when the lower rates of stimulation were used. Figure 1 shows some typical results during shortening at 12 mm/sec, the tension at 7 impulses/sec soon fell to about 10% of the isometric level, whereas at 50 impulses/sec the fall was a much smaller proportion of the total tension.

The tension during lengthening. Rapid forcible extension of an active muscle may lead to irreversible damage (Gasser & Hill, 1924). The lengthening movements used in the present experiments had no such deleterious effects on the cat soleus which continued to give repeatable results after numerous extensions of up to 10 mm at velocities up to 50 mm/sec.

The tension changes that occurred during lengthening were more complicated than during shortening, and they differed with different stimu-
lating conditions. Figure 2 shows the tension that developed in response to a constant velocity movement during stimulation at 50 impulses/sec (Fig. 2a) and 7 impulses/sec (Fig. 2b). In each case the tension rose steeply during the first 0.5 mm of movement, and in each case it rose more

\[ a \text{ 50 impulses/sec} \]

\[ b \text{ 7 impulses/sec} \]

Fig. 1. Muscle tension during shortening. Length records (below), and tension records (above) photographed from an oscilloscope display. (a) Stimulation at 50 impulses/sec in each of five channels. (b) 7 impulses/sec in each channel. In each case an isometric contraction was followed by shortening at 12.5 mm/sec.

Tension was also measured during other isometric contractions at some of the lengths that the muscle shortened through. These tensions have been put in (dashed lines) opposite the appropriate parts of the length records.

The ripple visible on the tension records during movement is due to vibration from the motor and lead screw.

\[ a \text{ 50 impulses/sec} \]

\[ b \text{ 7 impulses/sec} \]

Fig. 2. Muscle tension during lengthening. After an isometric contraction the muscle was extended at 7.2 mm/sec. Recorded as in Fig. 1. (a) Stimulation at 50 impulses/sec in each channel; (b) 7 impulses/sec in each channel.

The dashed lines indicate isometric tension plotted opposite appropriate parts of the length records.

gradually during the last part of the movement. But, whereas at 50 impulses/sec the steep initial rise in tension was followed by a further gradual rise, at 7 impulses/sec this initial rise was followed by a fall in tension which only began to rise again when the muscle had been stretched through about 3 mm. This fall often took the tension during lengthening
below the isometric tension that corresponded to the new muscle length, and although the tension gradually increased later in the movement, it often remained below the corresponding isometric tension for a considerable distance. At this point the muscle was being lengthened by a force smaller than it could have withstood in an isometric contraction at the same length.

![Graph showing tension during extension through different parts of the length range.](image)

Fig. 3. Tension during extension through different parts of the length range. Tension records from a number of different extensions similar to those shown in Fig. 2 have been traced (continuous line) to show how the tension during lengthening differs from the isometric tension in various parts of the length range. Positions of the ankle joint are shown below corresponding parts of the abscissa.

In each case the muscle was lengthened through 6 mm at 7.2 mm/sec. The interrupted lines are isometric length–tension plots.

The response of the muscle to lengthening depended on the muscle length as well as the rate of stimulation. Figure 3 shows the courses of a number of constant velocity movements similar to those shown in Fig. 2, but through different parts of the muscle length range. The dotted lines are isometric length–tension plots at three different stimulus rates. The continuous lines show the tension during separate 6 mm extensions at 7.2 mm/sec; as in Fig. 2 each movement started from an isometric contraction.

At each rate of stimulation the records of tension during extension formed a more or less orderly series (Fig. 3). At a high stimulus rate the tension rose above and generally remained above the isometric tension corresponding to the length that the muscle was passing through. With lower rates of stimulation there was a range of lengths within which the
tension during movement fell below the corresponding isometric length–tension curve. This effect was seen at lengths where the isometric tension increased rather steeply with increasing length (Fig. 3).

The fall in tension that sometimes occurred during lengthening was an unexpected finding, and quite different from the behaviour of a muscle tetanized at high rates. At first sight the tension during lengthening was surprisingly low, but it was only low when compared with the corresponding isometric tension. It was equally reasonable to regard the isometric tension as exceptionally high; we have come to prefer this latter viewpoint.

Figure 4 gives another view of the response to an imposed lengthening. One curve (crosses) shows the isometric tension during stimulation at different rates. The other curve (dots) shows the tension in the same muscle as it was extended through that same length at 7.2 mm/sec after 5 mm of movement. At the highest stimulus rates the tension during lengthening rose above the isometric tension, as it did in Fig. 2a, but at some lower stimulus rates it fell below the isometric tension as it did in Fig. 2b.

At the lowest rates of stimulation the situation was different again; the contraction was imperfectly fused, so that there was movement within the muscle even under isometric conditions. At these stimulus rates the additional externally imposed movement did not always reduce the tension further.

The effect of velocity on tension. Figure 5 shows the effect of velocity of movement on tension. At the high rate of stimulation the response to movements was in many respects similar to the response of other fully

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Fig. 4. The effect of stimulus rate on tension. Isometric tension x ; tension during lengthening at 7.2 mm/sec ○. Measurements were made at a muscle length corresponding to an angle of 70° at the ankle; all movements began 5 mm short of that length.
tetanized muscles (Levin & Wyman, 1927; Abbott & Aubert, 1952). During shortening the tension fell below, and during lengthening it rose above the isometric tension; though it did not always continue to increase with increasing velocities of lengthening.

During stimulation at a lower rate (7 impulses/sec in Fig. 5) the isometric tension exceeded the tension during either lengthening or shortening, but during very slow lengthening the muscle was evidently able to retain some part of the extra tension associated with isometric contraction. At 7 impulses/sec the isometric tension far exceeded the tension during even quite slow shortening; when in Fig. 5 the muscle shortened at 3 mm/sec it developed only about half its isometric tension, whereas at 35 impulses/sec the same velocity of movement reduced the tension by only about 20% of the isometric value. The 7 impulses/sec plot of Fig. 5 emphasizes the exceptional nature of the tension during isometric contraction, which was a good deal higher than could have been expected from a knowledge of the tension during movements.

At the onset of an isometric contraction the tension rises to its plateau at different speeds with different rates of stimulation (Cooper & Eccles, 1930; Buller & Lewis, 1965; Rack & Westbury, 1969). The foregoing results suggest an explanation for these differences. As the tension rises, the contractile parts of the muscle shorten at the expense of series elastic elements (Hill, 1949); when the force–velocity curve rises steeply to the zero velocity point (Fig. 5, 7 impulses/sec) this internal re-arrangement
will proceed slowly as the tension approaches its final value, and this final value will therefore only gradually be reached. In these experiments the tension in isometric contractions developed slowly when the muscle length and stimulus rate were in a range where the isometric length–tension curve was steep (Rack & Westbury, 1969); this was the same range within which the force–velocity curve rose steeply to the zero tension point.

![Graph](image)

Fig. 6. Tension during and after muscle lengthening. In each case the muscle was extended through 5 mm at 7.2 mm/sec, and held at the final length (uppermost trace). The tensions developed at three different rates of stimulation are shown below.

_Tension changes after the movement ceased._ Figure 6 shows the tension before, during and after a constant velocity extension with the muscle stimulated at three different rates. In each case the final tension was approximately the same as the muscle achieved during an isometric contraction at that length, but this tension was reached in different ways.

At 50 impulses/sec the tension during movement was greater than the isometric tension, and it fell to the final level when the movement ceased. At 7 impulses/sec the tension during movement became less than the isometric tension, and when movement ceased it climbed gradually to its final level after an initial fall. At this rate of stimulation the muscle could only develop its full isometric tension if it was held stationary for a long
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enough time, and once the muscle had been moved a further period of immobility was needed before the full isometric tension could again be achieved.

The tension always rose as lengthening began, and always fell immediately the movement ceased (Fig. 6), showing that the actual process of lengthening added something to the tension even though the tension during the movement was sometimes surprisingly low. Two factors were presumably operating; the actual process of lengthening was accompanied by an increase in tension, but at low stimulus rates the movement also led

![Diagram](image)

Fig. 7. The effects of movement on an unfused tetanus. Photographs of tension and length displayed as in Fig. 2, but during synchronized stimulation of the whole muscle at 8·5 impulses/sec. The muscle was lengthened, and shortened at 11·5 mm/sec.

to a loss of the 'extra' tension that was peculiar to isometric contraction; on balance the tension during lengthening often fell below the corresponding isometric tension when the stimulus rate was low.

In the 15 impulses/sec record of Fig. 6 the tension at the end of the movement was higher than the final isometric tension, but when the movement ceased the tension fell below the isometric tension and then climbed up again rather slowly. Presumably the additional tension associated with lengthening outweighed the loss of isometric tension during the movement, but this additional tension decreased rapidly when the movement ceased whereas the isometric tension took some time to redevelop.

**Fusion of tetani during movement.** When low rates of stimulation were used tension fluctuated at the stimulus frequency. This fluctuation was always more marked during lengthening or shortening movements than during an isometric contraction.

In these experiments minor tension fluctuations were often obscured by vibration transmitted from the motor and lead screw; when, however, stimuli were supplied synchronously to the whole muscle giving an unfused
tetanus, the effect of movement on this tension fluctuation was clearly seen. In Fig. 7 the muscle was stimulated synchronously at 8.5 impulses/sec; during isometric contraction the tension fluctuation was quite small (less than 4% of the mean tension), but during lengthening the fluctuation increased a great deal to become more than 20% of the mean tension. During shortening the tension fluctuation was less striking, but it was in fact an even larger proportion of the much smaller mean tension.

![Graph showing muscle tension fluctuations](image)

**Fig. 8.** The effect of vibration on muscle tension. After contracting isometrically the muscle was subjected to longitudinal sinusoidal vibration at 100 c/s (the movement did not in fact reach this final frequency for two or three cycles). The imposed vibration was through 0.56 mm (peak to peak), the preceding isometric contraction being at the shorter end of this movement cycle. The mean length during vibration was therefore 0.28 mm longer than during isometric contraction.

**The effect of vibration on muscle tension.** Externally imposed vibration is a convenient method of moving a muscle continuously with little or no alteration of its mean length. Vibratory movement is accompanied by a corresponding tension oscillation, but the mean tension is usually less than the isometric tension would have been at the same mean length (Buchthal & Kaiser, 1951; Matthews, 1966).

Longitudinal vibration of 0.1–1.0 mm (peak to peak) reduced the mean muscle tension below the isometric tension, but this reduction was only
large when low rates of stimulation were used. Figure 8 shows the tension changes that accompanied a vibration of amplitude 0.56 mm (peak to peak) at 100 c/s. During stimulation at 35 impulses/sec the mean tension fell only a little below the isometric tension, but during stimulation at 7 impulses/sec the mean tension fell to less than a quarter of the isometric tension. At these low rates of stimulation, tension was reduced below the isometric value by either lengthening or shortening movements, so it was hardly surprising that vibration which combines lengthening and shortening movements should reduce the tension in a similar way. Vibration of amplitudes less than 0.1 mm peak to peak had negligible effect on the mean muscle tension.

DISCUSSION

The cat soleus muscle has different properties at different lengths and at different rates of stimulation. The stimulus rate–tension plot has a steep section in which a small increase in rate causes a relatively large increase in tension, but at different muscle lengths this steep section occurs over different ranges of stimulus rate (Rack & Westbury, 1969). The isometric tension that the muscle developed in this range was unusual in a number of respects; it took longer to develop, it reached its final level only in the absence of movement, and it was greater than could have been expected from a knowledge of the muscle performance during movements.

Hypothesis. These findings can be explained in terms of the sliding filament theory of muscle contraction (A. F. Huxley & Niedergerke, 1954; H. E. Huxley & Hansen, 1954; Hansen & H. E. Huxley, 1955; A. F. Huxley, 1957) if certain assumptions are made.

Muscles are believed to generate tension by the formation of cross links between thin and thick filaments within the myofibrils, each link exerting a force that tends to move the filaments in relation to each other. The number of links in existence at any time must depend on their rates of formation and breakdown, and these may change independently in different circumstances. It is this independence of the processes of formation and destruction of links to which we wish to direct attention.

It is assumed that cross links may be formed when active sites on the thick and thin filaments bear an appropriate relation to each other, their rate of formation being related to the level of activation of the contractile machinery. The rate of destruction of links is assumed to change as the relationship between the filaments alters (Huxley, 1957); to explain the experimental results it is necessary to postulate that cross links are only slowly broken down as long as they remain in the position at which they were formed, but are more likely to be broken down when they are distorted by movement in either direction. The rate of break-down of links
would then be less in truly isometric conditions than during lengthening or shortening movements.

If such a muscle were stimulated at a high rate, the contractile mechanism would be powerfully activated so that there would be a strong tendency for cross links to be formed. If during such intense activation the filaments moved on each other, the increased rate of destruction of links that accompanied the movement might not too seriously diminish their number. During muscle lengthening links would be stretched or distorted from their initial position, with a probable increase in the force they exert; whereas during shortening the links would move in the opposite direction and exert less force. At high rates of stimulation, therefore, the tension could be expected to rise during lengthening and fall during shortening, as indeed it did in the experiments that have been described.

If the contractile mechanism were less intensely activated cross links would be formed more slowly, but in the absence of movement the rate of break-down of links is assumed to be low, so that given time a relatively large number of cross links might still be formed, with a correspondingly high muscle tension. If, however, the filaments then moved on each other in either direction, the rate of destruction of cross links would increase, and since they would reform relatively slowly the total number of links might decrease considerably, with a corresponding fall in tension. In a shortening movement the mean force exerted by each link would also decrease so that the tension would fall far below the isometric value.

If with a low level of activation the muscle were lengthened, the number of links would again be less than during isometric contraction, but individual links would then exert a greater force. If this extra force of the individual links outweighed the reduction in their number, the tension during lengthening would exceed the isometric tension, but if the number of links were greatly reduced the tension during lengthening would then fall below the isometric tension.

The changes in tension observed during imposed movement of soleus were those that would be expected from the model suggested above, if a low stimulus rate is taken to correspond to a low level of activation of the contractile machinery. With high rates of stimulation the tension rose above the isometric value during lengthening, and fell below it during shortening; but with lower stimulus rates the tension often fell below the isometric value during movement in either direction. At the lowest rates of stimulation the contraction was in our experiments always somewhat irregular, and the fibres moved within the muscle. A high rate of break-down of cross links could then be expected even during supposedly isometric contraction, and it was no surprise that imposed lengthening failed to reduce the tension further (Fig. 5, 3 impulses/sec).
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When a motor unit is stimulated at a low rate the tendency for cross links to be formed must presumably increase with each action potential, decreasing again between stimuli with a consequent fluctuation in the number of links. When a number of motor units are activated synchronously there is a corresponding fluctuation in the total muscle tension and some internal movement. If now the break-down of links is further accelerated by external movement, the fluctuation in their number is likely to be between wider limits; it is hardly surprising therefore that in an unfused tetanus the tension fluctuates more widely during movement than during an isometric contraction.

*The relation between stimulus rate and isometric tension.* If in a quite stationary muscle fibre cross links were destroyed at a rate proportional to their number, but were formed at a rate proportional to some product of the level of activation and the number of available unused sites (Huxley, 1957), the number of links present, and therefore the tension during sustained contraction, would depend on the level of activation in the way indicated in Fig. 9 (continuous line). With increasing activation the tension would rise toward a limiting value equivalent to the tension that would develop if every link that could be formed were formed.

At low rates of stimulation, however, some internal movement of the muscle occurred in our experiments; this movement could be expected to increase the rate of destruction of cross links with a corresponding fall in tension to give the stimulus rate–tension curve a sigmoid form (Fig. 9, long dashed line).

When the whole muscle was stimulated synchronously, there was even more internal movement, which also occurred with higher stimulus rates; such movement could be expected to decrease the tension further, and to have an effect on tension at higher stimulus rates, displacing the steep section of the sigmoid curve towards the right (Fig. 9, short dashed line).
These predicted curves are in fact similar in shape to the experimental stimulus rate–tension plots for soleus (Rack & Westbury, 1969).

The method of distributing impulses among different groups of muscle fibres was relatively crude, and a significant amount of internal movement was always present when the stimulus rate was low. By appropriate distribution of activity among adjacent fibres that are mechanically coupled together the animal may be able to generate an isometric tension that follows a pattern something like the continuous line in Fig. 9.

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