

ISOTONIC LENGTHENING AND SHORTENING MOVEMENTS OF CAT SOLEUS MUSCLE

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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 'step' changes in tension after which it lengthened or shortened isotonicly.
3. Isotonic lengthening movements usually began relatively slowly but proceeded with increasing velocity; this acceleration was most conspicuous when low rates of stimulation were used.
4. At low rates of stimulation the isotonic lengthening movement often continued beyond the length at which the muscle could have generated that tension in an isometric contraction. The muscle then shortened slowly back toward that length.
5. Isotonic shortening movements began relatively rapidly, but as shortening continued the movement became slower, and often had an irregular oscillatory course.
6. The isotonic movements are discussed in relation to the sliding filament theory of muscle contraction.
7. The compliance of the series elastic elements was calculated from the relative amplitudes of the 'step' changes in tension and length. The stiffness of this component increased with increasing muscle tension.

INTRODUCTION

Previous papers (Rack & Westbury, 1969; Joyce, Rack & Westbury, 1969) described the tension developed by cat soleus during isometric contractions, and during imposed movements at various constant velocities. The changes in tension in these experiments must necessarily have been

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accompanied by corresponding changes in the length of the tendon and other compliant elements in series with the contractile machinery, and it was uncertain how much of the external movement could be accounted for in that way.

When, however, a tetanized muscle is subjected to a sudden 'step' change in tension, and the tension is thereafter held constant while the muscle moves freely, the accompanying length changes occur in two distinct phases. There is first a very rapid 'step' change of length which is attributable to undamped or very lightly damped series elastic elements; this is then followed by a slower isotonic movement that is presumed to reflect the properties of the contractile components of the muscle fibres (Bouckaert, Capellen & de Blende, 1930; Jewell & Wilkie, 1958).

This subdivision of the muscle into contractile and series elastic elements (Levin & Wyman, 1927; Hill, 1949) proves very useful in the treatment of experimental results, but we do not intend to imply that the two components are anatomically separate, nor that the series elastic element is necessarily something entirely passive.

This paper describes length changes that occurred when, after contracting isometrically, the cat soleus was subjected to a sudden change in tension, after which it was free to lengthen or shorten isotonicly.

METHODS

Thirty-nine cats were used, their weights ranging from 2.1 to 4.2 kg. Many of these also contributed results that have been included in the preceding papers.

The anaesthesia, dissection, fixation of the animal, and the force transducer have already been described. Tetani were always at 2 min intervals and the stimulating pulses were distributed to different subdivisions of the soleus nerve supply in rotation (Rack & Westbury, 1969).

The muscle tendon and force transducer were coupled through a photo-electric position transducer (Joyce *et al.* 1969) to an assembly designed to give a constant tension load.

Constant tension was achieved by the use of Tensators (Tensator Ltd., Newport Pagnell, Bucks). These are coils of spring steel which when straightened return to their coiled form if they are free to do so. When a Tensator is mounted on a freely rotating bobbin, the outer end can only be pulled away from the bobbin by a force that overcomes the tendency of the metal to curl and the Tensator resists such an extension with an approximately constant force.

Selected pieces of Tensator were riveted together in pairs and mounted on light bobbins made of Nylatron (Polypenco Ltd., Welwyn Garden City, Herts.) and fitted with miniature ball races (Fig. 1). As the pair of Tensators moved through the gap between the bobbins they exerted an approximately constant force on the coupling rod. Nineteen such assemblies were available with forces ranging from 40 g to 4 kg.

Release mechanisms. The coupling rod to which the Tensators were attached carried a steel ball which could be gripped between a pair of levers (L in Fig. 1). These levers were held in position by an electro-magnetically controlled latch.

When this latch was opened, the levers were pulled apart by strong springs leaving the muscle coupled only to the Tensator assembly, and free to move.

The restraining levers along with the latch that controlled them could, when necessary, be moved longitudinally on a lead screw rotated by a velodyne, lengthening or shortening the muscle before release of the levers.

Inertia and friction. Some force was required to accelerate the moving parts and to overcome friction. This additional force could alter the tension on the muscle, and it was obviously desirable to keep it to a minimum.

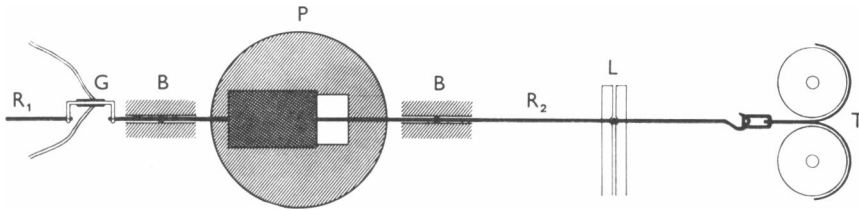


Fig. 1. Transducers, and the Tensator assembly. The muscle tendon was connected by the coupling rod R_1 to a force transducer G consisting of two semi-conductor strain gauges mounted on a beryllium copper link. The second coupling rod R_2 was mounted on Nylatron bearings B and connected the force transducer to the Tensator assembly T. This rod carried the diaphragm of the photoelectric position transducer P, and a steel ball that could be locked between the levers L.

The bearings on either side of the position transducer (B in Fig. 1) had significant friction whenever the direction of pull of the muscle was not quite axial. In each experiment, therefore, care was taken to align the muscle as perfectly as possible. The remaining friction still sometimes caused a small alteration of tension when the direction of movement reversed (Figs. 4 and 6 a).

The various couplings, the force transducer, and the moving parts of the position transducer weighed 4.7 g. The inertia of the Tensator assemblies varied with their size from 0.4 g for the smallest to 17.5 g for the largest. When the tension was 800 g or more, the effective mass of all moving parts was less than 10 g per kg applied force, though the mass was relatively larger when smaller forces were used.

Since the tendon was coupled directly to the force transducer by a rod weighing only 0.4 g, the tension record gave a good indication of any tension changes that did occur, whether they were the results of inertia, friction, or imperfections in the Tensator.

Compliance of mountings. Movements that occurred in the mountings of either the animal, or the position transducer would not appear on the length records, and could lead to error. In fact these mountings yielded by 0.08 mm/kg force between them; this small movement was usually disregarded.

RESULTS

When, after a short period of isometric contraction the levers that had restrained the muscle were suddenly released, the tension on the muscle changed rapidly to a new value, and the muscle was free to lengthen or shorten. The initial 'step' change in tension was accompanied by a similar

rapid length change; these initial rapid changes were complete in 10–20 msec, thereafter the muscle lengthened or shortened isotonically, and usually at a very much slower rate (Fig. 2).

With the tensions used (up to 4 kg) the muscle remained in good condition giving repeatable results for long periods. Permanent damage to the muscle (Gasser & Hill, 1924) was only seen when higher tensions were used.

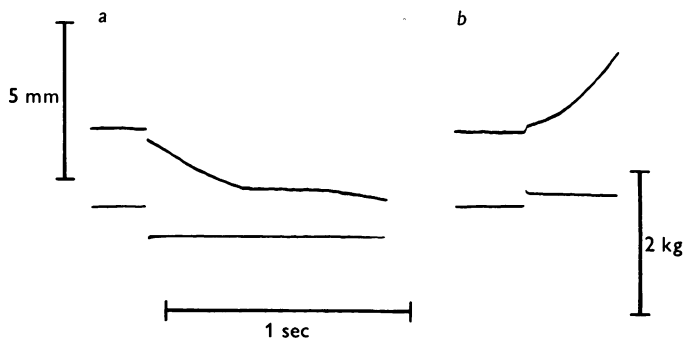


Fig. 2. The muscle length changes that accompany a 'step' change in tension. Oscilloscope photographs; the length record is above, tension below. Stimulus rate 10 impulses/sec in each of five channels. Isometric contractions at a length equivalent to an angle of 80° at the ankle were followed by a sudden decrease in tension (*a*), and a sudden increase (*b*). After the change in tension the muscle was in each case free to move isotonically.

Isotonic movements

After the first rapid movement the muscle lengthened or shortened isotonically, and the velocity of any part of this movement could be measured from the slope of the length record.

When cat soleus moves into a different length range, its contractile force changes, and the velocity of movement might be expected to change also (Abbott & Wilkie, 1953); the changes that occurred in these experiments were not, however, those that might have been anticipated from length changes alone.

When the tension on the muscle exceeded the isometric tension by a small amount, the initial 'step' was followed by isotonic lengthening which was at first quite slow, but then proceeded with increasing velocity (Fig. 2*b*), even though the muscle was being extended into a length range in which it could be expected to resist the movement more effectively. The muscle was evidently relatively good at resisting the first part of the movement, but as the lengthening proceeded the resistance offered by the muscle decreased and the movement accelerated. This sort of behaviour was seen with increments of tension up to about 30% of the isometric value.

Isotonic shortening movements on the other hand often began fairly rapidly but then became much slower, and sometimes stopped altogether for a time. The velocity of shortening could be expected to decrease as the muscle moved to a shorter length (Abbott & Wilkie, 1953), but the changes in velocity that occurred in these experiments could not be wholly accounted for in that way. In Fig. 2*a* the movement ceased for a time after 2 mm of shortening though the muscle was still 4 mm longer than the length at which it could develop that tension in an isometric contraction.

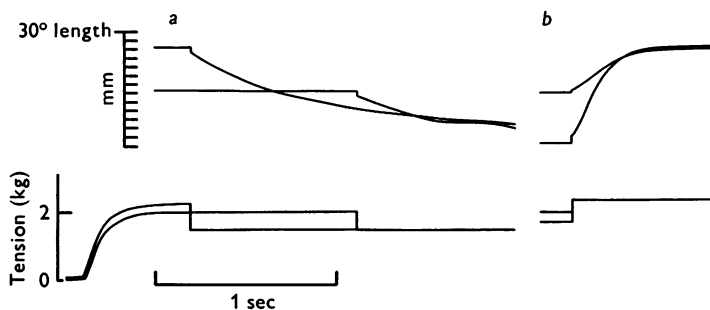


Fig. 3. Isotonic movements from different starting points. Tracings from oscilloscope photographs. Stimulation at 35 impulses/sec. (a) After isometric contractions at two different lengths the muscle was released and allowed to shorten isotonicly, the tension being the same in either case. (b) After isometric contractions the muscle was lengthened isotonicly.

It was clear that at any tension the velocity of an isotonic movement was modified both by the immediate history of movement, and by the changes in muscle performance that occur anyway at different lengths. In order to separate these two effects, isotonic movements were arranged to start from different muscle lengths. The velocity of lengthening or shortening could then be measured at the same length, and under the same tension, but with different previous histories of movement. The movements were usually so timed that measurements were made after approximately equal periods of stimulation.

Figure 3*a* shows the course of two such shortenings during stimulation at 35 impulses/sec. When movement began from the shorter length, the velocity after 1 mm of movement was about 8 mm/sec; when, however, the muscle was made to pass through the same length with the same tension, but after already moving 6 mm, it had only half that velocity. The preceding shortening movement had evidently affected the properties of the muscle in a way that made it less effective at shortening against a load than it was at the beginning of a movement. Aidley (1965) found that the velocity of shortening of frog rectus abdominis muscle immersed in solutions rich in potassium depended on their histories of previous movement

in a similar way. The irregular course of the later part of shortening (Fig. 3*a*) will be considered later.

During lengthening (Fig. 3*b*) the velocity was less when the muscle had just started to move than when it reached the same length after some millimetres of preceding movement. Again, the preceding movement made the muscle less effective, so that it was less well able to limit the velocity of lengthening.

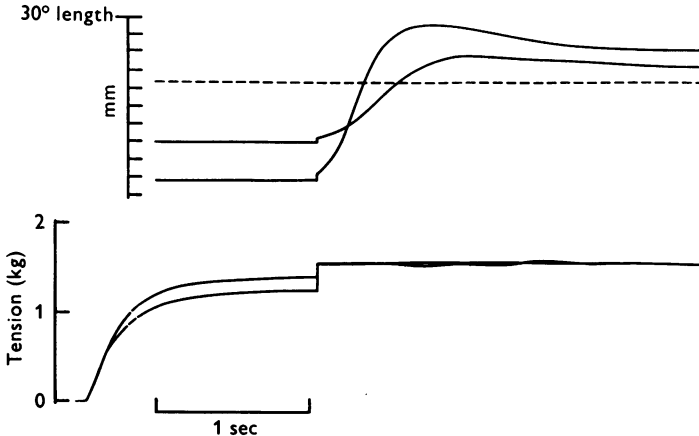


Fig. 4. Isotonic lengthening from different starting points. Similar to Fig. 3*b*, but during stimulation at 10 impulses/sec in each of five channels. The dashed line indicates the length at which the isometrically contracting muscle gave the same tension that had caused the isotonic lengthening movement.

The effect of stimulus rate. The differences between the muscle performance at the beginning of a movement, and late in its course were seen at all rates of stimulation, but these differences were always most striking when the lower stimulus rates were used. Figure 4 shows the courses of two isotonic lengthenings during distributed stimulation at 10 impulses/sec (in each filament). The tension during the movement was the same in both cases, but, as in Fig. 3, the movements began from different muscle lengths. At this rate of stimulation the preceding movement had a very marked effect on the velocity of isotonic lengthening; in Fig. 4, the first part of the isotonic lengthening from the longer starting point was at only about one tenth of the velocity with which the muscle lengthened through that point after 2.2 mm of preceding movement.

The more effective resistance to isotonic lengthening at the beginning of the movement corresponded to the relatively high tension that occurred at the beginning of an imposed extension (Joyce *et al.* 1969). In each case the difference between the muscle performance at the beginning of the

movement, and late in its course was most clearly seen at the low rates of stimulation. The isotonic movements show, however, that this difference is also present to a lesser extent at higher rates of stimulation (Fig. 3).

The force-velocity relation. The force-velocity relation at any length and stimulus rate clearly depends on the movements that preceded the measurements. A previous paper (Joyce *et al.* 1969) described the force-velocity relation for muscles that had already moved through 5 mm at

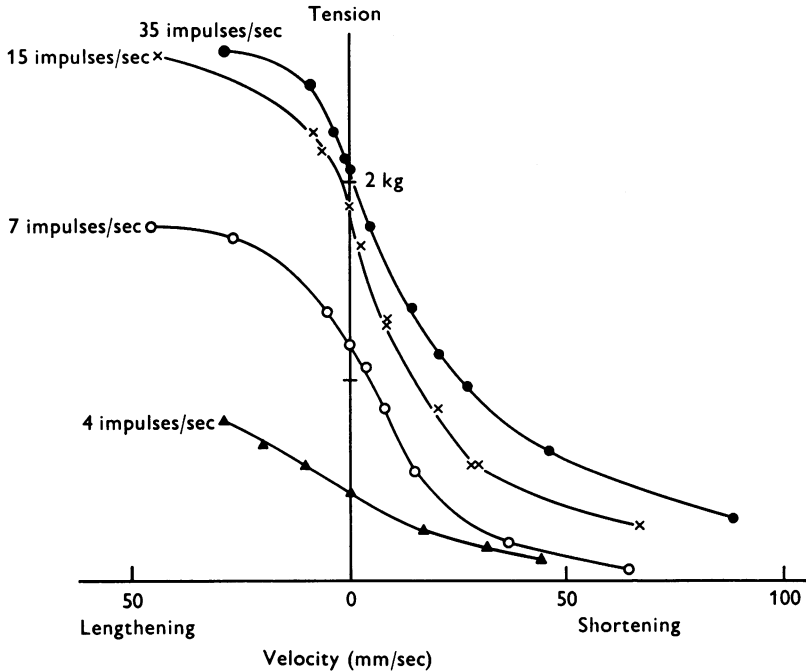


Fig. 5. Force-velocity plots at the beginning of isotonic movements. Velocity measured 15 msec after the tension step has been plotted against tension. Stimulation was through five channels at rates indicated on the Figure. All movements began after 1.6 sec isometric contraction at a length equivalent to an angle of 70° at the ankle.

constant velocity. By using tension 'steps' it has been possible to obtain force-velocity plots for the contractile elements of the muscle close to the beginning of the movement. Immediately after the tension 'step' both length and tension records were disturbed by vibration; measurements of velocity were therefore made from the length records at some short interval after the tension change. Figure 5 shows how the velocity of isotonic movement 15 msec after the initial 'step' varied with tension.

At the beginning of the movement the tension during lengthening always exceeded the isometric tension (Fig. 5), and at each stimulus rate a smooth

curve could be drawn through the zero velocity (isometric) point. These curves are quite different from those obtained later in the course of movement when at some stimulus rates isometric tension appeared as an exceptional point, higher than the tension during either lengthening or shortening.

The extra contractile power that the muscle developed during isometric contraction at these stimulus rates evidently persisted into the first part of an ensuing movement, improving the muscle performance. As the movement progressed this initial advantage was lost, and lengthening was less effectively resisted. Numerous other families of force-velocity curves could no doubt be constructed, each showing the performance of the muscle with a different set of preceding conditions.

It is not strictly correct to compare isotonic force-velocity plots with plots obtained during imposed movements in which the tension varied, since the tendon and other series elastic elements within the muscle would change in length as tension changed, and make an unknown contribution to the velocity of movement.

It might seem that this source of error could be avoided by using only isotonic movements and making measurements in different parts of their courses. In practice, however, the tension changes that accompany a prolonged slow or even moderately fast lengthening cannot usually be seen during isotonic lengthening movements, since a force that is large enough to extend the muscle through a sufficient distance very often does so with an increasing velocity, and prolonged slow lengthening movements do not occur. Under these circumstances the muscle is 'unstable' and once lengthening has begun it continues rapidly in a 'run away' state.

The later course of lengthening movements. When a muscle was lengthened isotonicly the velocity of movement at first increased, but eventually the muscle was lengthened into a range in which it could resist more effectively; the movement was then checked, and the velocity decreased again. If the stimulus rate was high (Fig. 3*b*) the movement continued with decreasing velocity toward a length at which the muscle could be expected to contain the movement in an isometric contraction. This last part of the movement was the sort of behaviour one would expect from an inert viscoelastic system, or from a muscle in which the tension during lengthening always exceeded the isometric tension.

When, however, the rate of stimulation was lower, isotonic lengthening often continued through the length at which the muscle could have generated that tension in an isometric contraction (dashed line in Fig. 4) to be arrested at some greater length from which it slowly shortened back toward the expected length for an isometric contraction of that tension. This excursion beyond the final length corresponded to the fall in tension below the isometric level that occurred during a constant velocity lengthening. The slow shortening back toward the final length corresponded to the slow rise in tension to the isometric level after the end of an imposed lengthening movement.

The later course of shortening movements. After the initial length 'step' and the rapid shortening that immediately followed it the subsequent course of the movement was often surprisingly irregular. The progress of shortening was often temporarily slowed or halted (Figs. 2*a* and 6), and occasionally the movement actually reversed (Fig. 6*a*). A second retardation of shortening was sometimes seen giving the appearance of a damped oscillation superimposed on the course of the movement. These irregularities were always most striking when the stimulus rate was rather low; they were less often present, and generally less well developed during stimulation at higher rates.

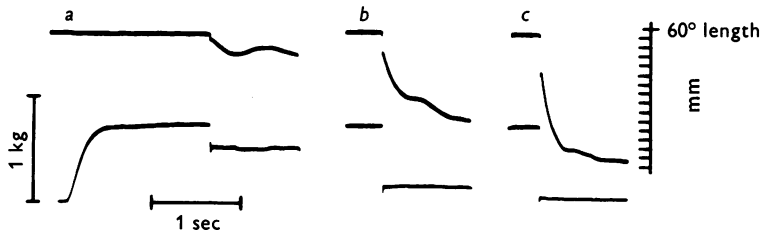


Fig. 6. Isotonic shortening against different tensions. Oscilloscope photographs. Length records are above, tension below. Stimulation at 15 impulses/sec in each of five channels. In *a* there was some change in tension, due to friction, as the movement reversed.

In most experiments only one upward deflexion was clearly visible, so that a frequency of oscillation could not properly be determined. However, the time interval between the force 'step' and the point at which the velocity of shortening reached its first minimum could easily be measured from an electrically differentiated length record; this time interval which varied between 0.25 and 0.65 sec was used as a measure of the period of the oscillation. The oscillations observed in these experiments were a whole order slower than those observed by Podolsky (1960), Civan & Podolsky (1966) or Armstrong, Huxley & Julian (1966), in frog muscle.

We have been unable to define in detail the factors that determine the time course of these oscillations. The period differed in different cats, and it was usually less during rapid than during slow shortening movements. Oscillation was prominent with stimulus rates of 20 impulses/sec or less, but the rate of stimulation did not seem to affect the period of the oscillation except in so far as it affected the velocity of movement. The distance that the muscle shortened before the velocity fell to its first minimum varied from 1 to 12 mm, being greatest when the movement was most rapid (Fig. 6).

The Tensators, transducers, and couplings had significant mass, so that oscillations could arise merely from the combination of their inertia, and elastic components in the muscle and the mounting frame; the frequency of such an oscillation would be determined by the mass, and elastic properties of the elements concerned. The high frequency length oscillations that occupied the first 10 msec after the force 'step' (Fig. 8) were accompanied by oscillations of force, and these could be accounted for in that way; but it was unlikely that the lower frequency oscillations described above arose from a mechanical arrangement of this sort. In order to exclude this possibility, however, extra weight was added to the couplings to increase the mass acting on the muscle 30 times. This extra mass caused a small increase in the amplitude of the slow oscillation, but had no appreciable effect on its time course.

Isotonic shortenings had the same irregular course when the arterial pressure was reduced to zero immediately after the animal had been killed. It was unlikely, therefore, that changes in the muscle blood flow had played any important part in these oscillations.

The effect of reversing the direction of movement. The force-velocity relationship measured at any time was modified by the movements that preceded the measurement. Isotonic or constant velocity movements each gave information about the effects on the velocity of lengthening of a preceding lengthening, and the effects on the velocity of shortening of a preceding shortening. To examine the effects of other different preceding conditions isotonic movements were arranged to begin immediately after a controlled lengthening or shortening.

Figure 7 shows a typical result. The muscle was lengthened isotonicly after a period of isometric contraction (Fig. 7*a*) and after a slow controlled shortening (Fig. 7*b*). Each of the isotonic movements began from the same muscle length, and the final tension was the same in either case. When the isotonic movement followed a slow shortening the muscle was less well able to resist the ensuing lengthening movement, and this proceeded faster than it had done after an isometric contraction. A period of isometric contraction 'improved' the performance of the muscle during the first part of a subsequent movement, but this effect clearly did not occur after movement of the muscle in either direction. When a controlled lengthening was immediately followed by isotonic shortening, the velocity of shortening was less than it would have been after an isometric contraction; again, the preceding movement had reduced the effectiveness of the muscle.

The foregoing paragraphs describe the behaviour of the muscle when shortening was immediately followed by lengthening or vice versa. If the two movements were separated by a short isometric contraction the situation was much more complicated; in particular a slow lengthening movement could sometimes, after an interval, actually enhance the ability of the muscle to shorten, or to resist lengthening.

The initial 'step' change in length

A 'step' reduction in tension was accompanied by an initial very rapid shortening separated from the subsequent isotonic movement by a more or less definite corner (Fig. 2). The response to a small increase in tension was similar, and again there were fast and slow phases of movement separated by a corner. When, however, the increment in tension was large

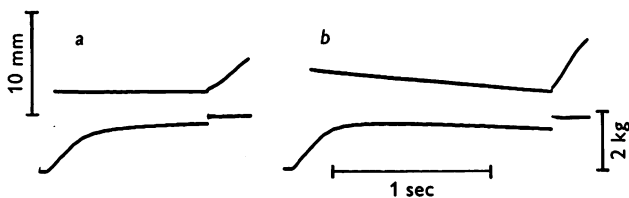


Fig. 7. The effect of previous shortening on isotonic lengthening. Oscilloscope photographs. 'Step' increments in tension were followed by isotonic lengthening movements, (a) after a period of isometric contraction, and (b) after a slow shortening movement. Each tension 'step' began at the same muscle length, and the final tension was the same in either case. Stimulus rate 15 impulses/sec in each of five channels.

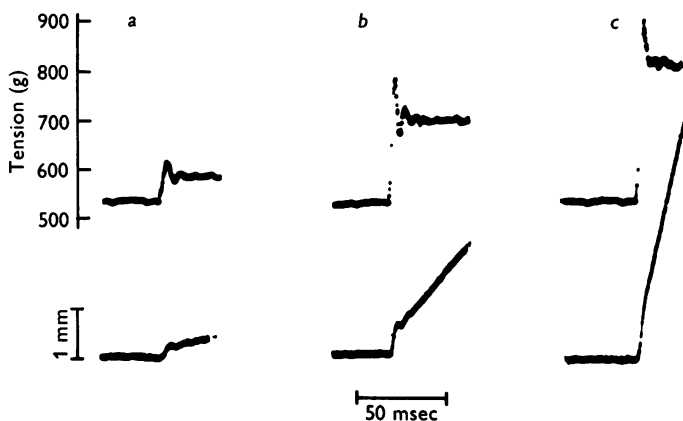


Fig. 8. Length and tension changes at the onset of movement. The tension record is above, length below. Stimulation at 10 impulses/sec in five different channels. After an isometric contraction the restraining levers were released, and the muscle was extended by different Tensator assemblies.

(more than about 50% of the isometric tension), the two phases of lengthening merged into each other and could not be clearly separated (Fig. 8c).

The series elastic element. On the assumption that the initial rapid lengthening is the response of an undamped or lightly damped series elastic element to the 'step' change in tension (Hill 1950; Jewell & Wilkie,

1958), it was possible to determine the elastic properties of this component of the muscle from the relative amplitudes of the length and tension 'steps'. Unfortunately, however, neither length nor tension changed as a perfect 'step', and the length changes could not be directly measured at the time of release. The record of this first part of the isotonic phase of the movement was therefore extrapolated backward to the release time, and length measurements were made to this extrapolation (Jewell & Wilkie, 1958).

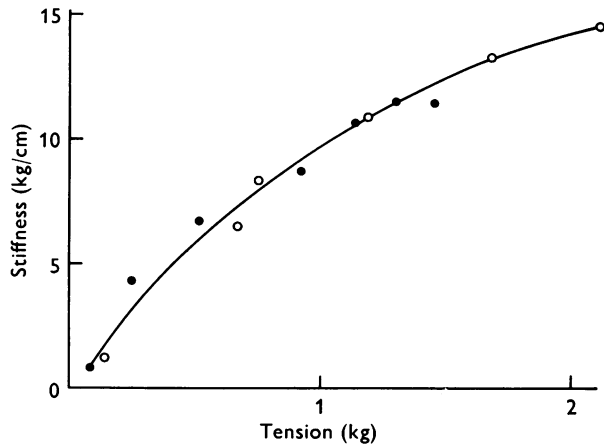


Fig. 9. The stiffness of the series elastic element at different tensions. 'Step' changes in tension were imposed on the muscle during distributed stimulation at different rates. The stiffness of the series elastic element was calculated from the relative amplitudes of 'steps' of length and tension. This stiffness has been plotted against a tension midway between the tensions at the beginning and end of the 'step'. Results calculated from shortening steps: ●, from lengthening steps: ○. The steps used in constructing this Figure involved length changes of 0.5 mm or less.

The properties of the series elastic elements were determined by this method at different muscle lengths, and with different rates of stimulation. Changes in either length or stimulus rate altered the muscle tension, and these tension variations were accompanied by changes in the series elastic element of the muscle, which was relatively compliant when the tension was low, but became stiffer as the tension increased (Fig. 9). In Fig. 9 different stimulus rates were used to obtain different tensions; similar records were obtained at a constant stimulus rate when the tension was modified by changing the muscle length. Similar variations of the stiffness of the series elastic element with changing tension appear in the results of Hill (1949), Jewell & Wilkie (1958), Wells (1965) and Bahler (1967).

In Fig. 9 the stiffness of the series elastic element has been plotted against a tension midway between the isometric tension that preceded the 'step', and the constant tension that followed it. If instead the stiffness was plotted against the preceding isometric tension only, the points obtained during lengthening generally fell above those obtained during shortening; viewed in this way the series elastic element of the muscle could be said to be stiffer in its response to a sudden lengthening than to a corresponding shortening movement.

Some part of the series elastic element is in the tendon, this part could be measured by direct observation (Jewell & Wilkie, 1958). A marker (a fine silk thread) was sewn into the tendon where the lower muscle fibres joined it, and a mark was made on the rod that coupled the tendon to the transducers. During isometric contractions at various stimulus rates two observers with microscopes fixed pointers over these two marks; the distance between these could then be measured with a travelling microscope after the contraction had ceased. This method allowed an accuracy of ± 0.1 mm.

The tendon length increased with increasing tension in an approximately linear manner, the tendon having a stiffness of about 20 kg/cm. The part of soleus tendon that covered the posterior surface of the muscle was not included between the markers, the complete tendon would therefore have been more compliant than these measurements indicate.

DISCUSSION

When the cat soleus is stimulated at physiological rates it often develops more tension during an isometric contraction than during lengthening or shortening (Joyce *et al.* 1969). When an isometric contraction was followed by movement, some of the extra effectiveness associated with the isometric state persisted into the beginning of the movement but was lost as the movement progressed. These changes in the muscle performance could be seen during the first part of a directly imposed movement, but they were more readily analysed when the muscle lengthened or shortened isotonicly.

Lengthening. Many features of the muscle behaviour during lengthening could be explained in terms of a hypothesis (Joyce *et al.* 1969) based on the sliding filament theory of muscle contraction (H. E. Huxley & Hanson, 1954; A. F. Huxley & Niedergerke, 1954; Hanson & H. E. Huxley, 1955; A. F. Huxley, 1957). It was assumed that cross bridges between thick and thin filaments were broken down rather slowly when there was no movement; a large number of intact links might then exist even at quite low rates of stimulation. If now the tension applied to the muscle were suddenly increased some lengthening would occur at once, with distortion of these links and an increase in their rate of break-down. As more links were

broken the remaining ones would bear a greater load and be distorted further, with a further increase in their rate of break-down. The process of lengthening would thus accelerate, and it is not surprising that isotonic lengthening at low stimulus rates may lead to a 'run away' condition in which the muscle lengthens very rapidly until it reaches a new length at which it is able more effectively to resist the movement (Fig. 4). When the muscle was stimulated at high rates, links broken during lengthening would be more rapidly re-formed, so that their total number would remain larger, and exert a correspondingly greater restraint on the movement preventing this 'run away' situation.

During movement in either direction there would be fewer links than in an isometric contraction; it is not surprising therefore that an isotonic lengthening that immediately follows a shortening movement proceeds faster than one that begins after a period of isometric contraction.

Shortening. During shortening the tension fell below the isometric value, and such a fall is explicable in terms of the sliding filament theory (A. F. Huxley, 1957). It was surprising, however, that the velocity of shortening fell rather suddenly after the muscle had shortened through a number of millimetres. In Fig. 6c there was an initial rapid isotonic movement through 8 mm (a distance equivalent to 2500–3500 Å/half sarcomere) before the sudden decrease in velocity. It is difficult to see how cross links formed during the isometric contraction could affect the velocity after so large a movement; some other explanation must be sought.

The sudden changes in velocity were more than could be simply attributed to the changing effectiveness of the muscles fibres at the different lengths they passed through (Abbott & Wilkie, 1953); but, the sort of movements we have reported might well occur if the change in contractile effectiveness followed the length change after a time delay. A delay in the effect of length on tension could also account for the oscillatory course of the shortening movements seen in Figs. 2, 3a and 6, and would no doubt also contribute to the overshoot that occurred after isotonic lengthening movements at low stimulus rates (Fig. 4).

It was suggested (Rack & Westbury, 1969) that the alterations in contractile force that accompany length changes might be the result of changes in the geometry of the transverse tubules within the muscle fibres. Any such distortion of these tubules would involve changes in their volume, and a flow of fluid into or out of them. Such a movement of fluid in narrow tubes could well take time, and perhaps account for the postulated delay in the muscle response to a change in length.

The oscillations that occurred at the beginning of shortening movements of frog muscle fibres (Podolsky, 1960; Armstrong *et al.* 1966) were much smaller in amplitude and higher in frequency than we have seen; these could well have quite a different origin (Civan & Podolsky, 1966).

The series elastic elements. Measurements of the length and tension 'steps' indicate a series elastic element the compliance of which varies with the isometric tension, although the compliance of the tendon remains constant. Clearly some part of this series elastic element is within the muscle, and it is that part that alters as the tension changes.

If for each 'step' the part of the length change attributable to the tendon were calculated and subtracted, the remainder of the length 'step' would give a measure of the elastic properties of that part of the series elastic element that lay within the muscle substance. Unfortunately our knowledge of the elastic properties of the tendon is incomplete since the tendon of origin, and that part of the tendon of insertion that lies along the surface of the muscle contribute some compliance that cannot be assessed. It is clear, however, that the elastic modulus of that part of the series elastic element that lies within the muscle rises steeply with increasing tension.

If (Hanson & Huxley, 1955; Huxley, 1960) the part of the series elastic element that lies within the muscle substance includes the sum of the elastic properties of the existing cross links, then its elastic modulus could be expected to be greater at high tensions when the number of cross links is large. The present results are compatible with that suggestion.

Physiological implications of the results. A cat normally stands with an angle of about 120° between the lower leg and foot. The achilles tendon is then under tension, and it is likely that soleus is continuously active, and bears a considerable part of this load (Denny Brown, 1929; see also Vrbová, 1963). The muscle is evidently well adapted to sustain isometric contraction at low rates of stimulation.

When the isometrically contracting muscle was suddenly lengthened, it offered a high resistance to the beginning of the movement, meeting the first small length change with a large change in force. The ankle joint would therefore be relatively stiff in its response to a small rapid dorsiflexion and this stiffness would not depend on reflex activity. If the force continued to act, lengthening the muscle further, the changes in tension were relatively smaller, so that, other things being equal, the ankle joint would be less stiff in its response to a large deflexion than to a small one.

In the intact animal, however, a change in muscle length would, through the stretch reflex, modify the activity in the muscle fibres, though a significant time would elapse before this could affect the tension (Jansen & Rack, 1966). Stretch reflex activity could thus increase the stiffness with which the muscle meets a prolonged deflecting force, but could have no effect on the first part of the movement.

The immediate resistance of a limb to a sudden disturbing force is not therefore under direct control of the central nervous system, but depends

on the initial high level of muscle stiffness, and the inertia of the moving part. It is tempting to believe that these are usually sufficient to check the extent and velocity of movement for long enough to allow the stretch reflex to operate and resist further postural disturbance. The stiffness with which the limb meets the later part of the movement would then be under direct control of the central nervous system through the fusimotor nerve fibres. The striking sensitivity of the muscle spindles to small movements (Matthews & Stein, 1968, 1969) would ensure that stretch reflex activity is initiated at the very beginning of a movement, and the delay kept to a minimum.

Such a mechanism would break down if the limb were subjected to a force that was large enough to extend the muscle to a point at which it began to 'run away' before an effective reflex resistance could develop. Presumably the inertia of the limb, the muscle properties, and the delay in the stretch reflex are matched to each other in such a way that this seldom occurs during normal activity.

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