

THE BEHAVIOUR OF A MAMMALIAN MUSCLE  
DURING SINUSOIDAL STRETCHING

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SUMMARY

1. Tension changes have been recorded in tetanized and passive cat soleus muscles during sinusoidal stretching at frequencies between 0.25 and 12.5 c/s.
2. During sinusoidal stretching the muscle tension varied in an approximately sinusoidal manner. The tension record showed an angular advance on muscle length. A method of measuring mean angular advance in nonlinear systems is described.
3. In tetanized muscle, resistance to lengthening increased with increasing frequency of stretching. With increasing frequency the elastic stiffness increased more rapidly than the viscous stiffness, so that at the higher frequencies the angular separation between length and tension became smaller.
4. With increasing stretch amplitude the elastic stiffness of the tetanized muscle declined, and the mean angular advance of tension became larger.
5. In passive muscle the viscous stiffness increased at the higher frequencies, and the mean angular advance of tension on length was correspondingly increased.
6. The functional significance of these findings and their relation to the findings of other workers are discussed.

INTRODUCTION

The shortening and the increase in stiffness of muscles after excitation have been extensively studied, and are of obvious importance. The muscles, however, perform an important function in absorbing and largely dissipating energy transmitted to the animal body by external mechanical forces. This function has attracted less attention.

When a moving object strikes a limb, expends its kinetic energy and

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falls to the ground, the limb is deflected, but resists the deflection force with mounting resistance until the energy transfer is complete. The limb then returns to its approximate previous position with little or no oscillation. The limb is behaving as a damped elastic structure, and there can be little doubt that the muscles play the major part in determining this behaviour.

When a muscle is extended by an external force the work done may be divided into two components, a part done against the elasticity of the muscle, which re-appears during shortening, and a part done against the viscous component of the muscle which does not re-emerge. Furthermore, some of the potential energy stored in the elastic components during lengthening may be expended in overcoming the viscous resistance to shortening. (The terms elastic and viscous are not intended to imply constant elasticity, or linear Newtonian viscosity.)

The non-linear behaviour of striated muscle presents an obstacle to the investigation of its properties, but this can be partly overcome by the use of sinusoidal stretching, since it is then possible to separate the tension that develops into two components: the tension due to the elastic component which is in phase with length, and the tension due to the viscous component which is in phase with velocity of extension.

The properties of the cat soleus muscle have been investigated during sinusoidal stretching. This paper reports the behaviour of the passive and tetanized muscle.

Similar experiments have been performed on small fibre bundles from frog muscle by Buchtal & Kaiser (1951), and on insect muscles by Machin & Pringle (1960).

METHODS

Fifteen adult cats were used. Two were anaesthetized with Nembutal (sodium pentobarbitone) the others were decerebrated by mid-brain section under ether anaesthesia. No difference was observed between the muscles of decerebrated and anaesthetized cats. The tendon of soleus was separated from the gastrocnemius, and detached from its insertion. The soleus nerve was dissected through gastrocnemius and divided.

The animals were rigidly mounted with two pairs of steel pins in the tibia, and clamps on the iliac crests and thoracic vertebrae.

**Stimulation.** The soleus nerve was stimulated through twin silver wire electrodes in a paraffin pool. Square waves were used 0.1 msec in duration, at frequencies 50/sec, 70/sec or 100/sec. The stimulus voltage was always above that necessary for maximal muscle tension.

**Method of stretching.** The mechanical stretcher used is illustrated diagrammatically in Fig. 1. An eccentrically mounted ball race was rotated by a 1/2 h.p. variable speed motor; two nylon vibration isolators were incorporated in the drive shaft. The bolt b was mounted in nylon bearings and held firmly against the ball race by a spring. As the ball race rotated this bolt moved sinusoidally, and its movement was used to stretch the muscle. An accurately sinusoidal movement could be obtained with frequencies of 0.25-12.5 c/s. By the use of different eccentrics, four different stretch amplitudes were available, 0.7, 1, 1.6 and 3.8 mm (peak to peak).

The mean muscle length altered by moving the whole animal in relation to the stretcher. The length of the muscle during full flexion at the ankle joint in the intact was taken to be the limit of physiological extension.

**Method of recording length, velocity and tension.** In the earlier experiments length was recorded by the change in resistance on a rotary potentiometer attached to the ball race through gears. This proved unsatisfactory at the higher frequencies, and was therefore replaced by a spring (S<sub>1</sub>) which acted on a suitably mounted RCA 5734 transducer valve (V<sub>1</sub>). The extension of this spring was recorded from a second transducer valve (V<sub>2</sub>) acted on by spring S<sub>2</sub>. The extension of this spring was arranged to be 1/10° out of phase with the length, and its tension therefore reflected the velocity of movement. Since the lever is eighty times longer than its arc of movement, the depression from linearity incurred by this method was negligible.

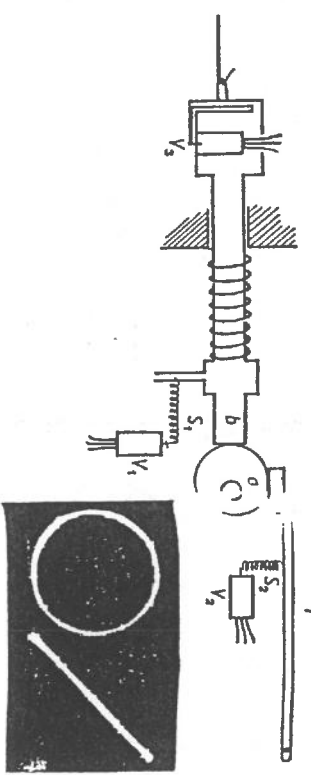


Fig. 1. Diagram of stretching machine. Rotation of the eccentric (a) causes horizontal movement of the bolt (b) which is communicated to the muscle through a myograph containing transducer valve (V<sub>1</sub>). Movement of the bolt is recorded by the valve (V<sub>1</sub>) which measures tension in the spring (S<sub>1</sub>). Velocity of movement of the bolt is measured by valve (V<sub>2</sub>) which records tension in the spring (S<sub>2</sub>); the spring (S<sub>2</sub>) is stretched by movement of the lever (l) which is arranged to move at 90° to the movement of the bolt. *Inset*: Velocity-tension figure (left), and length-tension figure (right) recorded while sinusoidally stretching a spring. The L-T figure is a line, indicating that the spring has no measurable viscosity.

Muscle tension was recorded by a myograph using the valve V<sub>2</sub> as transducing element. Vibration was transmitted through the frame holding animal. Some vibration was transmitted through the drive shaft and moving bolt; this was just palpable on the bolt at the higher frequencies. These vibrations could be on the tension display when their frequency reached the resonant frequency of the myograph, but it is unlikely that this had any important effect on the experimental results. **Inertia of springs.** The link and hook joining the roller to the stretcher weighed and the cat soleus weighs approximately 4 g. If the coupling hooks plus half the weight of the muscle be considered to act as an inertial load then these will exert a force on myograph opposite in direction to the elastic component of the muscle tension. Since force was only 5 g when the largest available amplitude of stretch was used at the largest available frequency it was usually disregarded.

**Display of results.** Results were displayed in either of two ways: (a) Muscle length, and muscle tension, were separately displayed as vertical deflection, a horizontally moving trace.

(b) The length signal (from valve V<sub>1</sub>, Fig. 1) was supplied to the horizontal deflection of the oscilloscope while the tension signal deflected the same beam vertically, so that

length-tension plot was obtained in the form of a repeating figure. In the oscope used (Toktronix 565) a second independent beam was available; this was also deflected vertically by the tension signal while its horizontal movement recorded the velocity of stretching through the output of the valve  $V_2$  (Fig. 1). The brightness of this trace was modulated at 50 c/s to provide a time marker. The length-tension (L-T) and velocity-tension (V-T) figures were photographed by a camera which was triggered from the stretching machine so that alternate cycles were recorded.

**Interpretation of results.** When a perfectly elastic material is stretched sinusoidally, the tension also alters sinusoidally in phase with length. The L-T figure is a straight line, while the V-T figure is an ellipse or circle. (The inset photograph in Fig. 1 illustrates this situation. The L-T and V-T figures shown there were obtained by stretching a coiled spring through a range within which its properties were linear.)

When the material stretched combines elasticity and Newtonian viscosity, the tension still alters sinusoidally, but, since tension then depends on the velocity of lengthening as well as on length, maximum tension develops before maximum length, and the tension shows phase advance on length. The L-T record during lengthening then differs from the record during shortening, and in a complete cycle the L-T figure is an ellipse traced in a clockwise direction.

The work done on the muscle in one complete cycle is represented by the area of the L-T figure and, when the horizontal measurements of the two figures are made equal, the ratio: area of L-T figure/area of V-T figure gives the tangent of the angle of phase advance (see Appendix).

When materials with stable but non-linear properties are examined, the above two statements remain true, though the term 'phase angle' cannot properly be used since tension does not then vary in a pure harmonic manner. However, the area of the L-T figure still measures the work done on the muscle in a cycle, and the L-T area/V-T area still gives the tangent of the mean angular advance.

The tension developed during sinusoidal stretching of a visco-elastic structure may be regarded as the sum of two vector components: a component in phase with length, and a component  $90^\circ$  in advance of length. Two components of muscle stiffness may be similarly derived: elastic stiffness is force in phase with length/unit stretch amplitude, and viscous stiffness is force  $90^\circ$  in advance of length/unit stretch amplitude. The viscous and elastic stiffness of muscle under the experimental conditions may be determined from the L-T and V-T figures (see Appendix).

RESULTS

The cat soleus was examined during sinusoidal stretching through amplitudes 0.7-3.8 mm (peak to peak), at frequencies 0.25-12.5 c/s. Measurements were made only while the records were consistently repeatable. The lowest frequencies were used sparingly since the rather long periods of stimulation fatigued the muscle quite rapidly.

Variations in the frequency of stimulation between 50 and 100/sec had no detectable effect on the muscle behaviour.

Figure 2 shows the muscle tension (lower trace) during sinusoidal stretching. Tetanic stimulation of the motor nerve began during this record, and the right-hand side of the figure shows the relation between length and tension in the tetanized muscle. The tension follows a curve that is very approximately sinusoidal, but this curve shows an angular advance on the

length record (upper trace). This angular advance always occurred during sinusoidal stretching of a tetanized muscle. The results of sinusoidal stretching were more usually displayed in the form of L-T and V-T figures. In Fig. 3 the L-T figures are the continuous lines and maximum length is to the right; the V-T figures are interrupted lines with velocity of lengthening to the left. Both L-T and V-T figures were traced in a clockwise direction. This method of display was the most convenient, as variations in the muscle properties could then be readily seen, and measurements were more easily made.

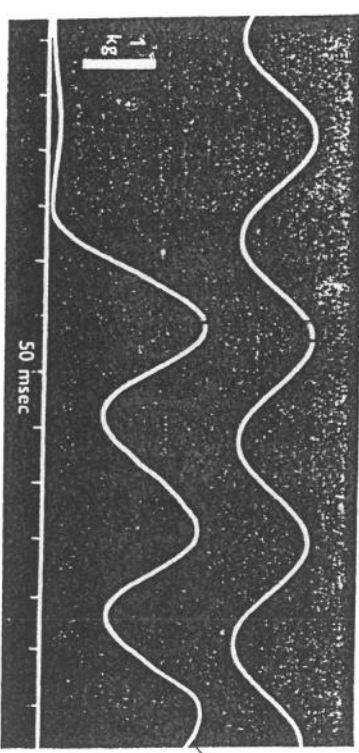


Fig. 2. Sinusoidal stretching of soleus through 1.6 mm (peak to peak) at approximately 5 c/s. Muscle length is recorded above, and tension below. Stimulation of the soleus nerve (0.1 msec square waves, 50/sec) was started during recording. The tension recorded in both tetanized and the passive muscle varied in an approximately sinusoidal manner. The tension showed an angular advance on length.

**The effects of varying stretch frequency.** Figure 3 shows a series of results obtained while stretching a tetanized muscle sinusoidally at three different frequencies. Changes in the frequency of stretching led to quite small changes in the peak tension. The trough (lowest) tension, however, fell to a lower level at the higher frequencies, and it was evident that the muscle tension was small when the velocity of shortening was large.

The areas of the L-T and V-T figures altered as the frequency of stretching changed, but in contrast to simple linear visco-elastic systems it was the elastic stiffness (measured from the V-T figure, see Appendix) that increased with increasing frequency, while the viscous stiffness and work absorbed changed rather little.

In many experiments stretch frequencies down to 0.25 c/s were used, but the changes in the L-T and V-T figures between 0.25 and 1 c/s were small. It seemed probable that at 0.25 c/s the L-T figure was becoming close to the hysteresis loop that occurs at 'zero frequency' (Buchthal & Kaiser, 1951).

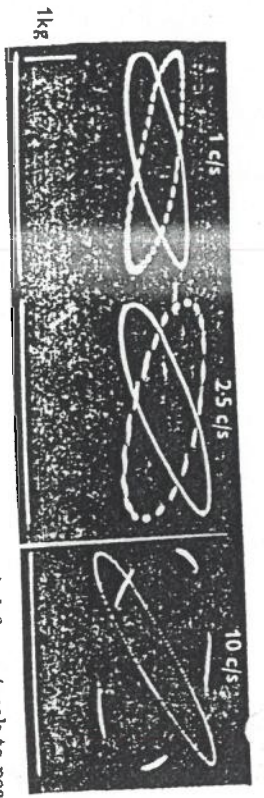


Fig. 3. Sinusoidal stretching of tetanized muscle through 1.6 mm (peak to peak) at 1, 2.5, and 10 c/s. Stimulation: 0.1 sec square waves, 50/sec. The continuous lines are plots of muscle length (abscissa) against tension (ordinate); maximum length is to the right. The interrupted lines are plots of velocity of lengthening (abscissa) against tension (ordinate); maximum velocity of lengthening is to the left. The trace is interrupted 50 times/sec. With increasing frequency there is a fall in the trough tension, but little change in the peak tension. The area of the V-T figure increases with increasing frequency, but the area of the L-T figure is smaller at the highest frequency.

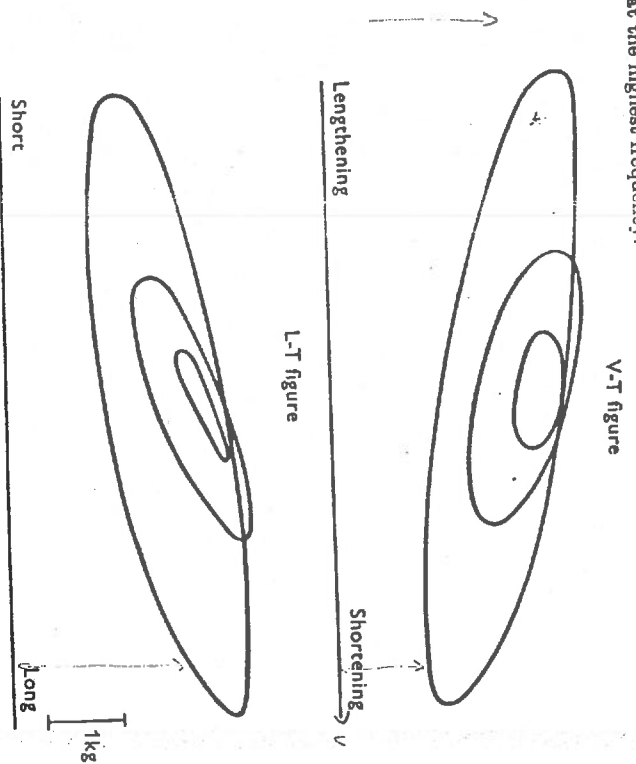


Fig. 4. Sinusoidal stretching of tetanized muscle at 3.3 c/s. Stimulus: 0.1 msec square waves, 50/sec. The mean muscle length was kept constant, but three different stretch amplitudes were used: 0.7, 1.6 and 3.8 mm (peak to peak). The V-T figure became relatively *larger* when the stretch amplitude was large, indicating a decline in elastic stiffness with increasing amplitude. The L-T figure changed less in its proportions, indicating that the changes in viscous stiffness were less than the changes in elastic stiffness.

*2.5 c/s*

The effect of stretch *width*. Figure 4 shows L-T and V-T figures obtained while stretching a muscle through 0.7, 1.6 and 3.8 mm (peak to peak) at the same mean muscle length.

Although similar in general form, these figures altered in relative proportions as the stretch amplitude changed. The V-T figure was relatively broader when the amplitude was small, indicating that the elastic stiffness was greater during the small than during the larger amplitude stretch.

The L-T figure on the other hand changed in shape much less, and it was at the intermediate amplitude (1.6 mm) that the L-T figure was relatively broader, and the viscous stiffness greater.

The effect of varying mean muscle length. The mean muscle length could be altered over a large range without any significant effect on the response to tetanic stimulation. When the muscle length was close to the estimated physiological limit, both peak tension and elastic stiffness increased. This increase in tension was, however, no greater (and usually less) than occurred in the passive muscle under the same conditions. The general pattern of response to the various frequencies and amplitudes of stretching remained unchanged.

When the muscle was examined at very short lengths (10-15 mm less than its physiological limit), the tension was smaller, and when the larger amplitudes of stretching were used at the faster speeds, the tension fell to zero in the latter part of shortening. Under these circumstances the viscous and elastic stiffnesses were very much smaller with large than with small amplitudes, since there was a limit to the fall in trough tension that could occur.

*Absorption of work, and muscle stiffness*

A series of measurements from a single experiment are presented in Fig. 5. The upper part of each graph consists of a plot of the work absorbed/cycle against frequency of stretching. At each stretch amplitude the work absorbed increased with increasing frequency up to about 3.3 c/s but thereafter there was little change in the work absorbed with further increases in frequency.

The lower part of Fig. 5 shows the peak and trough tensions at various frequencies and amplitudes. The trough tension changed with frequency much more than the peak tension, and the fall in trough tension with increasing frequency was much greater when the larger stretch amplitudes were used. This finding is in keeping with the known relation between muscle tension and velocity of shortening.

In Fig. 6 viscous and elastic stiffnesses of the muscle at different frequencies and amplitudes are plotted in the form of a Nyquist diagram. In this figure a line joining any point to the origin forms an angle with the horizontal that is equal to the mean angular advance of tension on length. (The same experimental results were used in constructing both Figs. 5 and 6.)

At each frequency examined, the mean angular advance was greater with large than with small stretch amplitudes. At each stretch amplitude

the mean angular advance changed little with changes in frequency between 0.25 and 3.3 c/s, but at the higher frequencies of stretching the increase in viscous stiffness with frequency became progressively smaller, and the angular advance correspondingly decreased. With further increase in frequency the viscous stiffness declined.

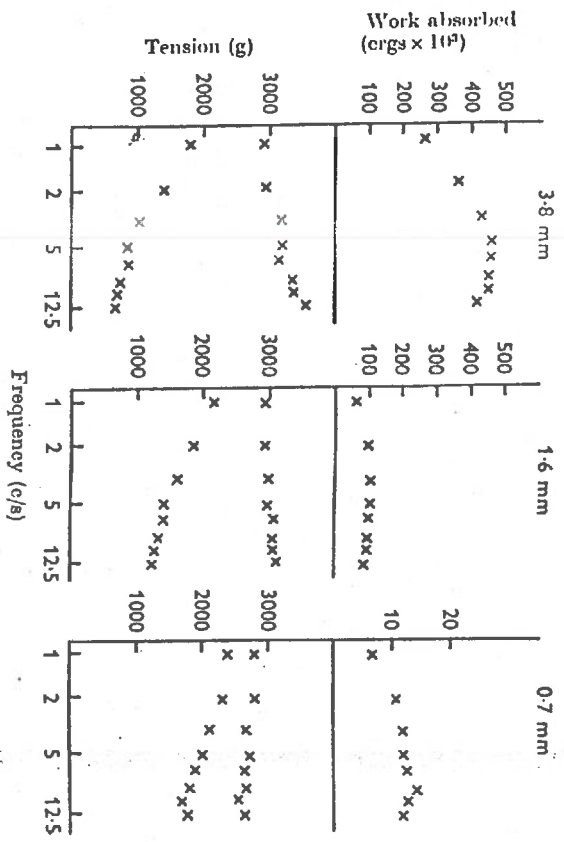


Fig. 5. The work absorbed, and the muscle tensions during sinusoidal stretching of a tetanized muscle through three different amplitudes. At each stretch amplitude the work absorbed/cycle, and the peak and trough tensions have been plotted at a number of frequencies. Stimulations: 0.1 msec square waves, 50/sec. The work absorbed/cycle increased with increasing frequency up to about 3.3 c/s, but then declined at highest frequencies. The work absorbed during the larger amplitude stretch cycles was very much greater than with the smaller amplitudes. (Note difference in scale in the 0.7 mm plot.) The difference between peak and trough tensions increased with increasing frequency, and this increase was greater when the amplitude was larger. The changes in the peak-trough tension difference were due mainly to changes in trough tension.

*Passive muscle*

The length-tension diagram of the cat soleus muscle has been described by Matthews (1959). Tension rises approximately exponentially with increasing length, the rise becoming steep as the maximum physiological length is approached. Rates of extension up to 5 mm/sec did not affect the slope of this curve. During slow release of the extended muscle, the L-T diagram differs from the curve followed during lengthening, the tension at each length being always lower during shortening than during lengthening.

Roberts (1963) subjected the passive cat soleus to sinusoidal extension. He recorded clockwise L-T figures which did not alter in shape with frequency changes between 0.7 and 17.0 sec/cycle. In the present investigation the passive cat soleus has been investigated by the methods already described for the tetanized muscle. The results confirm Roberts's finding that the L-T figures do not change in shape significantly with frequency as long as the frequency is kept below 2 c/s. When, however, the frequency was increased beyond 2 c/s, wider L-T figures were recorded, which had correspondingly larger areas. The peak and trough tensions and the areas of the V-T figures altered only a very small amount.

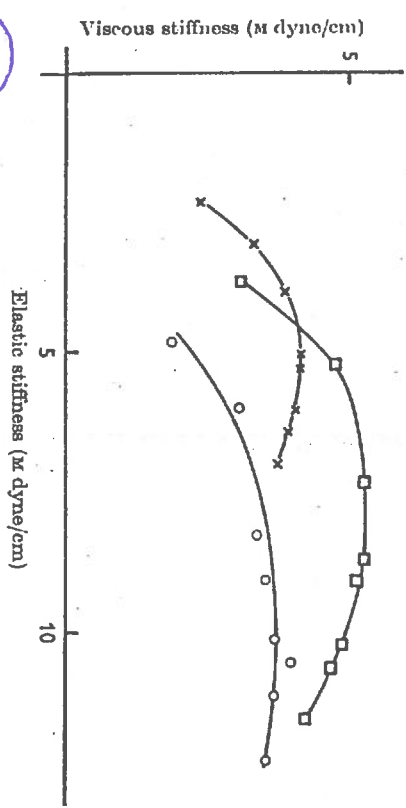


Fig. 6. The results from which Fig. 5 was constructed are presented in a different form. Viscous stiffness (ordinate) is plotted against elastic stiffness (abscissa) for three stretch amplitudes: x, 3.8 mm; □, 1.6 mm; O, 0.7 mm (peak to peak). In each series, the frequencies were: 1, 2, 3.3, 5, 6.3, 8.5, 10, and 12.5 c/s, reading from left to right. With this type of plot a line joining any point to the origin has a length that represents the modulus of muscle stiffness under the experimental conditions, and the angle that this line makes with the horizontal indicates the angular advance of tension on length. At each stretch amplitude, the elastic stiffness increased with frequency. At each frequency the elastic stiffness was greater with the small than with the large stretch amplitudes. In the amplitude range used the angular advance was greater with the large than with the small stretch amplitudes. The angular advance always declined at the higher stretch frequencies.

The effects of stretch frequency on the properties of passive muscle are illustrated in Fig. 7. The work absorbed/cycle is plotted against the frequency of stretching; the work rose steeply at the higher frequencies, but peak tension increased only a small amount with frequency, and the trough tension did not change. Three of the L-T figures from which these measurements were made are illustrated on the right. The changes in behaviour of passive muscle with changing frequency

were very different from the changes that occurred in tetanized muscle. Passive muscle resisted movement with a viscous stiffness that rose steeply as the frequency of stretching increased beyond about 5 c/s; and the mean angular advance of tension increased from about  $18^\circ$  at 2 c/s to

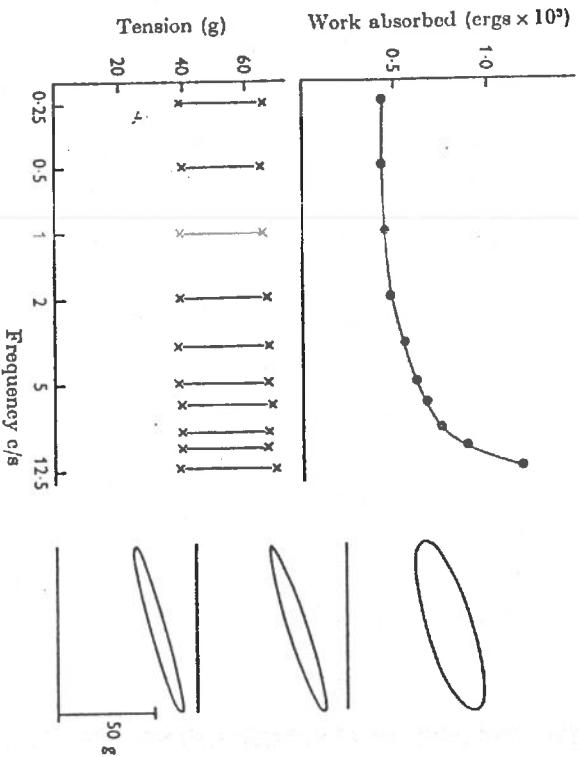


Fig. 7. A passive muscle was sinusoidally stretched through 0.7 mm (peak to peak) the maximum length being 7 mm less than the physiological limit of the muscle. The upper graph is a plot of work absorbed/cycle at various frequencies; the corresponding peak and trough tensions are shown below. On the right are three of the L-T figures from which measurements were made; from above downwards 12.5, 3.3 and 0.25 c/s. The peak tension increased only slightly with increasing frequency. The area of the L-T figure (and therefore the work absorbed/cycle) increased considerably at the higher stretch frequencies. The work absorbed at the highest frequency was, however, still about ten times smaller than the corresponding figure for tetanized muscle (compare with Fig. 5).

about  $40^\circ$  at 12.5 c/s. In tetanized muscle, however, the viscous stiffness did not increase with a rise in frequency above 5 c/s; the elastic stiffness on the other hand did rise progressively with increasing frequency, and the mean angular advance decreased.

#### DISCUSSION

*Comparison with carrier work.* Most of the previous experimental work on the mechanical properties of skeletal muscle has been done on the muscles of amphibia and fishes at low temperature, so that comparisons with the present results can be qualitative only.

Buchta] & Kaiser (19) described a method of sinusoidal extension of fibre bundles from frog semitendinosus. They used frequencies from 20 to 200 c/s, and demonstrated the difference between the static and dynamic elastic stiffness. They also found a decrease in the elastic stiffness of tetanized muscle with increasing stretch amplitude.

Hill (1938) demonstrated that although the muscle tension during shortening is inversely related to the velocity of shortening the tension during lengthening does not increase in the same way in proportion to the velocity of lengthening. With the more rapid stretch velocities the muscle 'gives' and the tension generated is thus limited (see also Katz 1939; Abbot & Aubert, 1952).

These findings throw some light on the differences in behaviour of the muscle during shortening and during lengthening. The fall in trough tension with increasing frequency or increasing amplitude is in keeping with the force-velocity relation described by Hill, and the limited rise in peak tension during rapid, or large, amplitude stretching presumably represents 'give' in the muscle fibres.

Hill's equation (Hill, 1938) which describes the relation between tension and velocity of shortening can only be applied after corrections are made for the series elastic elements of the muscle. During shortening the V-T curve (see Fig. 3) passes through a low point at which for an instant tension is not changing. At this point the length of the series elastic element in the muscle is not changing, so that the force-velocity relation is then a property of the contractile elements only. In fact measurement of a number of such records yields an isotonic V-T diagram that very approximately fits Hill's equation.

*Functional significance of the present results.* The velocities of lengthening and shortening that have been used are within the range calculated from speeds of angular movement known to occur at the ankle joints of living cats (see Engberg, 1964). The method of stimulation of the muscle is non-physiological, but it is worth noting that similar patterns of behaviour were recorded in soleus muscles that were continuously active in the so-called 'alpha cat' after dorsal root section, decerebration and cerebellectomy (Jansen & Rack, unpublished results). The present results can probably therefore be taken to reflect the behaviour of muscle in a state of continuous activation from any cause.

During sinusoidal stretching the muscle resists lengthening with a stiffness that increases as the frequency of stretching increases. The stiffness is under these circumstances much better able to resist rapid displacement to a limb than could have been expected from a knowledge of its static length-tension diagram. The rise in tension is greater when the stretch amplitude is greater, but often less than it would be in a linear system. In other words, the muscle is able to resist sinusoidal stretching with a greater stiffness when the amplitude of movement is small.

*Damping properties of muscle.* Periodic oscillation may occur when an elastic member is linked to an inertial load. If the elastic member has viscous properties also, oscillation is either prevented or damped so that it decreases in amplitude. When a visco-elastic material behaves in linear fashion, a knowledge of its viscous and elastic properties enables prediction of the way it will behave with a particular inertial load. It is then possible to predict whether oscillation will occur, at what frequency, and at what rate its amplitude will decline.

The elastic and viscous properties of muscle vary with both frequency and amplitude of oscillation, and furthermore pure sinusoidal oscillation could not be expected. Predictions about the damping properties of tetanized muscle therefore require assumptions and approximations that render them rather speculative. The present results do, however, suggest that with loads that the soleus could be expected to withstand (up to about 4 kg) the muscle would after transient deflexion undergo a heavily damped oscillation. The frequency of such an oscillation would increase as the amplitude diminished, since the elastic stiffness of muscle is greater at small amplitudes.

APPENDIX

Symbols used:

- $l$  = muscle length,
- $l_0$  = mean muscle length,
- $r$  = amplitude of movement (mean to peak),
- $p$  = tension,
- $v$  = velocity or movement,
- $\omega$  = angular velocity,
- $\phi$  = angular displacement between length and tension,
- $t$  = time.

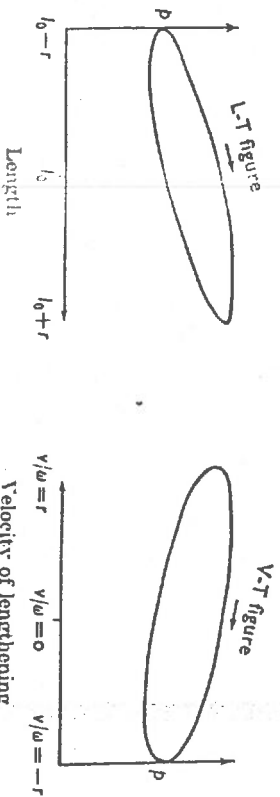


Fig. 8. Diagrammatic L-T and V-T figures to illustrate the method of treating the experimental results.

Since muscle length varies sinusoidally

$$l = l_0 + r \cdot \sin \omega t. \tag{1}$$

The tension during this imposed length change is a periodic non-harmonic function of length, and may therefore be described by the Fourier series

$$p_{(\omega)} = \sum_{n=1}^{\infty} a_n \cdot \sin n\omega t + b_0 + \sum_{n=1}^{\infty} b_n \cdot \cos n\omega t, \tag{2}$$

where tension is expressed as a function of angular movement  $\omega t$ .

The coefficients  $a_n$  and  $b_n$  represent the amplitudes of the sine and cosine components, and are defined by Fourier's theorem as

$$a_n = \frac{1}{\pi} \int_0^{2\pi} p_{(\omega)} \cdot \sin n\omega t \cdot d(\omega t), \tag{3}$$

$$b_n = \frac{1}{\pi} \int_0^{2\pi} p_{(\omega)} \cdot \cos n\omega t \cdot d(\omega t) \tag{4}$$

In a complete force cycle, work is done on a sinusoidal movement only by the component of force that varies at the same frequency as the movement. (This subject is fully treated in engineering manuals such as Den Hartog, 1956.)

In the present situation only the fundamental terms  $a_1 \sin \omega t$ , and  $b_1 \cos \omega t$  represent force components varying with the same frequency as the movement. The sine component of force is in phase with length, and the cosine component is in phase with the velocity of movement.

If the fundamental terms in the Fourier expansion are considered alone, the angular displacement between length and tension is given by

$$\tan \phi = b_1/a_1 \tag{5}$$

where the amplitudes  $a_1$  and  $b_1$  are defined by eqns. (3) and (4).

The area of the L-T figure is described by the integral  $\int p \cdot dl$ .

$$\int p \cdot dl = r \int_0^{2\pi} p \cdot \cos \omega t \cdot d(\omega t) = \pi r^2 a_1. \tag{6}$$

Since the V-T figure is always traced with its horizontal axis equal to that of the L-T figure, it is in reality a plot of  $v/\omega$  against tension (see Fig. 8), and its area is given by the integral  $-\int \phi(p/\omega) dv$

$$-\int \phi(p/\omega) dv = r \int_0^{2\pi} p \cdot \sin \omega t \cdot d(\omega t) = \pi r^2 a_1 \tag{7}$$

Since  $b_1/a_1 = \tan \phi$ ,  $\phi$  is the angular displacement between muscle length and the fundamental component of muscle tension;  $\phi$  gives a measure of the 'mean angular advance' of tension on length. From eqns. (5), (6) and (7)  $L-T \text{ area}/V-T \text{ area} = \tan \phi$ .

In treating the experimental results it is convenient to use the component of force that is in phase with length as a measure of elastic resistance, and the force that is 90° ahead of length as a measure of viscous resistance. Elastic stiffness is then described by the expression

$$a_1/r' (= V-L \text{ area}/\pi r^2)$$

and viscous stiffness by the expression  $b_1/r' (= L-L \text{ area}/\pi r^2)$ .

The elastic and viscous stiffness so measured describe the properties of the muscle only under the particular conditions of frequency and amplitude for which they are determined.

The work done by the force  $b_1 \cos \omega t$  on movement

$$l_0 + r \sin \omega t \text{ is } \int_1^{\omega} b_1 \cos \omega t \cdot dl$$

$$\text{and } \int_1^{\omega} b_1 \cos \omega t \cdot dl = b_1 r' \int_0^{\omega} \cos^2 \omega t \cdot d(\omega t). \quad (8)$$

Performing this integration between 0 and  $2\pi$  the work done in a complete cycle is found to be  $\pi r b_1$ , which is the area of the  $L-L$  figure.

The work done by the force  $a_1 \sin \omega t$  may be examined by the same method, but when the appropriate integration is performed it is found that no work is done by this component in a complete force cycle. (In fact the work done by this component of force during lengthening equals the work done on the same component during shortening.)

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## THE REFLEX RESPONSE TO SINUSOIDAL STRETCHING OF SOLEUS IN THE DECEREBRATE CAT

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#### SUMMARY

1. Soleus muscle in the decerebrate cat was stretched sinusoidally through various distances, at various frequencies while tension and e.m.g. activity were recorded.

2. Two patterns of stretch reflex activity were seen. In one, slow stretching led to a large increase in tension, whereas in the other tension increased little during slow stretching, but rose steeply during a more rapid stretch. Intermediate states were also seen.

3. Both these reflex patterns were abolished when the fusimotor fibres were blocked with Xylocaine.

4. At low frequencies of stretching the e.m.g. activity was greatest at peak muscle length; at higher frequencies the greatest activity was found during lengthening. This angular advance of e.m.g. activity on length was greatest at 3.3-5 c/s. At the higher frequencies the e.m.g. activity was less in advance of muscle length.

5. Angular advance of e.m.g. activity was greatest in the preparations that were also the most sensitive to slow stretching.

6. Muscle contraction follows an electrical stimulus with a small delay. The delay between the end of stimulation and the end of muscle relaxation is longer, and may exceed 200 msec in cat soleus.

7. The timing of the reflex tension during sinusoidal stretching depended on how far the angular advance of the e.m.g. combined with the damping properties of muscle offset the time delays in the reflex pathway.

8. Changes in muscle tension generally preceded changes in muscle length. When, however, stretch amplitudes of 1 mm (peak to peak) were used, a phase delay of tension was sometimes seen. This only occurred in preparations that also showed little sensitivity to slow stretching.

9. Phase delay of tension was usually found with frequencies of

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