

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

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(Received 6 May 1965)

### 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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approximately 6–8 c/s, and this corresponds to the clonus frequency for soleus.

10. The mechanisms of the two types of reflex behaviour, and the damping properties of the system are discussed.

#### INTRODUCTION

Stretch reflexes in the decerebrate cat have been extensively studied under static conditions (Liddell & Sherrington, 1924; Granit, 1958), and during slow stretching (Matthews, 1959*a*, *b*). The reflex response to rapid stretching has received less attention.

It is generally believed (cf. Granit, 1955; Hunt & Perl, 1960) that the muscle spindles and their primary afferent fibres are the principal sensory components of this reflex, and Merton (1951) has suggested that since the fusimotor nerve fibres alter the response of the muscle spindles to extension, they have an indirect effect on muscle contraction which amounts to a servo control of muscle length.

Afferent impulses from the muscle spindles do not have an instantaneous effect on muscle tension, and the stretch reflex can be regarded as a feedback control system with time delays. A simple position control system with time delays is unstable, and oscillation may occur, because corrections are always applied at an interval after displacement. This situation is well known to control engineers, and the instability is often overcome by constructing a system in which the resistance to deflexion is a function of the velocity of deflexion as well as its extent.

In skeletal muscle with an intact stretch reflex there exist mechanisms whereby the velocity of lengthening or shortening may modify the tension. Active muscle offers a resistance to changes in length that varies with velocity (Hill, 1938; Katz, 1939). The afferent discharge from the muscle spindles is also known to depend on their rate of extension as well as their actual length (Matthews, 1933); furthermore, there is evidence that the response of the muscle spindles to length and to velocity of lengthening can to some extent be altered independently by fusimotor activity. The behaviour of the muscle spindles has recently been reviewed by Matthews (1964).

In examining the performance of a control system, it is desirable to test its response to dynamic as well as static deflexions, and controlled sinusoidal deflexions can conveniently be used for this purpose. It is then possible to measure the work necessary to maintain the movement, and this gives an indication of the stability of the system. When external work is required to maintain the sinusoidal movement, there is a phase advance of force on displacement, and the system has positive damping properties for movement at that frequency and amplitude. When,

however, the oscillation is maintained without external work, the system is undamped.

This paper describes the behaviour of the decerebrate cat's soleus muscle during sinusoidal stretching. Similar experiments have been reported by: Lippold, Redfearn & Vučo (1958), Partridge & Glaser (1960), and by Roberts (1963). The use of higher frequencies, and smaller stretch amplitudes, with concurrent electromyogram (e.m.g.) recording has led to some new findings.

#### METHODS

*Preparation.* Twenty cats were used, but the principal results were obtained from thirteen of them.

The animals were decerebrated by transection of the mesencephalon under ether anaesthesia after common carotid ligation. The tendon of soleus was dissected, and the foot disarticulated. The nerve to soleus was preserved, but nerves to the other muscles of the limb were cut. In some experiments the innervation of tibialis anterior was left intact. In most experiments the lumbar spinal nerve roots and cord were exposed by laminectomy.

The method of application of stretch has already been described (Rack, 1966). Essentially the experiments consisted of stretching the muscle sinusoidally at various frequencies and amplitudes, while recording the tension and the e.m.g.

At the end of each experiment the muscle nerve was cut, and the properties of the passive muscle were recorded at the same muscle lengths, stretch amplitudes, and stretch frequencies as had been used during the earlier records.

Recording was not started less than 2 hr after decerebration. The rectal temperature was kept between 36 and 39° C during the recording periods.

*Electromyography.* Potential changes were recorded between a silver plate placed on the belly of the soleus muscle, and a hook which was inserted into the soft tissues near the proximal end of the muscle. A Tektronix 122 preamplifier was used, and the records were displayed on a Tektronix 565 oscilloscope along with the tension record.

*Integration of the e.m.g.* In addition to the direct display of the amplified e.m.g., the output of the preamplifier was fed into an integrating circuit. The circuit used was based on one described by Starr & Livingston (1963), but this was modified by shortening the time constant of the amplifier to 0.6 msec, increasing the time constants of the integrating CR circuit to a possible maximum of 6½ min, and inserting filters to exclude amplifier noise. Frequencies above 5000 c/s, and amplitudes less than 20 mV were excluded. The integrator had a frequency range from 250 to 5000 c/s and integration was acceptably linear for the range of amplitudes required (up to 500 mV). The time constant of decay of the integrated potential was never less than 100 times the duration of the cycle. The integrator was re-set to zero during alternate stretch cycles by shorting the integrating condensers through a relay operated from the driving motor.

*Display of results.* The methods of recording and of measuring the records have been described in a preceding paper (Rack, 1966). The tension was usually displayed as the vertical deflexion of an oscilloscope beam which was deflected horizontally by the length signal (Fig. 1). A repeating length-tension figure was thus obtained, and it was always easy to see at once whether or not the behaviour of the preparation was stable. When this form of display was used, the e.m.g. was also displayed on a beam deflected horizontally by the length signal, and in order to separate the traces during lengthening and shortening a biasing potential was introduced during shortening (Fig. 1). This was done through a micro-switch operated by a cam on the stretcher drive shaft.

## RESULTS

The decerebrate cat is a variable and unpredictable preparation. Some animals remain in a stable state of reflex excitability for many hours, whereas others alter more or less rapidly from time to time. By taking a large number of photographs in rapid succession, it was always possible to decide whether the reflex remained in a steady state during the recording period. Spontaneous changes often gave interesting information, but the main conclusions of this paper have been based on records of activity that remained constant for long enough to be examined by sinusoidal stretching at a number of different frequencies.

*The types of reflex behaviour*

Different patterns of reflex behaviour were found in different preparations. In some there was a steep increase in e.m.g. activity and tension when the muscle was slowly extended, and this activity remained as long as the muscle was held extended. These were the very rigid preparations that have often been described as typical decerebrate cats. In other preparations the tension and e.m.g. activity remained small when the muscle was slowly stretched to its physiological limit, but by contrast, rapid stretching was accompanied by a burst of electrical activity and by a large increase in tension. The preparations could be classified according to their response to slow or static stretch, and they varied between those that showed no reflex response at all, and those in which the tension rose to as much as 1800 g at the maximum physiological length. For simplicity, the preparations will hereafter be described as being more or less statically sensitive.

It was not possible to discover the factors that determined which type of reflex would occur in a particular animal. One might perhaps expect the level at which the brain stem was cut to be important, but in fact each type of reflex was seen after both high and low decerebrations, and we did not succeed in altering the pattern of an established reflex by removing more mid-brain. Variations in the magnitude of the reflex, on the other hand, were common and these occurred spontaneously as well as after the removal of more mesencephalon.

*The e.m.g. during sinusoidal stretching*

Changes in muscle tension could only be explained in the light of the accompanying electrical activity; the e.m.g. will therefore be described first. The e.m.g. was usually displayed with the tension record by an oscilloscope beam which was deflected horizontally by the muscle length signal; in interpreting these records it is necessary to remember that

horizontal movement does not give a linear measure of time, the time scale is compressed at either end of the figure, and expanded in the centre, so that evenly distributed electrical activity would appear denser at the ends than in the centre.

During slow sinusoidal stretching of the more statically sensitive preparations through small amplitudes, the e.m.g. activity was continuous (Fig. 1, 0.25 c/s), but in the less statically sensitive preparations the activity was rather feeble. (Fig. 2, 0.25 c/s shows only a few motor units discharging.)

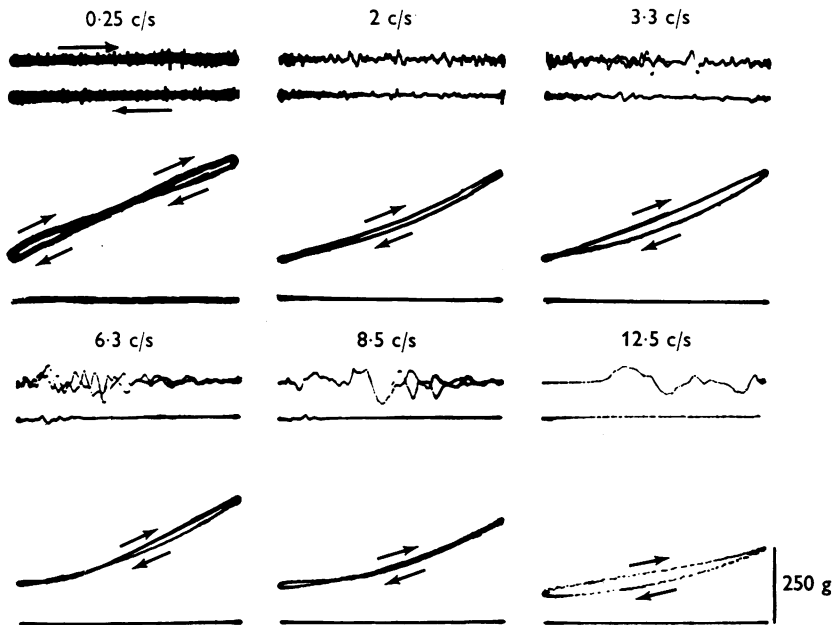


Fig. 1. L-T figures, and e.m.g. records during 1 mm (peak to peak) stretching of one of the more statically sensitive preparations. Initial length 15 mm less than physiological limit. Both e.m.g. and tension are displayed as functions of length. E.m.g. slightly retouched. The highest trace represents e.m.g. during lengthening, and below is shown the e.m.g. during shortening. All L-T figures run in clockwise direction. The e.m.g. shows continuous vigorous activity at the slowest speed, but becomes silent during shortening at the higher speeds. Note decline in peak muscle tension at the faster speeds. The muscle developed no passive tension at this length.

When the frequency of stretching was increased, the e.m.g. activity of the two types of preparation became more alike. At 2 and 3.3 c/s (Figs. 1 and 2) both types of preparation showed vigorous electrical activity during lengthening, but much less during shortening. The e.m.g. activity could then be described as showing an angular advance on muscle length. With further increase in the frequency the e.m.g. activity

became concentrated into a short 'burst', and its duration became shorter as frequency increased.

The timing of the e.m.g. activity within the cycle changed with frequency of stretching in a characteristic way. As the frequency was increased up to about 5 c/s the maximum activity occurred progressively earlier in the cycle. When, however, the frequency was increased beyond that point the timing altered in the opposite direction, and the maximum activity occurred progressively later in the cycle.

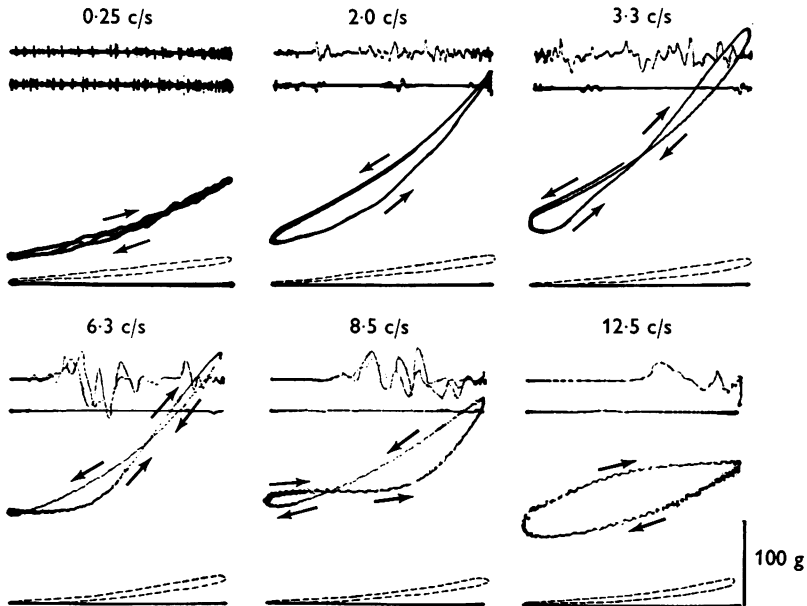


Fig. 2. L-T figures, and e.m.g. during 1 mm (peak to peak) stretching of one of the less statically sensitive preparations. Initial length 10 mm less than physiological limit. E.m.g. is displayed as in Fig. 1, with the activity during lengthening shown above. (E.m.g. retouched.) At the lowest frequency the e.m.g. records activity in a few motor units only, at higher frequencies activity is vigorous during lengthening. Note the changes in peak tension with frequency, and the anti-clockwise L-T figures at 2 and 8.5 c/s. Interrupted lines indicate L-T figure after nerve section.

In Fig. 3*A* the angular advance of the 'mid-point' of the e.m.g. on maximum muscle length has been plotted at different frequencies of stretching. The mid-point was measured from the integrated e.m.g., and was taken to be the point at which the charge on the integrator had reached half its maximum. The measurements were made on projections of traces like the one displayed in Fig. 3*B*, using a ruler so calibrated that angular displacement could be read directly from the horizontal axis. Measure-

ments of this mid-point were only made when there was a period of electrical silence in the cycle to provide a base line.

The e.m.g. activity in the two types of reflex differed in various respects. The more statically sensitive preparations showed continuous activity at low frequencies of stretching, but as frequency was increased this activity was interrupted by a silent interval during shortening. With increasing frequency this interval became relatively longer, until the e.m.g. activity was confined to a part of muscle lengthening only. In the less statically

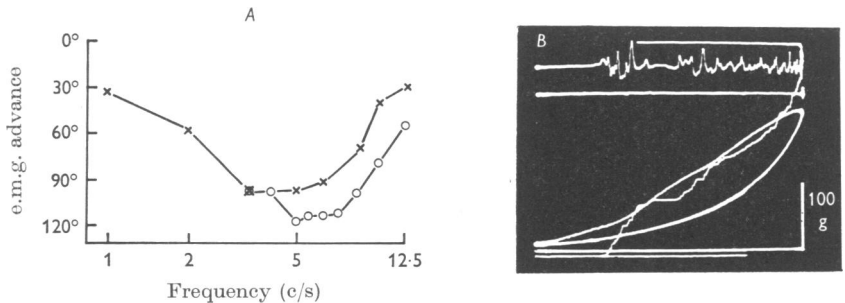


Fig. 3. *A.* The amount by which the mid-point of the e.m.g. activity precedes peak muscle length is plotted at various frequencies of stretching. Open circles indicate the more statically sensitive preparation (shown in Fig. 1), crosses the less statically sensitive preparation shown in Fig. 2. The e.m.g. 'phase advance' is greatest at the intermediate frequencies.

*B.* L-T figure and e.m.g. during 3.8 mm (peak to peak) sinusoidal stretching of one of the less statically sensitive preparations at 2 c/s. The e.m.g. and the L-T figure are shown as in Figs. 1 and 2, but a record of the integrated e.m.g. is also shown; this starts from its own base line and climbs obliquely across the trace while the e.m.g. is active during lengthening, but returns as a horizontal line when the e.m.g. is silent during shortening.

sensitive preparations, however, there was much less activity at the lowest frequencies (and sometimes none at all), but at the higher frequencies more activity appeared during lengthening. The two sorts of preparation were thus much more alike at high than at low frequencies of stretching, but even at high frequencies the duration of e.m.g. activity was always longer in the more statically sensitive preparations.

Another difference between the two types of preparation was in the extent by which the e.m.g. activity was in advance of length. Comparing Figs. 1 and 2 it will be seen that at the highest frequencies the e.m.g. activity occurred earlier in the more statically sensitive than in the less statically sensitive preparations. This can also be seen in Fig. 3*A.* This 'angular advance' of the e.m.g. was so great in the more statically sensitive preparations that the e.m.g. amplitude was sometimes greatest at the beginning of lengthening (Fig. 1, 6.3 c/s).

*The tension during sinusoidal stretching*

The series of L-T figures displayed in Fig. 1 was obtained while stretching sinusoidally one of the more statically sensitive preparations. In this preparation a peak tension of about 450 g was recorded, and this remained constant at the lower frequencies of stretching. When, however, the frequency of stretching was increased beyond 6.3 c/s the tension declined in spite of the increasing velocity of stretching, and at 12.5 c/s the peak tension was only about 250 g.

Figure 2 contains a series of L-T figures obtained from one of the less statically sensitive preparations. The tension during slow stretching was rather small, but at intermediate frequencies the e.m.g. activity during lengthening was accompanied by a steep rise in tension and a higher peak tension. At higher frequencies the peak tension declined as it did in the less statically sensitive preparations. This decline was seen when the maximum e.m.g. activity occurred less than 40 msec before the maximum muscle length. Apparently the muscle did not then develop its greatest stiffness until rapid stretching was over, so that the peak tension was rather small at the highest frequencies in either type of preparation.

In the less statically sensitive preparations the trough (minimum) tension rose when the frequency of stretching increased above about 2 c/s; the interval between the end of the e.m.g. activity, and minimum length was then less than 250 msec. With a further increase in frequency the trough tension increased, but at the highest frequencies the trough tension declined. Presumably the velocity of shortening was then so great that the tension fell in spite of the muscle activity. A similar effect was seen in tetanized muscle (Rack, 1966).

*Work done on the muscle.* The L-T curve during lengthening differed from the curve during shortening, so that in a complete cycle a figure was described. The area of this figure indicated the energy transferred between the machine and the muscle. When the figure ran clockwise work was done by the machine on the muscle, but when it ran anticlockwise the muscle did work on the machine.

The work absorbed by the muscle during 1 mm stretching has been plotted in Fig. 4 for one of the more statically sensitive preparations, and in Fig. 5 for one of the less statically sensitive preparations. In the more statically sensitive preparations work was required to maintain the movement at all frequencies (Fig. 4), and the L-T figures ran clockwise (Fig. 1). In the less statically sensitive preparations, however, the muscle did work on the machine at some frequencies (Fig. 5), and the L-T figures then ran predominantly anticlockwise (Fig. 2).



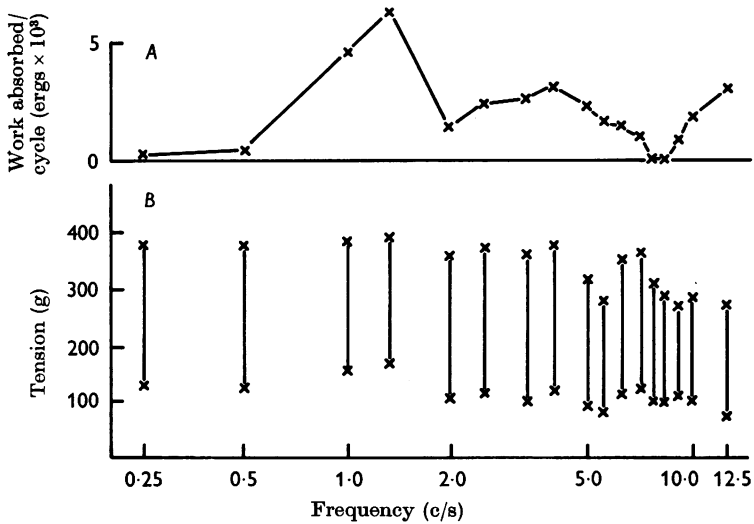


Fig. 4. Work absorbed (*A*), and tension changes (*B*), during 1 mm (peak to peak) stretching of one of the more statically sensitive preparations (the same as in Fig. 1). Initial length 15 mm less than physiological limit. At this length the muscle developed no tension after its motor nerve was cut. Note low points in the work absorption plot at 2 and 8.5 c/s.

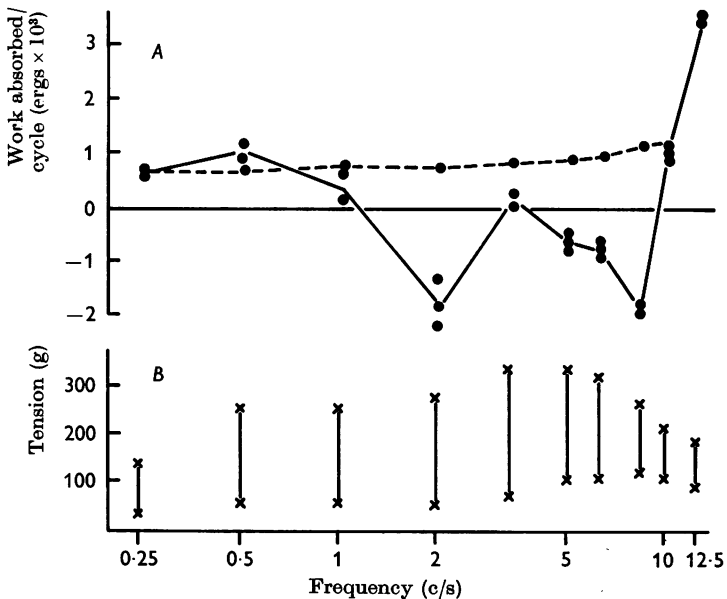


Fig. 5. Work absorbed (*A*), and tension changes (*B*), during 1 mm (peak to peak) stretching of one of the less statically sensitive preparations (the same as in Fig. 2). Initial length 10 mm less than physiological limit. The interrupted line indicates the work absorbed by the muscle after its motor nerve was cut. Note the changes in peak and trough tensions with changing frequency. There are two low points in the work absorption plot, at 2 and 8.5 c/s; at both these frequencies the 'work absorption' is negative, i.e. the muscle is doing work on the machine.

*The relation between e.m.g. and tension*

The shape and direction of the L-T figures could be correlated with the e.m.g. activity that accompanied them. Vigorous e.m.g. activity early in lengthening was always associated with a steep rise in tension during lengthening, and since this exceeded the tension during shortening the L-T figure then ran clockwise, and external work was required to maintain the movement.

When the e.m.g. was relatively inactive at the beginning of lengthening, but increased later in lengthening, the tension during shortening might exceed the tension during lengthening and the L-T figure then ran predominantly anticlockwise (Fig. 2, 2 and 8.5 c/s). This state of affairs was commonly seen during 1 mm stretching of the less statically sensitive preparations at 5-8.5 c/s, and less often also at 2 c/s (Fig. 2). Anticlockwise figures did not occur in the more statically sensitive preparations with their generally greater 'angular advance' of the e.m.g. activity on length.

With frequencies of 10 c/s or more, the L-T figures always ran clockwise in spite of the lateness of the e.m.g. activity; the shape of the L-T figures suggested that the muscle then remained in an 'active state' during a significant part of the ensuing lengthening, so that tension rose considerably as lengthening began.

The work absorption/frequency plot from the less statically sensitive preparation (Fig. 5) shows a low point at 2 c/s. This was not always seen. In some of the less statically sensitive preparations there was no reflex activity during the slowest stretches, and hardly any at 2 c/s; the work absorption/frequency plot then followed the pattern of the passive muscle at the slower speeds. Some small amount of static sensitivity seemed to be necessary for work to be done by the muscle on the machine at the slower speeds.

Some of the tension changes are difficult to visualize when they are displayed against muscle length, and we have sometimes found it useful to examine the same sort of results on a linear time base. In Fig. 6 the muscle length and tension, the e.m.g., and the integrated e.m.g. are separately displayed. This kind of display gives another view of the sequence of events when a preparation of low static but high dynamic sensitivity was sinusoidally stretched. In interpreting these figures it is necessary to remember that an L-T figure traced in a clockwise direction implies an angular advance of tension on length, whereas an anticlockwise figure implies an angular delay.

At the lowest frequency of stretching (Fig. 6, 1 c/s) the e.m.g. activity occurred mainly in the later part of lengthening, and at maximum length.

The tension developed was small, and showed a little angular advance on length.

At 2 c/s, the delay between the e.m.g. activity and the muscle tension it generated occupied a larger fraction of the cycle; the peak tension occurred relatively later, and muscle activity persisted well into the period of shortening, so that the tension during the last part of shortening was greater than during the first part of lengthening. The trough tension was reached later than the minimum length, and there was a mean angular delay of tension on length.

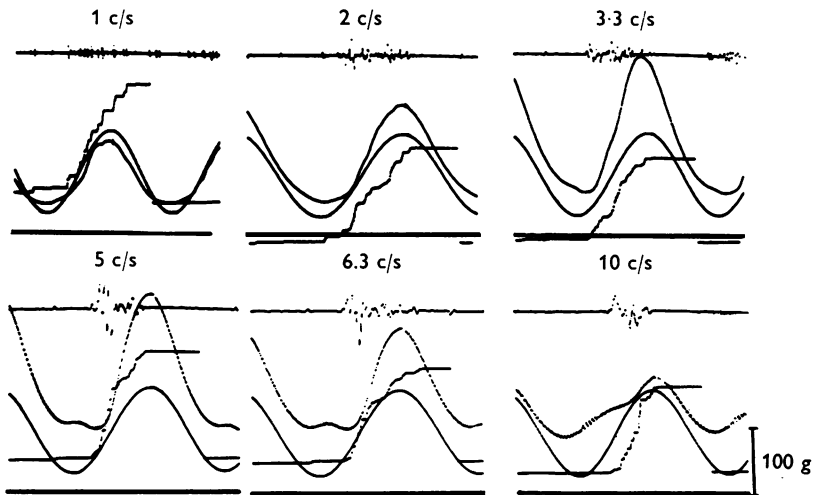


Fig. 6. The response to 1 mm (peak to peak) stretching of one of the less statically sensitive preparations. Initial length 9 mm less than physiological limit. The results are displayed on a linear time base. Frequency is indicated above each set of records. The length signal appears as a sine curve constant in all the records. Tension is indicated by the irregular but approximately sinusoidal trace. E.m.g. activity is shown above, and the integrated e.m.g. record climbs obliquely across each record. The tension base line is below. The alterations in the tension record with increasing frequency are described in detail in the text.

When the muscle was stretched at 3.3 c/s, the e.m.g. activity occurred earlier in the cycle, and the peak tension occurred correspondingly earlier preceding maximum length. The contractile activity lasted through shortening, and the sudden fall in tension at minimum length marks its decline. The peak tension preceded the maximum length, while the trough tension was delayed after the minimum length, and this trace corresponds to the figure-of-eight seen in Fig. 2 at the same frequency.

At 6.3 c/s the e.m.g. activity again occurred late in extension, the peak tension was therefore later, and was no longer ahead of maximum length.

The muscle activity now persisted right through shortening, and the inflexion in the tension trace that marks the decline in contractile activity occurred after minimum length. The trough tension was later than minimum length, and there was a mean angular delay of tension.

The highest frequency in Fig. 6 is 10 c/s. The e.m.g. activity then occurred late in extension, and the peak tension occurred after maximum length. Activity, however, lasted well into the following lengthening, and the tension in the early part of extension was considerable, the trough tension was now well ahead of minimum length, and there was a mean angular advance of tension on length.

Both Figs. 2 and 6 show intermittent e.m.g. activity at the higher frequencies, and the effect of each burst of activity can be seen in the tension record. At 2 c/s active tension lasts for at least 200 msec after the end of the electrical activity, but at 6.3 c/s an inflexion in the tension record only about 85 msec after the e.m.g. activity indicates a decline in active tension. Intermediate frequencies show intermediate time intervals between the end of e.m.g. activity and the decay of active tension.

The apparent discrepancy in these results is probably explicable as follows: After the electrical impulse, contractile elements in the muscle pass into an active state during which their stiffness is increased (Hill, 1949; Ritchie, 1954). This stiffness then slowly declines. During the decline a point is reached at which the contractile elements cease to shorten, and begin to be re-extended by either the series elastic elements of the muscle, or by external movement. In an isometric muscle this point marks the beginning of the decline in tension, and it occurs earlier when the tension is high in an unfused tetanus than when tension is lower in a single twitch. The interval between the end of the electrical activity and the beginning of the decline in muscle tension is not constant, therefore, but depends on the muscle tension.

When this property of muscle is taken into consideration, the results shown in Figs. 2 and 6 present less difficulty.

#### *Intermittent stimulation during sinusoidal stretching*

The rather complicated relation between e.m.g. activity and muscle tension during 1 mm sinusoidal stretching was unexpected. In order to confirm and clarify these findings some additional experiments were carried out in which the motor activity in the stretch reflex was imitated by interrupted tetanic stimulation of the ventral nerve roots.

Three cats were anaesthetized with sodium pentobarbitone (Nembutal). The L7 and S1 roots were detached from the spinal cord, and their distal ends prepared for stimulation in a paraffin pool. The rest of the dissection of the leg was exactly as before, and the recording methods were the same. Interrupted tetani were provided by leading the output of a stimulator through a contact breaker on the stretcher drive shaft. This contact breaker could

be adjusted to transmit a burst of stimuli of any desired duration in any part of the cycle. In order to approximately match the reflex tension, the stimulus was usually confined to the S1 root.

In these experiments the relation between the electrical activity and muscle tension was found to be the same as in the stretch reflex records, and this was a useful confirmation of the earlier findings. Figure 7 shows how the direction of the L-T figure depends on the timing of the stimulus (here recorded as an e.m.g.) within the cycle. When an electrical stimulus occurred early in extension, the tension rose early, and the L-T figure ran clockwise, but when the stimulus occurred late in extension the L-T figure ran anticlockwise, and the muscle did work on the machine.

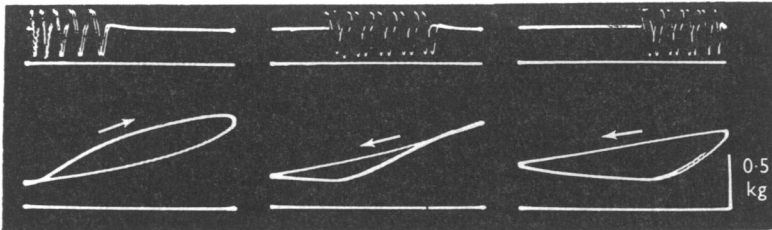


Fig. 7. L-T figures, and e.m.g. during 1 mm (peak to peak) sinusoidal stretching at 3.3 c/s. The spinal roots have been cut, and trains of 5 impulses at 10 msec intervals are delivered to the S1 root in various parts of the cycle. (The e.m.g. shows two imperfectly superimposed traces, as the camera shutter was open for more than a complete cycle). The L-T figure changes from a clockwise to an anticlockwise direction as the stimuli are delivered later in the cycle.

In the isometric muscle, tension was still appreciable 250 msec after the end of a brief tetanus, and during sinusoidal stretching the interval between the last stimulus and the apparent decline in active tension altered with frequency in the same sort of way that it did in the reflex experiments.

### *Clonus*

When the muscle did work on the stretching machine, it was assisting its own forced oscillation. The preparations that did this also exhibited sustained clonus when loaded with an appropriate weight. A record of clonus in such a muscle is shown in Fig. 8. The lower trace records the muscle length, and the upper trace the e.m.g. The clonus frequency in this preparation was approximately 6 c/s, and this coincided with the frequency at which the sinusoidally stretched muscle did most work on the stretching machine.

In some other preparations clonus frequencies of about 8 c/s were recorded. This value also corresponded to the frequency at which those muscles did most work on the stretching machine. Clonus was never seen

in the more statically sensitive preparations, and this was not surprising since work always had to be done on these preparations to maintain sinusoidal movement.

*Changes in magnitude of reflex activity.* The magnitude of the reflex activity varied in different decerebrate preparations, and changed from time to time in each preparation. The results illustrated in Figs. 1 and 2 were from preparations with fairly active reflexes, other preparations were seen in which the reflex tension was smaller, and the behaviour was closer to that of passive muscle.

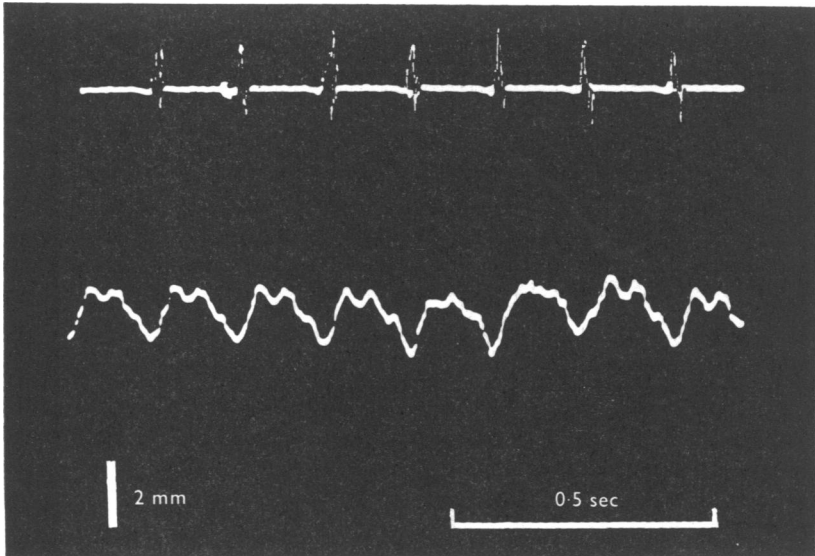


Fig. 8. Clonus in one of the less statically sensitive preparations loaded with 50 g weight. Upper trace records e.m.g. Lower trace records muscle length (recorded by measuring changes of tension in a fine spring joining the tendon to the anode pin of an RCA 5734 transducer valve). E.m.g. retouched. The clonus frequency (6 c/s) corresponded to the frequency at which this muscle did most work on the machine during sinusoidal stretching. (The higher frequency irregularities in the length record are probably artifacts from the recording system.)

The transfer of work between the stretcher and the muscle was also affected by the magnitude of reflex activity, and when the level of reflex activity fell the amount of work absorbed by the muscle in a cycle approached the figure obtained for passive muscle. In the less statically sensitive preparations the reflex activity had different effects on the work absorbed at different frequencies of stretching (Fig. 5); at 12.5 c/s an increase in reflex activity led to an increase in the work absorbed by the muscle, but at 6.3 c/s the effect of reflex activity was to reduce the work absorbed below the passive level, and in the more active preparations this

reduction was so great that the work absorbed by the muscle was negative, i.e. the muscle was doing work on the machine.

*The effect of stretch amplitude.* The foregoing descriptions have been based on the effects of stretching the muscle through 1 mm. Stretch amplitudes of 0.7, 1.6 and 3.8 mm were also available, and each type of reflex was examined at all these amplitudes.

With 3.8 mm (peak to peak) stretching, the e.m.g. activity was distributed in the cycle in the same way as with the smaller amplitudes, and its mid-point altered with frequency in the same way (Fig. 9), the 'phase advance' being greatest at 3.3 c/s.

In spite of the similarities in the e.m.g. records, the tensions that developed during sinusoidal stretching differed in important respects, and these differences were reflected in the shape of the L-T figures. In the less statically sensitive preparations 1 mm sinusoidal stretching led at some frequencies to anticlockwise L-T figures. When, however, the stretch amplitude was increased to 3.8 mm, the L-T figures always ran clockwise. A preparation that did work on the machine when the amplitude of stretching was small would cease to do so when the amplitude was increased, and with a further increase in amplitude the muscle would absorb work from the machine. Figure 3 shows an L-T figure obtained during 3.8 mm stretching of one of the less statically sensitive preparations.

This increase in work absorbed by the muscle as the amplitude of movement increases is in keeping with the known properties of skeletal muscle. During shortening the tension developed in active muscle is inversely related to the velocity of shortening (Hill, 1938). When the amplitude of sinusoidal stretching is increased, the velocity of shortening is correspondingly increased, so that tension during shortening becomes smaller. Muscle activity during shortening has therefore a progressively smaller effect on tension as the amplitude of movement increases, and any increase that may occur in the magnitude of the reflex activity during shortening has negligible effect compared with the effect of the increase in velocity.

This important property of muscle ensures that work will always be absorbed when the amplitude of sinusoidal movement is sufficiently large, and this is the important factor in limiting the amplitude of spontaneous clonus.

Figure 9 contains plots of the work absorbed, the tension changes, and the angular advance of the e.m.g. activity during 3.8 mm stretching of a preparation with low static sensitivity. This figure shows that although the muscle always absorbed work from the stretching machine the amount of work absorbed in a cycle varied with different frequencies of stretching. The work absorbed always fell to a relatively low level at fre-

quencies 5–10 c/s, and in this respect the findings resembled the results of stretching through 1 mm (Fig. 5).

A second dip in the frequency/work absorption plot was also seen at 2 c/s in some preparations, but this was never so obvious as with the smaller stretch amplitudes.

The amount of work absorbed in a cycle varied with frequency in the same sort of way irrespective of the amplitude of stretching, but an increase in the amplitude above 1 mm biased all the values in the direction of more work absorption by the muscle.

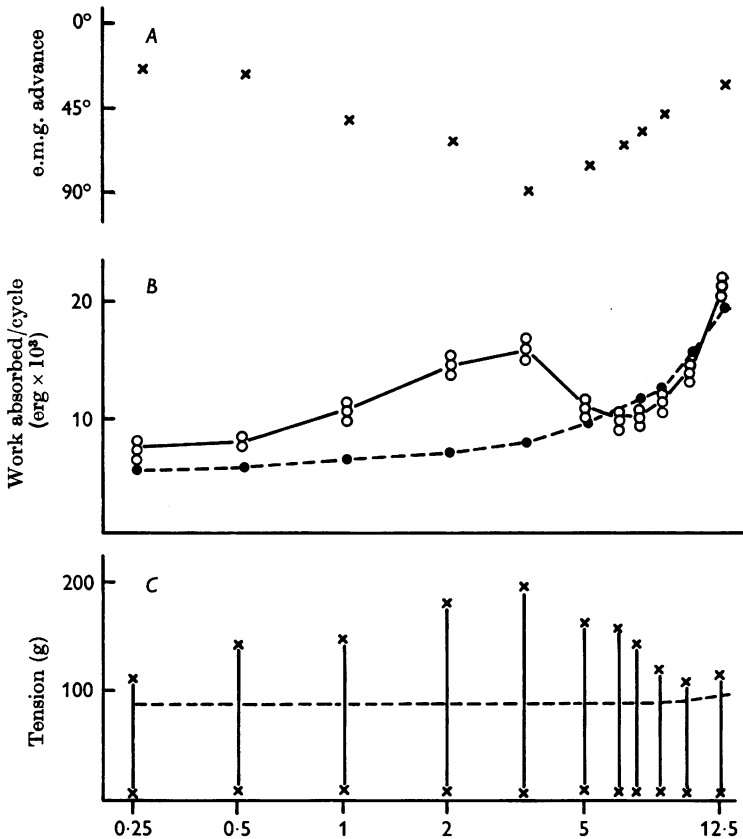


Fig. 9. E.m.g. 'phase advance' (A), work absorbed (B), and tension changes (C), during 3.8 mm (peak to peak) sinusoidal stretching of one of the less statically sensitive preparations. Initial (shortest) length 10 mm less than physiological limit. The e.m.g. changed with frequency in the same way as it did with smaller amplitude stretching (compare Fig. 3). The work absorbed/cycle was always positive (compare Fig. 5), but fell below the value for passive muscle (interrupted line) at 6.3–10 c/s. Peak and trough tensions changed in the same way as with smaller amplitude stretching; the lower interrupted line indicates the peak tensions of the passive muscle.



Reduction of the stretch amplitude to 0.7 mm (peak to peak) reduced the changes in the work absorption/frequency plot, so that they were always less striking than those seen during 1 mm stretching. The work absorbed/cycle was closer to the figure for passive muscle, and only rarely at 6.3 c/s did the muscle do work on the machine.

The rather small changes in the work absorption during stretching through smaller amplitudes were probably associated with a reduction in the e.m.g. activity, of the less statically sensitive preparations, but no reliable measurement of total e.m.g. activity was possible in these experiments.

*The effect of altering initial muscle length.* The very large differences in the sensitivity of different preparations to static stretch have already been discussed. At one extreme are preparations that develop a high tension when held extended; at the other extreme are those that develop a tension no greater than the denervated muscle at that length.

Although reflexes that were quite insensitive to static stretch did occur, it was more usual to find some increase in the reflex activity with an increase in muscle length even though the extra reflex tension developed was rather small. Whenever the reflex activity did increase with length there was some alteration in the pattern of reflex behaviour also, the 'bursts' of e.m.g. activity at the higher stretch frequencies became longer, and began earlier in the cycle.

In other words, if a muscle had any sensitivity to static stretch, increasing its length changed its response in the direction of the more statically sensitive preparation.

*The integrity of the fusimotor fibres.* During the course of these experiments, it seemed possible that the two types of preparation that have been described might merely reflect different total amounts of fusimotor activity. To obtain further information on this point, conduction in the small fibres of the soleus nerve was blocked with lignocaine (Xylocaine) (Matthews & Rushworth, 1957; Critchlow & von Euler, 1963).

Pieces of filter paper soaked in a solution of Xylocaine (0.25, or 0.125 g/100 ml.) were placed on the nerve as it lay in a paraffin pool. The integrity of the alpha motor fibres was tested from time to time by measuring the isometric twitch tension during stimulation of the nerve proximal to the treated segment.

Six applications of Xylocaine were made in three different reflex preparations. One of these preparations showed a high sensitivity to static stretching, and the other two a low static sensitivity. On each occasion there was a very active reflex before application of Xylocaine and the changes in tension and work absorption at different frequencies were characteristic.

Application of Xylocaine always gradually reduced the reflex activity until the e.m.g. became silent, and the L-T figures resembled those obtained after nerve section. This reduction of activity toward the passive state took place without any significant blockage of conduction in the alpha motor fibres (as measured by the isometric twitch tension); the decline in reflex activity was therefore attributed to the blocking of small fibres in the motor nerve.

During the decline in reflex activity, there was nothing to suggest that one type of reflex was changing into the other. The e.m.g. activity became steadily less, without any change in its timing, and the L-T figure became progressively closer to the type seen in passive muscle. In particular, the behaviour of the more statically sensitive preparation did not at any stage come to resemble the less statically sensitive preparations.

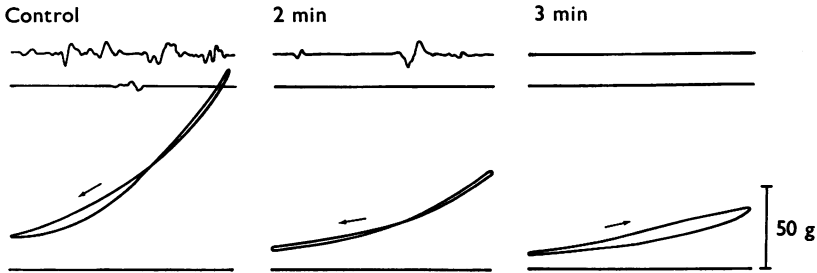


Fig. 10. The effect of applying Xylocaine to the muscle nerve. One millimetre stretching of one of the less statically sensitive preparations at 3.3 c/s. Before Xylocaine treatment the L-T figure was a figure-of-eight, and the e.m.g. was active during most of lengthening. A filter paper soaked in 0.25% Xylocaine was placed on the soleus nerve. Two minutes later the e.m.g. activity was less, and the tension was reduced, but the distribution of e.m.g. activity and the shape of the L-T figure were unchanged. Three minutes after Xylocaine application all e.m.g. activity had disappeared, and the L-T figure was the same as in the passive muscle. Conduction in the alpha motor neurone was unaffected. Reflex activity returned to its previous level 10 min after removal of the Xylocaine.

Figure 10 illustrates the effect of Xylocaine on one of the less statically sensitive preparations during sinusoidal stretching through 1 mm at 3.3 c/s. Two minutes after application of Xylocaine the e.m.g. activity was less, and the tension had declined, but the general shape of the L-T figures was unchanged. Three minutes after application of Xylocaine the e.m.g. activity had ceased, and the L-T figure was the same as in the passive muscle.

This progressive reduction in reflex response was attributed to blockage of thin fibres in the soleus nerve (Matthews & Rushworth, 1957). Of these the fusimotor fibres were probably the most significant, since the small afferent fibres probably play little part in the stretch reflex of extensor muscles (Hunt & Perl, 1960). It was concluded therefore that each type of reflex behaviour depended on a background level of fusimotor activity, and the differences between the two sorts of preparation were not merely differences in the total amounts of fusimotor activity.

## DISCUSSION

*Timing of the e.m.g. activity.* The afferent discharge from innervated muscle spindles has not been examined in detail during sinusoidal stretching. The muscle spindles are known, however, to be sensitive to the velocity of lengthening as well as to length itself (Matthews, 1933). During sinusoidal stretching, therefore, the greatest afferent activity will occur in advance of peak muscle length. This angular advance will be less than  $90^\circ$  since there is no evidence that the innervated muscle spindles are sensitive to acceleration of lengthening. The angular advance will probably increase as frequency (and therefore velocity of lengthening) increases.

The e.m.g. during sinusoidal stretching shows an angular advance that often reaches, and may exceed,  $90^\circ$ ; a further advance must therefore occur as the reflex signal passes through the spinal cord. It is possible to envisage ways that this could occur; for example, recurrent inhibition of the motor neurones through their axon collaterals might block transmission of the later part of the muscle spindle discharge, so that only its earlier part is translated into motor neurone activity. It is unlikely that an inhibitory effect from the soleus tendon organs plays an important part in this mechanism, since the tendon organ discharge is related to muscle tension (Matthews, 1933; Jansen & Rudjord, 1964), and angular advance was not significantly altered when the tension was reduced to a low level by an incomplete fusimotor block.

The increase in the angular advance of the e.m.g. activity that occurred with a moderate increase in frequency of stretching is in keeping with the known properties of the muscle spindles, but the smaller angular advance that occurred at the higher frequencies was unexpected. It was found, however, that at higher frequencies active tension persisted from the previous cycle into the earlier part of muscle lengthening. This activity presumably had an 'unloading' effect on the muscle spindles, diminishing their afferent discharge in the same way that a twitch in isometric muscle causes a silent period in the discharge of the muscle spindle afferents. Such a mechanism would delay the response of the muscle spindles to extension of the whole muscle; the effect would be more striking in the less statically sensitive preparations which change in stiffness more obviously as the activity from the previous cycle decays. At the higher frequencies of stretching the e.m.g. activity does in fact occur later in the less statically sensitive than in the more statically sensitive preparations.

*The two types of stretch reflex.* The foregoing experiments have demonstrated two different patterns of reflex activity in the decerebrate cat, neither of which can exist after fusimotor activity has been abolished.

The differences in reflex behaviour may be due to differences in the

fusimotor control of the muscle spindles, or to differences in the spinal synaptic mechanism, or to both. A good deal of information is available about the fusimotor control of the muscle spindles (Matthews, 1964), and about their behaviour in the soleus muscle of the decerebrate cat (Jansen & Matthews, 1962). It is therefore worth considering how far the present observations can be related to the known behaviour of the muscle spindles.

There is convincing evidence that the sensitivity of the muscle spindles to static stretch and to dynamic stretching can be independently influenced by two different kinds of fusimotor fibres (Matthews, 1964). In the decerebrate cat, the response of the muscle spindle primary endings is usually at a high level as a result of background fusimotor activity, but the responses to static stretch and dynamic stretching vary in different preparations; these variations have been attributed to different mixtures of static and dynamic fusimotor activity (Jansen & Matthews, 1962).

It is tempting to assume that the different patterns of reflex behaviour seen in the present experiments correspond to the different sorts of fusimotor activity found by Jansen & Matthews, and the fact that intermediate reflex states did occur presents no difficulty.

Certain features of the more statically sensitive preparations suggest vigorous activity in the static fusimotor fibres. The vigorous response of both tension and e.m.g. to a slow or static stretch could be a consequence of static fusimotor activity, and the fact that the e.m.g. remains active during shortening at moderate speeds is very suggestive of activity in the static fusimotor fibres (Crowe & Matthews, 1964; Jansen & Rudjord, 1965). In contrast, the less statically sensitive preparations showed a lack of response to slow stretching, and a lack of activity during shortening, which both suggest a low level of activity in the static fusimotor fibres.

In the less statically sensitive preparations the peak tension rose during moderate increases in frequency of stretching, which suggests that dynamic fusimotor activity was enhancing the sensitivity of the muscle spindles to rapid stretching. The changing angular advance of the e.m.g. activity with moderate increases in frequency was also the sort of behaviour that could be expected during dynamic fusimotor activity; this was found in both types of preparation.

The experimental results suggest therefore that dynamic fusimotor activity was present in both types of preparation, but static fusimotor activity was prominent only in the preparations that were more sensitive to static stretch.

*The relation of muscle tension to e.m.g. activity.* The effect of e.m.g. activity on muscle tension during sinusoidal stretching could perhaps have been predicted from the known properties of skeletal muscle.

Electrical activity in muscle is followed by an 'active state' which develops rapidly, but decays over a much longer period (Ritchie, 1954). E.m.g. activity early in lengthening therefore leads to muscle activity when the velocity of lengthening is greatest. Extension of this active, and therefore stiff, muscle leads to a high tension during lengthening, and since a part of the stiffness is viscous (Rack, 1966) work is required to maintain the movement whether the activity continues during shortening or not.

If therefore the e.m.g. activity begins sufficiently in advance of muscle length, the muscle will always absorb work from the stretching machine, whatever happens during the rest of the cycle.

*Muscle damping in the decerebrate cat.* When during sinusoidal stretching a muscle absorbs work from the machine, it opposes and tends to damp movement. When, however, the muscle does work on the machine, it assists its own movement, and the damping tendency is said to be negative. In these experiments the machine was much more powerful than the muscle so that the movement was not in fact significantly affected by the muscle behaviour. If, however, the muscle were acting on an inertial load, then the damping properties of the muscle at each frequency and amplitude would govern the course of an oscillation at that frequency and amplitude.

Absorption of work, and damping, are associated with a phase advance of tension on length, but work done by the muscle on the machine implies phase delay, and negative damping. The phase relation between length and tension in any frequency-amplitude situation depends on how far the angular advance of the e.m.g. and the damping properties of the muscle itself can offset the delays in the reflex pathway.

The complexity of the stretch reflex, and the non-linearities of its component parts prevent useful mathematical description of its properties. It is, however, possible to suggest the sort of effects that the different parts of the reflex pathway will have on the phase relations between length and tension during sinusoidal stretching:

(1) The muscle spindle discharge shows an angular advance on peak length that first increases with frequency, but diminishes at the highest frequencies.

(2) This reflex signal is further advanced as it passes through the spinal cord.

(3) The motor neurone discharge 'triggers' a state of contractile activity in the muscle fibres, which slowly declines over about 250 msec.

(4) The muscle has a powerful damping effect as long as a significant part of the contractile activity occurs during lengthening.

From the functional point of view, the damping properties of the muscle cannot be separated from the angular advance of the reflex signal,

since the muscle has important damping properties only if it is activated early in extension.

The authors are grateful to Mr T. Rudjord for many helpful discussions, to Dr P. B. C. Matthews for his comments on results and the manuscript, and to Mr J. Rausanaksel for technical assistance. One of us (P. M. H. R.) was supported by the United Birmingham Hospitals and Regional Hospital Board, and received a travel grant from the Wellcome Trust.

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