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ELASTIC PROPERTIES OF THE CAT SOLEUS TENDON AND THEIR FUNCTIONAL IMPORTANCE

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SUMMARY

1. A new method has been used to measure the stiffness of the entire tendinous component of the soleus muscle of the cat. During sinusoidal stretching of the muscle–tendon combination, the motor nerves were stimulated repetitively in such a way that the force of contraction offset the movement, and the muscle fibres remained at constant length. The afferent endings of muscle spindles were used to detect extension of the muscle fibres. In this null situation, when the spindles did not ‘see’ any movement, all of the applied movement was assumed to have been taken up in the tendinous components, and measurements of the movement and force allowed the stiffness to be calculated. Precautions were taken to avoid the effects of fusimotor stimulation.

2. The stiffness of the entire tendinous component increased with increasing muscle force by approximately 2 N/mm per Newton mean force from 2 N/mm at low force to about 25 N/mm at 11 N; the method could not be used for larger forces.

3. Independent measurements of the stiffness of the external part of the tendon were made by both static and dynamic methods. The entire tendinous component was much less stiff than the external tendon.

4. Measurements of the dimensions of the tendon allowed Young’s modulus for the tendon to be calculated. It increased from about 250 N/mm² at 2·5 N to about 450 N/mm² at 10 N mean force.

5. Measurements of dissected muscles allowed comparisons to be made between the stiffness of the external tendon and the stiffness of the entire tendinous component in these muscles. Scaling of the stiffness of the external part of the tendon to the length of the entire tendinous component gave a value of stiffness which was similar to that measured by the spindle null method.

6. The compliance of tendons has implications for the control of movement which are discussed.

INTRODUCTION

Most skeletal muscle fibres are attached to bone through tendons which are essentially elastic. A contraction of the muscle fibres may therefore not necessarily cause the same movement at the muscle attachments, since some movement will be taken up in extending the tendon. Conversely, an externally imposed movement may
not be communicated faithfully to the muscle fibres, since some of this movement may also be taken up in the tendon. The actual distribution of movement between the muscle fibres and the tendon will depend on their relative stiffnesses.

Muscle spindles are located among the muscle fibres, so that the part of an external movement that they ‘see’ will also depend on the distribution of the movement between muscle fibres and tendon. Under passive conditions, muscle fibres are much more compliant than tendon, so that movement which is applied to the tendon of a passive muscle will be transmitted faithfully to the spindles. However, when the muscle fibres are active they increase in stiffness, and less of the external movement will then be seen by the spindles. In many normal situations, the muscle length and the muscle activation are both changing at the same time, so that the relationship between external movement and spindle movement may become complicated (Rack, Ross, Thilmann & Walters, 1983); any attempt to understand the muscle spindle activity and the consequent reflex responses will then require a knowledge of the tendon properties.

There have been previous measurements of the mechanical properties of tendons but these have considered only those parts of the tendon that lie outside the main bulk of the muscle (Rigby, Hirai, Spikes & Eyring, 1959; Diamant, Keller, Baer, Litt & Arridge, 1972; Woo, Ritter, Amiel, Sanders, Gomez, Kuei, Garfin & Akeson, 1980; Ker, 1981). Tendinous fibres extend over the surface of many muscles and often within the muscle substance, and we lack knowledge of the properties of these tendinous elements. It has sometimes been assumed that the tendon fibres which serve a bundle of muscle fibres retain their separate identity, and have similar mechanical properties throughout their length, so that the compliance of the entire tendon may be calculated from the compliance of a part (Alexander & Vernon, 1975; Rack et al. 1983), but this assumption has not previously been tested experimentally.

In the present investigation we have measured the properties of the entire tendinous components of a muscle by using muscle spindles to detect movement, or lack of movement, of the muscle fibres. The muscle–tendon combination was subjected to periodic sinusoidal movements, but during each cycle of movement the muscle was also stimulated to contract. The movement and the stimulus were then adjusted until their effects on the discharge of the muscle spindles offset each other so that the afferent activity no longer changed with the movement. In this null situation it was assumed that the muscle fibres were remaining at constant length and that all of the imposed movement was being taken up in their tendinous components. The resistance to movement would then give a measure of the stiffness of the tendinous components.

The results support earlier assumptions, and add useful information about the properties of the cat soleus tendon at different forces. A preliminary account of the work has already appeared (Rack & Westbury, 1983).

METHODS

The experiments were performed upon eight adult cats weighing between 2.25 and 2.75 kg; six of these contributed to the main body of the results. The animals were anaesthetized by an intraperitoneal injection of pentobarbitone sodium (Sagatal, May & Baker), further quantities being given intravenously as required. Rectal temperature was maintained at 36–38 °C.
The methods of dissection, fixation and stimulation of soleus have previously been described in detail (Rack & Westbury, 1969). The muscle was exposed and dissected free from surrounding structures, other muscles in the limb being denervated. A flake of the calcaneum was left attached to the Achilles tendon. The tendon of plantaris was removed, and the tendinous fibres which formed the insertion of the gastrocnemius were removed by blunt dissection, care being taken to preserve those fibres that arose from soleus. The fibres could be separated to within about 7 mm of the insertion but no attempt was made to dissect the most distal part of the tendon where the fibres from the different muscles become intertwined. A clamp was then attached to the distal end of the tendon; it did not grip the tendon tightly, but the fragment of calcaneum became engaged behind it (Fig. 1). In some experiments the flake of bone was embedded in epoxy resin to fix it further. This ensured that movements of the clamp were faithfully transmitted to the tendon.

Fig. 1. Schematic diagram showing the arrangement of the experiment. c, tendon clamp; m, dissecting microscope; s.g., strain gauge; s, ventral root stimulators.

The mechanical arrangement
The cat was mounted in a rigid metal frame, similar to the one that was used previously (Rack & Westbury, 1969). The tibia was secured by two pairs of steel pins and in this mounting it moved by less than 2 μm/N force. The tendon clamp was coupled to a machine which generated sinusoidal movements from a rotating wheel and crank. This was the same mechanism that had been used to move human joints (Evans, Fellows, Rack, Ross & Walters, 1983), though it was modified to give smaller amplitudes of movement. Similar position and force transducers were used. The force transducer, and other couplings that joined the position transducer to the tendon clamp, yielded by less than 1 μm/N. Taken together, the mechanical couplings to the tendon and to the tibia yielded by only 3 μm/N. This movement would not have been detected by the position transducer, but the error incurred was small; it was disregarded.

The muscle was kept in a pool of Krebs–Henseleit solution which was maintained at a temperature of 35–37 °C by an immersion heater. The same solution was dripped continuously onto the tendon.

Muscle stimulation
The ventral nerve roots of the seventh lumbar and first sacral segments were subdivided until the divisions could be arranged into five or more groups, each of which supplied a similar amount of the soleus muscle. The muscle could then be activated by a pulse distributor which supplied stimuli to each of these divisions in sequence to obtain a smooth contraction of the muscle with a relatively low rate of impulses in each motor unit and a correspondingly low force (Rack & Westbury, 1969). The ventral root filaments were stimulated at a rate which was modulated.
sinusoidally around a mean level. This was achieved by the use of a voltage-controlled pulse generator whose input was a sinusoidal wave form generated from the rotating wheel (Fig. 1). The mean stimulus frequency, its depth of modulation and its phase relation to the movement could all be adjusted.

**Afferent recording**

The dorsal nerve roots were subdivided to obtain filaments which contained single primary afferent fibres from soleus muscle spindles. Afferents were identified in the usual way by their response to muscle extension and to muscle stimulation (Matthews, 1972). In the presence of an array of stimulating electrodes on ventral roots it was difficult to record from more than two afferents simultaneously, and we were usually content to record from one at a time.

**Experimental procedure**

When the necessary ventral and dorsal root filaments had been arranged on electrodes, the muscle was subjected to sinusoidal stretching at 20-2.5 Hz. The muscle was kept at a mean length that corresponded to an angle at the ankle of 45° (see Rack & Westbury, 1969). Muscle spindle afferents respond to sinusoidal movement with a train of action potentials whose rate fluctuates at the frequency of the movement (Matthews & Stein, 1969; Poppele & Bowman, 1970). When a sinusoidally modulated stimulus was added, the fluctuations in the rate of discharge could become greater or smaller, depending upon the timing of the stimulus pulses in relation to the movement. Our purpose was to adjust the phase relation between the modulated stimulus train and the movement, and to adjust either the depth of stimulus modulation or the amplitude of the movement until the afferent discharge from the spindle became steady, and ceased to fluctuate at the frequency of the movement. To assist us in these adjustments, we employed a PDP 11/34 computer to carry out a cycle-by-cycle sinusoidal analysis of the afferent impulse trains (see Brown, Rack & Ross, 1982a). We could then make changes in the parameters of stimulation and movement while observing their effects. When the display indicated that a satisfactory null point had been reached, so that there was no muscle spindle response to the movement, we made tape recordings of the movement, the force, the afferent pulse train and the stimulating pulses. Once a satisfactory null had been reached in the response of the afferent ending, the force record was analysed by conventional methods to determine the mean force, and the amplitude and phase of force fluctuation in relation to movement. Stiffness could then be calculated from these measurements (Brown, Rack & Ross, 1982a).

**Structure of the muscle**

Following the physiological measurements, the structure and dimensions of each of the muscles were determined by dissection and direct measurement. With the muscle held at the length at which physiological measurements had been made, we split it longitudinally in the plane of the muscle fibres and measured the length of the muscle fibre bundles and the over-all length of the muscle including all of the tendon.

The cross-sectional area of the external part of each tendon was determined by a gravimetric method (Ellis, 1969; Ker, 1981). A measured portion of the external tendon was cut and weighed. Its density was then found by flotation in a mixture of chloroform and benzene. The cross-sectional area could then be calculated.

**Measurement of stiffness of external tendon**

For all tendons, a static method was employed for measurement of stiffness. The length of a marked segment of the tendon was measured with a travelling microscope while different loads were applied. In this way a length-force curve could be plotted for the range of forces that were used in the main experiments. In two experiments the stiffness was also measured by a dynamic method; this is described in a later section.

**RESULTS**

The principal results of this investigation are measurements of mechanical stiffness. However, these could only be obtained after analysis of the afferent muscle spindle responses to movement and appropriate adjustment of muscle stimulation.
Muscle spindle responses

Sinusoidal movement was applied to the muscle–tendon combination at a frequency of about 2 Hz. When the muscle was passive, this caused the primary endings of muscle spindles to discharge during the extension phase of each cycle of movement (Fig. 2A). This relationship between the afferent discharge and the movement is seen more clearly when the responses to many cycles of the movement are averaged and displayed as a cycle histogram (Fig. 3A). This result confirms the profound modulation of the primary afferent discharge by a small (±0.16 mm) movement (Matthews & Stein, 1969; Poppele & Bowman, 1970).

Fig. 2. Records of primary afferent activity during applied sinusoidal movement (amplitude ±0.16 mm). Each record shows (from top downwards) afferent discharge, force and movement. In A the muscle was passive, i.e. unstimulated. In B a modulated stimulus (visible below the afferent record as dots) was applied to the ventral roots. The timing of the stimulus pulses had been adjusted to give a null in the afferent response to the movement.

For our purposes, it was also useful to represent the afferent activity in a third way. We have (in effect) fitted a sinusoid to each cycle histogram and then plotted its relationship to the movement. In Fig. 4 the amplitude and phase of this sinusoid are plotted on polar coordinates as . The distance of the point from the origin thus indicates the depth of afferent modulation, and the position of the point indicates the phase angle (about 80°) by which the afferent activity leads the movement.

When the muscle was stimulated through its ventral roots, and the stimulus modulation was adjusted appropriately, the fluctuations in the afferent discharge could be minimized, although the receptors continued to discharge at a mean rate that was comparable to that of the passive muscle. In this null situation the timing
Fig. 3. Averaged records from many cycles of movement (frequency, 2-2 Hz; amplitude, \pm 0.16 mm). In each Figure the records represent (from top downwards) frequency of muscle spindle afferent discharge, force, stimulus rate in each of the five ventral root filaments, and muscle length. For clarity the responses to the cycle of movement are displayed twice. The records are from the same muscle spindle as in Fig. 2. A, passive muscle, movement but no stimulus (average of forty-two cycles; mean rate of afferent discharge, 26 impulses/s). B, muscle stimulated at the same mean rate as in D, but no modulation of the stimulus (fifty-nine cycles; mean afferent rate, 20 impulses/s). C, muscle stimulated with the same mean rate and the same modulation as in D, but no movement (fifty-seven cycles; mean afferent rate, 23 impulses/s). D, both the movement and the appropriately modulated stimulus were applied to give a null in the muscle spindle afferent response to the movement (one hundred and twenty cycles; mean afferent rate, 14 impulses/s).

of the afferent action potentials was no longer closely related to the applied movement (Fig. 2B), and the histogram of averaged responses (Fig. 3D) shows that the component of discharge related to the 2 Hz movement was greatly reduced. On the polar diagram (Fig. 4) the point (\(\triangle\)) fell close to the origin and this method of display gave an immediate (on-line) indication that a null had been achieved.

In this null situation we presume that virtually all of the applied movement was being taken up in the tendinous components so that the muscle fibres and muscle spindles moved very little.

Fig. 3B and C shows controls. Figs. 3B and 4 (\(\bullet\)) show that the application of a ventral root stimulus at the same mean rate that was used to reach a null, but without modulation, had little effect on the afferent response to the movement, though there
Fig. 3D shows the relationship between movement and stimulus rate which was required to reach a null in the afferent discharge for this spindle. 

For most of the muscle spindles that we investigated we found conditions of ventral root stimulation that led to a satisfactory null in the afferent response. There was then little change in the response from cycle to cycle (the standard deviations of the measurements that contributed to the averages of Fig. 4 lay within the symbols). Even so, the afferent discharge was not entirely regular (Fig. 2B), and inspection of the cycle histogram (Fig. 3D) reveals that there was some consistent variation within the cycle. In that record (and in many others) the spindle discharge showed two peaks in each cycle: one when the muscle was approaching peak length, and the other when force was rapidly falling. The effects of the two peaks balance each other in the null situation, leaving no component at the frequency of movement.

For a minority of spindles we were unable to establish stimulating conditions which gave a null in the afferent response to each individual cycle, and although there was a null in the averaged response, the standard deviation was then larger. These muscle spindles were usually found to be strongly affected by stimulation of one of the ventral root filaments, so that when this filament was stimulated in a particular phase of the movement it had an unduly large effect on the afferent activity. Since the ventral root filaments were stimulated in sequence, the timing of stimulation of each filament often changed progressively from cycle to cycle, and the activity of the 'sensitive' afferent followed a similar course; its timing changed from cycle to cycle in a way that resembled beating. To avoid or minimize this effect, we took care to divide and arrange the ventral root filaments in ways that gave a smooth contraction, without visible movement of the surface of the muscle. The outcome was, however, largely a matter of chance. Division of the roots into less than five parts did not give satisfactory results.

The problem of fusimotor stimulation. An absence of afferent modulation can only be assumed to indicate a lack of movement so long as concomitant fusimotor activation has been avoided. There
are two possible sources of fusimotor activation: the $\gamma$-motor fibres provide an exclusive motor supply to the spindles, and the $\beta$-fibres provide a supply to both extrafusal and intrafusal fibres.

The most powerful fusimotor actions come from the small-diameter $\gamma$-axons, which have higher thresholds to electrical stimulation than the $\alpha$-motor axons (Harvey & Matthews, 1961; Westbury, 1980). To avoid activating these, the stimulus applied to each ventral root division was carefully adjusted until it was just supramaximal for the muscle contraction. The effect of tetanic stimulation of each ventral root filament on each muscle spindle afferent was then tested using rates of stimulation that were similar to those employed in the subsequent experiment for the measurements of stiffness. In a small number of cases stimulation of a ventral root division still caused excitation of the afferent; results from these spindles were discarded. (In these few cases, the modulation of the stimulus rate that did lead to a null in the spindle response to movement was quite different from the usual pattern.)

![Graph showing Viscous stiffness vs Elastic stiffness](image)

**Fig. 5.** Polar diagram showing the amplitude and phase of the force records of Fig. 3A, B and D. The force was divided by the movement to give the stiffness of the muscle. $\Box$, the passive muscle without ventral root stimulation, as in Fig. 3A; $\triangle$, the stiffness when the muscle was stimulated to produce a null in the spindle response, as in Fig. 3D; $\bullet$, the stiffness when the muscle was stimulated at the same mean rate as in the null situation but without modulation, as in Fig. 3B.

There was no way of avoiding stimulation of $\beta$-axons, and the possibility remains that some fusimotor activation occurred by this route. Effective fusimotor action usually requires a higher rate of stimulation than does extrafusal contraction (Bessou, Emonet-Dénand & Laporte, 1965; Emonet-Dénand & Laporte, 1983), so it is likely that the fusimotor effects of our relatively low rates of stimulation will have been small. By using distributed stimulation of the subdivided ventral roots, forces of contraction up to 7 N could be achieved with mean rates of stimulation of less than 10/s; at these rates the fusimotor action of $\beta$-axons would probably have been small and the effects of their modulation negligible. At higher rates of stimulation some fusimotor effects may have occurred, and these could account for some discrepancies in the estimates of stiffness (see below).

**The resistance to movement**

When no stimulus was applied to the ventral roots, the muscle force was very low and it changed little during the movement (Fig. 3A). This low value of stiffness of the passive muscle appears as a point very close to the origin of a polar plot of stiffness (Fig. 5, $\Box$). Stimulation of the muscle increased the mean force and it increased the
fluctuation of force which accompanied the movement. Fig. 3D shows the force recorded when stimulation was adjusted appropriately for there to be a null in the spindle afferent response. In this null situation the muscle fibres were assumed to remain at a constant length, so that all of the movement was being taken up in the tendon and its expansions within the muscle; the stiffness of the entire tendinous component could thus be calculated from the force record of Fig. 3D. This stiffness is displayed as a vector in Fig. 5 (Δ); in this experiment it amounted to 11 N/mm. The force variation was almost in phase with the movement (the point lies close to the horizontal axis), implying that the resistance to movement was essentially elastic in nature.

In Fig. 3B, where the muscle was stimulated at a steady rate, the relationship between the force and movement gives the stiffness of the whole muscle plus tendon (represented as ⬤ in Fig. 5). This value may be compared with measurements of tendon stiffness (see Discussion).
The amplitude range. It was impossible to modulate the muscle activation deeply enough to offset the effects of large movements, so that all the successful experiments were carried out with movements of small amplitude (less than ±0.2 mm). When, in order to achieve higher forces, a high mean rate of stimulation was used, sinusoidal modulation of the stimulus rate caused a relatively smaller modulation of the muscle force, and we were then limited to even smaller movements. Changes in amplitude within this limited range did not, however, appear to affect the measurements of stiffness.

![Graph showing the relationship between stiffness and muscle force](image)

Fig. 7. Graph showing the relationship between stiffness and muscle force for all of the eighty-eight measurements obtained with thirteen muscle spindle afferents in six soleus muscles. The tendinous components of the muscles varied in length from 55 to 65 mm, and no corrections have been made for these variations.

The effect of force on stiffness

When the mean rate of ventral root stimulation was changed, this led to a change in the mean muscle force. If the conditions of stimulation were then adjusted to re-establish a null, the stiffness of the tendinous components could be estimated again at a different mean force. The separate points in Fig. 6 show the values of stiffness which were found for a series of different mean forces in a single experiment.

Fig. 7 shows all of the stiffness measurements made by this method. It incorporates results from six muscles using thirteen afferents. The stiffness increased as the mean force increased, from about 2 N/mm at low forces up to 25 N/mm or more at 8–10 N. The increase was equivalent to about 2 N/mm per Newton mean force over the range of these measurements.

In most of the experiments several different muscle spindle afferents were used as null detectors, and sometimes two spindles were recorded simultaneously. Stiffness measurements made using the different receptors were usually similar, though with forces greater than 6 N some divergence did occur. Such discrepancies were not usually large.

When forces were high, the spindle null point method did not give satisfactory measurements of tendon stiffness. The properties of muscle are such that it is impossible by nerve stimulation to modulate a high mean force through a wide range at 2 Hz. Thus, as the mean stimulus rate and
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force were increased, a null could be achieved only with smaller and smaller movements, with a consequent loss of accuracy. At higher forces the mean rate of spindle afferent discharge was less, and they were then less sensitive indicators. Furthermore, higher rates of stimulation might have caused significant fusimotor effects through skeleto-fusimotor (β) axons.

For these reasons, useful results could only be obtained with mean forces of 10 N or less, and even then the higher force measurements were probably the least reliable. Some of the high stiffness values recorded at 8–10 N (Fig. 7) are probably attributable to these complicating factors.

Anatomy of the cat’s soleus muscle

Most of the fibres of the cat’s soleus muscle arise from a tendon of origin but some fibres arise directly from bone. The bundles of fibres lie in parallel, and are of similar length (Rack & Westbury, 1969) so that those that arise more distally are attached more distally to the tendon of insertion. Taking both tendons together, each bundle of muscle fibres was thus attached to bones through tendinous fibres that were of approximately the same length. Measurements of the lengths of the muscle fibre bundles were made through a dissecting microscope. From these measurements, and measurements of the whole muscle length including the tendon, the length of the tendinous components of the muscle fibres could be determined by subtraction. The angle of attachment of the muscle fibres to the tendon was sufficiently obtuse that this did not introduce significant error.

Measurements were made on the six animals that had been used for the spindle null experiments, with the muscle still at the same length. The over-all length of the muscle with its tendons ranged between 90 and 110 mm with a mean of 103 mm. The lengths of the muscle fibres themselves ranged from 35 to 45 mm with an average length of 42 mm. These measurements indicate that each muscle fibre was attached through 55–65 mm of tendon (mean, 61 mm).

These measurements were made at a muscle length that was equivalent to an angle at the ankle of 45° and they are comparable with those previously reported (Rack & Westbury, 1969).

Direct measurements of tendon stiffness

The stiffness of that part of the tendon that lies outside the muscle was measured directly for comparison with the values obtained by the spindle null method. Two different methods were used.

Static method. Stiffness was determined by applying loads and measuring the changes in length of a marked segment of tendon. The stiffness was then calculated from the slope of the length–force relationship. Two methods were used to apply force to the tendon. In some experiments the ventral roots were stimulated and the force was measured with the strain gauge attached to the tendon, while in other experiments the tendon was removed from the animal and force was applied by attaching weights. In both cases the extension of the marked segment of tendon was measured with a travelling microscope.

These measurements may be compared with measurements obtained from the same muscle by using the spindle null method; in Fig. 6 the continuous line shows the stiffness of a 1 cm length of the tendon plotted as a function of the mean force at which it was measured. The tendon did not obey Hooke’s law, but had a stiffness which increased with increasing force. This segment of the tendon was much stiffer
than the whole tendinous component of the muscle; this was to be expected since it was relatively short.

The cross-sectional area of each tendon was measured gravimetrically; the values ranged from 1.2 to 2.4 mm² with a mean of 1.84 mm². The stress and the Young's modulus of stiffness could then be calculated. The scale above Fig. 6 gives values of stress calculated for that tendon, and the scale on the right is arranged so that the continuous line indicates the Young's modulus at each stress. The modulus varied with force throughout the range that we could measure. Taking all of the different tendons it ranged from 350 to 600 N/mm² at a force of 10 N (a mean of 450 N/mm² at a mean stress of 5.6 N/mm²), and at a force of 2.5 N, it ranged from 185 to 460 N/mm² (a mean of 250 N/mm² at a mean stress of 1.4 N/mm²).

**Dynamic method.** When measurements of the tendon stiffness were made under static conditions, each addition of weights and subsequent measurement took about 1 min, and some creep may have occurred (Van Brocklin & Ellis, 1965; Hooley, McCrum & Cohen, 1980) which would lead to values for stiffness lower than those determined by a dynamic method. For this reason, in two experiments, a further estimation of the stiffness was made by a different method. This method was similar in principle to the spindle null method but the null was the absence of visible movement of a marked point on the tendon. The tendon was observed through a high-power dissecting microscope (Fig. 1), while the parameters of ventral root stimulation were adjusted until the chosen point was seen to be stationary. All of the imposed movement was then taken up in the part of the tendon distal to this point and the stiffness of this part could be measured. The method gave consistent and reproducible results, but the stiffness values obtained in this way were about 35% higher than with the static method.

**DISCUSSION**

*The spindle null method*

The method presented here for measuring the stiffness of the entire tendinous component makes use of the fact that the muscle spindles act as sensors of muscle fibre length. The primary endings of muscle spindles are very sensitive to small changes in length (Matthews & Stein, 1969), and should therefore be ideal for this purpose. In all of the measurements presented here, the amplitudes of movement were less than ±0.2 mm and thus fell within the small-amplitude, high-sensitivity range of the primary endings.

The anatomical arrangements of muscle spindles are not, however, simple (Barker, 1974), and although soleus is a muscle with parallel fibres of about equal length, the individual spindles do not respond equally to the contraction of all motor units (Binder, Kroin, Moore, Stauffer & Stuart, 1976; Windhorst & Schwestka, 1982). This variability of spindle behaviour probably explains the fact that it was sometimes difficult to achieve a null in the response of the muscle spindle to the applied movement. When, however, an arrangement of ventral root stimulation led to a smooth contraction of the muscle, and no single subdivision of the ventral roots had a particularly powerful effect on the spindle, we had little difficulty in establishing conditions of stimulation that led to a null in the afferent response.

With rates of stimulation that gave a high force of contraction, the method was
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less satisfactory since smaller movements had to be used, and the fusimotor effects of $\beta$-fibre stimulation may have been significant. These factors could have given stiffness values that were too high, and they may account for some of the high values recorded with forces greater than 7 N (Fig. 7).

The stiffness of different parts of the tendon

With forces up to about 7 N (about 35% of maximal), the spindle null method yielded consistent stiffness measurements, and we assume that these reflect the properties of the entire tendinous components of the soleus muscle fibres. These values may be compared with the more direct measurements of the distal, visible part of the tendon.

Static length–tension plots showed that the external part of the tendon was much stiffer than the values measured by the spindle null method (Fig. 6), indicating that the tendinous fibres within the muscle yield appreciably during the movement, and thus reduce the over-all stiffness.

The product of a measured stiffness and the length of tendon for which it was obtained gives a value of stiffness that is independent of length (the force required for unit strain). At each level of mean force this had a similar value whether it was obtained from measurements of a short piece of tendon or from the entire tendinous component by the spindle null method. This result implies that the tendinous fibres add up to give a similar stiffness whether they are distributed throughout the muscle or drawn together into the tendon of insertion. Furthermore, the result implies that the properties of the entire tendinous component can be estimated by dividing the measurement of stiffness of an external part of the tendon by the ratio of its length to the total length of the tendinous fibres measured by dissection.

Although stiffness measurements obtained from a static length–tension plot could be scaled in this way to give a value for the stiffness of the complete tendon, the values so calculated were usually somewhat lower than values measured by the spindle null method (this was true for Fig. 6). Static tendon measurements are, however, likely to be affected by creep; when a dynamic method of measurement was used, with a visual null point, it gave a better prediction of the total stiffness.

Tendon stiffness at different forces

Most previous workers have been concerned with the responses of tendons to the relatively large loads involved in vigorous exertion (Alexander & Bennet-Clark, 1977; Alexander, Maloiy, Ker, Jayes & Warui, 1982; Alexander & Vernon, 1975) and most measurements relate to tendon stresses of 15 N/mm$^2$ or more. Tendons then have a Young's modulus that is approximately constant; Woo et al. (1980) found a value of 1800 N/mm$^2$ for digital extensor tendons of pig, and Ker (1981) found 1650 N/mm$^2$ for sheep plantaris tendons.

With smaller forces, the tendon stiffness decreases (Gratz, 1931; Rigby et al. 1959; Diamant et al. 1972; Ker, 1981), and in the present experiments the Young's modulus varied throughout the range of forces that we could use. The values that we obtained (250–450 N/mm$^2$ at stresses of 1.5–6 N/mm$^2$) cannot therefore be compared directly with those earlier results. However, measurements from the figures of Woo et al. (1980) and from the records of R. F. Ker (personal communication) indicate that our
measurements of the Young's modulus of cat soleus tendon are consistent with the properties of sheep and pig tendons at low forces.

The relative movement of muscle and tendon

When a muscle is lengthened or shortened, the movement is distributed between the tendon and the muscle fibres in inverse ratio to their stiffnesses. A knowledge of the tendon stiffness (e.g. △ in Fig. 5) and the stiffness of the whole tendon–muscle combination (e.g. ● in Fig. 5) enables us to calculate this distribution for different muscle forces. The relationship is seen more easily if the measurements are presented as compliance (the reciprocal of stiffness). In Fig. 8A the height of each bar indicates the compliance of the muscle–tendon combination at each force, while the shaded part is the compliance of the tendon alone. The unshaded part is thus the compliance of the muscle fibres. As the mean force increased, the compliance of both the tendon and the muscle fibres decreased (stiffness increased) but they did not change by the same amount. At low forces the muscle fibres were much more compliant than the
tendon, but at about 10 N the two were approximately equal. When the force is low, most of the applied movement would therefore occur in the more compliant muscle fibres, whereas at higher forces the movement would be more equally distributed, so that relatively less would reach the muscle fibres. Since the muscle spindles would 'see' only the movement of the muscle fibres, their view of an imposed movement would also change with changing force, and when at high forces the tendon absorbed more of an imposed movement, the spindles would 'see' less of it.

Fig. 8A is, however, a simplification: whereas the tendinous elements behave in an elastic manner, the resistance of the muscle fibres to imposed movement has both elastic and viscous components (Rack & Westbury, 1974). This gives rise to the phase advance of the force record in Fig. 3B and of the whole muscle stiffness in Fig. 5 (●). As a consequence, movement of the muscle fibres will not merely be attenuated, it will also lag behind the external movement; this will be true also for the muscle spindles, which will 'see' a movement that is both attenuated and delayed. In Fig. 8B the data of Fig. 8A have been replotted to show the relative movement of the muscle fibres and their associated muscle spindles. In this Figure the distance of each point from the origin indicates the fraction of the movement that reached the muscle fibres; the angular displacement of the point from the horizontal axis corresponds to the phase lag of the muscle fibres behind the external movement. At low forces (the points on the right) most of the movement reached the muscle fibres, but when the force was increased a larger proportion was lost in the tendon, so that at the highest forces (10 N) the muscle fibres 'saw' only half of it (points nearer to the origin). This reduction in the relative movement of the muscle fibres was accompanied by an increase in the phase lag, so that at the highest forces the muscle fibres lagged behind the external movement by about 18°.

In a muscle with a longer and more compliant tendon, a larger fraction of the movement would be taken up in the tendon, and in a diagram such as Fig. 8B the points would move still closer to the origin with a further phase delay of the part of the movement which did reach the muscle fibres. The muscle spindles would then 'see' even less of the imposed movement and would 'see' it even later.

In the living animal, muscle force may depend upon the number of active motor units as well as upon their rate of discharge. The relationship may then be more complicated than the above paragraphs imply.

A theoretical consideration of systems that consist of an elastic component in series with a visco-elastic one shows that with changes in their relative stiffness a point that represents the proportion of movement in the visco-elastic component (at a given frequency) would move round in an arc (dashed line in Fig. 8B) the radius of which depends upon the characteristics of the viscoelastic element. If the tendon were very compliant compared with the muscle fibres, the point would lie towards the left end of the arc, near to the origin, but if the tendon were relatively stiff the point would lie at the other end of the arc, near to the value of 1.0.

Previous investigations of the cat soleus have not allowed for the large change in stiffness of the tendon with force. Morgan (1977) and Walmsley & Proske (1981) took the stiffness of the tendinous component to be constant, whereas the present results indicate that it varies considerably, and may at a low force be as small as 2 N/mm. A re-evaluation of their results is clearly necessary. In previous calculations (Rack & Westbury, 1974) we too assumed a constant stiffness of 20 N/mm. The present results show that the muscle fibres would in fact have 'seen' less of the movement
than was thought, so that their short-range stiffness would have operated over a smaller range, and within this range the fibres would have been somewhat stiffer. An appropriate adjustment of these results brings them closer to those obtained by Huxley & Simmonds (1971) for frog muscle fibres. The present results show that the short-range stiffness of the muscle fibres would be 0.9–2.1 N/mm per Newton mean force so that at half-maximal force (10 N) the force would increase by 2.3–5.3 % for an extension of 1 nm per half sarcomere. In a sudden transition from a lengthening to a shortening movement, this stiffness could be expected to operate over a distance of about 25 nm per half sarcomere.

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Elastic properties of the cat soleus tendon and their functional importance.
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