Mechanical properties of various mammalian tendons

M. B. BENNETT, R. F. KER, NICOLA J. DIMERY* AND R. McN. ALEXANDER

Department of Pure and Applied Zoology,
University of Leeds, Leeds LS2 9JT

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(With 3 figures in the text)

Dynamic tensile tests have been performed, using physiologically relevant frequencies and stress ranges, on various tendons from the legs and tails of 10 species of mammal. No consistent differences were found between tendons from different species or different anatomical sites. Tangent Young's modulus increases from low values at low stresses to about 1.5 GPa at stresses exceeding 30 MPa. Percentage energy dissipations of 6 to 11% have been measured for different species, but the lower values are probably the most reliable. There is little or no dependence of modulus or energy dissipation on frequency, in the range 0.2-11 Hz. The tensile strength of tendon (at strain rates of the order of 0.05 s⁻¹) is at least 100 MPa.

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Introduction

The elastic properties of tendon are important in running (Alexander, 1984) and have implications for the control of movement (Rack & Ross, 1984). Do all tendons have similar properties, or do tendons from different animals or different parts of the same animal have properties adapted to their particular functions?

Most studies of tendon properties have been limited to a single species, usually man (Van Brocklin & Ellis, 1965; Benedict, Walker & Harris, 1968; Hubbard & Soutas-Little, 1984), the cat (Matthews & Ellis, 1968; Rack & Westbury, 1984) or the rat (Rigby, Hirai, Spikes & Eyring, 1959; Svendsen & Thomson, 1984). Few have made comparisons (as did Benedict et al., 1968) between different tendons from the same animal. Only a few have involved dynamic tests at physiologically relevant frequencies (Ker, 1981; Rack & Ross, 1984; Rack & Westbury, 1984).

In this paper, we present data for tendons from the limbs and tails of 10 species of mammal.

*Present address: Department of Anatomy, Royal Veterinary College, London NW1 0TU

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Some of the data have already appeared in papers on the mechanics of the feet of individual species, but many are published here for the first time. Most of the dynamic tests were performed at frequencies of the same order of magnitude as those used in locomotion.

Materials and methods

Results of tests on the following tendons will be reported. All the animals were adults. References are given to papers in which some of the data have already appeared.

Red-necked wallaby (*Macropus rufogriseus*): tendons from the hind leg (Ker, Dimery & Alexander, 1986) and from the tail.

Common porpoise (*Phocaena phocaena*) and White-sided dolphin (*Lagenorhynchus acutus*): tendons of sacrocaudalis dorsalis and ventralis.

Domestic pig (*Sus scrofa*): leg tendons.

Arabian camel (*Camelus dromedarius*): plantaris tendon (Alexander, Maloiy, Ker, Jayes & Warui, 1982).

Roe deer (*Capreolus capreolus*) and Fallow deer (*Dama dama*): tendons from fore and hind legs (Dimery, Ker & Alexander, 1986).

Sheep (*Ovis aries*): plantaris tendon (Ker, 1981).


Horse (*Equus caballus*): leg tendons.

The carcasses of the wallabies, deer, sheep and Donkeys were delivered to our laboratory in apparently good condition within 2 days of death, and stored in plastic sacks at $-20^\circ$C until required. The camel tendon was stored in a refrigerator or at room temperature for 5 days following the death of the animal and then for a few weeks at $-20^\circ$C. It was kept moist by wrapping it in a damp cloth or a polythene bag. The carcasses of the whales reached us in fair condition within 1 week of death. One was dissected immediately and the other was stored at $-20^\circ$C. Tendons not used immediately after dissection were stored in plastic bags in the freezing compartment of a refrigerator. Ker (1981) found no perceptible difference in elastic properties between sheep plantaris tendons that were tested fresh and ones that had been stored frozen at $-20^\circ$C.

The papers cited above include data for the interosseous 'tendons' of deer and Donkeys. These do not consist solely of tendon, but include substantial fractions of muscle fibre and fat. They have, therefore, been excluded from the data presented here.

All the data were obtained by tests on an Instron 8031 dynamic testing machine. Specimens 0.09 to 0.4 m long were held either in the clamps described by Ker (1981), the shaped clamps described by Ker et al. (1986), or freezing clamps like those described by Riemersma & Schamhardt (1982). Most of the data were obtained from dynamic tests in which the actuator was made to move sinusoidally in position control, alternately stretching the tendon and allowing it to recoil. Most tests were made at 2.2 Hz, a convenient frequency of the same order of magnitude as the stride frequencies of the quadrupeds and the tail-beat frequencies of the whales, but a few tests were made at other frequencies. Forces were obtained from the output of the machine's load cell and displacements, either from the output that gives actuator displacement, or by means of the extensometer described by Ker (1981). The merits and limitations of these two methods were discussed by Ker et al. (1986). The most important point is that end effects, due to distortion in the clamps, are greatly reduced when the extensometer is used. After the test had been running for a few cycles, the outputs over a single cycle were stored in a pair of synchronized digital recorders. They were subsequently plotted on an XY plotter as a graph of force against displacement.

For measurements of ultimate strength, the actuator was made to move down at a speed of 7.5 or 10 mm/s until the tendon broke. These fairly low speeds made it unnecessary to use the digital recorders: the output was plotted directly on the XY recorder during the test.
The tendons were kept moist throughout the experiments, by wrapping them in plastic film or by moistening them frequently with 0.9% saline.

The cross-sectional areas of the sheep tendons were measured by the gravimetric method described by Ker (1981). Those of the other tendons were calculated from their masses, assuming a density of 1120 kg/m³ (Ker, 1981).

The determinations of Young’s modulus also require knowledge of the length of the specimen. This presents no difficulty when the extensometer is used (Ker, 1981), but there is some ambiguity when extensions are obtained directly from the displacements of the actuator. The difficulty is that the clamps do not attach to well-defined points on the tendon, but grip segments of finite length. In the experiments with freezing clamps, we assumed that the segments within the clamps were frozen and rigid. We measured the distance from the lower edge of the upper clamp to the upper edge of the lower clamp (the ‘daylight length’) while applying a small tensile load, and took that to be the length of the test specimen. In experiments with the other clamps, we used the distance between the mid-points of the serrated grips in the clamps. This distance was 33 mm longer than the daylight length.

Young’s modulus

Figure 1a shows the record of a typical tensile test. Load is plotted against displacement so gradients represent stiffnesses and can be used in calculating Young’s modulus. Stiffness is low at low loads, due to the initial crimp in the collagen fibres (Rigby et al., 1959; Diament, Keller, Baer, Litt & Arridge, 1972), but increases as load increases. There is therefore no unique Young’s modulus. Tangent moduli have been calculated from the gradients of tangents to the parts of the records in which load is high and increasing. Such a tangent is shown as a broken line in Fig. 1a.

Figures 1b and c show the results of three experiments designed to test our assumptions about the effective lengths of test specimens, when extensions are obtained directly from the displacements of the actuator. In each case, a tendon was subjected to a series of dynamic tests at the same frequency and approximately the same peak load but using successively shorter lengths. Compliance (the reciprocal of stiffness) is plotted against daylight length. Lines have been fitted to the sets of points by least squares regression. The line for the experiment with freezing clamps (Fig. 1b) passes very close to the origin, indicating that zero compliance would be attained at zero daylight length. This tends to justify our assumption that, for such experiments, the effective length of the specimen equalled the daylight length. However, the 95% confidence band is wide enough to admit effective lengths 25 mm greater or less than daylight length. The regression lines for non-freezing clamps (Fig. 1c) intersect the length axis at -36 and -51 mm, indicating effective lengths 36 and 51 mm longer than daylight length. They do not falsify our assumption that the effective length was 33 mm longer than daylight length, but the confidence bands are too wide for them to give it strong support.

The possible errors, due to inaccurate assessment of effective length, can be reduced by using long tendons. The wallaby and whale tendons were long enough to allow daylight lengths of 200–400 mm, but the shortest tendons (deer gastrocnemius) allowed daylight lengths of only 55 mm.

Ker (1981) presented evidence that, in experiments with the extensometer, the effective length of the specimen was the distance between the jaws of the extensometer. However, the confidence range for the effective length was quite wide. He made a (possibly over-cautious) assessment of possible errors in his values for Young’s modulus, due to uncertain end effects.

Calculations of Young’s modulus are also subject to errors due to uncertainty about cross-sectional areas. The mass per unit length (from which we calculated cross-sectional area) increases when a tendon takes up water and decreases as it dries.

We performed an experiment to discover how much and how fast the water content of tendons might change. Long segments of seven tendons were dissected from a sheep’s hind leg, and weighed immediately. They were immersed in 0.9% saline and removed periodically for weighing. Their weights increased and
eventually attained equilibrium values of 128 ± 4% (mean and standard deviation) of the initial values. The tendons were then removed from the saline and left exposed to the atmosphere of the laboratory. Their final (air dry) weights were 50 ± 4% of their initial weights. Rates of loss of weight as the weight passes its initial value ranged from 0.06% min⁻¹ for the gastrocnemius tendon (cross-sectional area 53 mm²) to 0.5% min⁻¹ for a digital extensor tendon (4 mm²). Large errors could occur, in measurements of cross-sectional area, both if tendons were allowed to dry and if they were moistened too assiduously with saline. We tried to avoid both these faults.
Figure 2a shows records of a series of tests in which the same tendon was subjected to successively larger peak stresses. In Fig. 2b, tangent moduli from these tests are plotted against peak stress. As stress increases, tangent modulus approaches an asymptote. It is close to the asymptotic value at all stresses above 30 MPa.

Figure 3 shows tangent modulus plotted against peak stress, for a wide variety of tendons from many species. In this graph (unlike Fig. 2b), every point refers to an experiment on a different tendon. This graph shows a great deal of scatter, but gives a general impression that tendons approach asymptotic moduli of about 1.5 GPa at stresses above 30 MPa.

Table I is based on the same data as Fig. 3, but shows only the moduli from experiments involving peak
stresses above 30 MPa. These can be assumed to be the asymptotic value of the modulus for each tendon. Means for all tested tendons are given on the right of the table, for each individual species. Only the value for Donkey (1.25 GPa) is significantly different from the grand mean of 1.50 GPa. The Donkey tendons included the thickest tendons investigated. It is possible that these tendons were not gripped satisfactorily in the clamps, and that end effects due to their splaying in the clamps may have been exceptionally severe. The freezing clamps, which would have been particularly suitable for such stout tendons, were not made until after the tests on Donkey tendons. Means for homologous tendons (irrespective of species) are given at the bottom of Table I. None of them is significantly different from 1.50 GPa. The low mean value for the gastrocnemius tendon is largely due to two exceptionally low values for Roe deer.

Table I includes several examples of widely divergent moduli for homologous tendons of the same species. The values range from 1.22 to 2.00 GPa for dolphin tail tendons, and from 1.27 to 1.92 GPa for Roe deer plantaris tendons. Some of this variability may be due to inconsistent tightening of the clamps: the end effects may not have been identical, even in experiments with well-matched tendons. Also, some of the variability may have been due to inconsistencies in our measurements of cross-sectional area, due to gain or loss of water by the tendons.

Ker (1981) measured the asymptotic moduli of sheep plantaris tendon at frequencies ranging from 0.22 Hz to 11 Hz. Within this range, he found no significant effect of frequency on asymptotic tangent modulus.
## Table I

Tangent Young's modulus for various tendons, calculated as explained in the text from the results of dynamic tensile tests involving peak stresses of at least 30 MPa

<table>
<thead>
<tr>
<th></th>
<th>Foreleg</th>
<th>Hind leg</th>
<th>Tail</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Superficial flexor</td>
<td>Deep flexor</td>
<td>Gastrocnemius</td>
</tr>
<tr>
<td>Wallaby</td>
<td>1.72, 1.18</td>
<td>1.51</td>
<td>1.36, 1.52</td>
</tr>
<tr>
<td>Porpoise</td>
<td>1.43, 1.70</td>
<td>1.55, 1.47</td>
<td>1.52</td>
</tr>
<tr>
<td>Dolphin</td>
<td>1.92, 1.29</td>
<td>1.85, 1.71</td>
<td>1.76, 1.72</td>
</tr>
<tr>
<td>Roe deer</td>
<td>1.73, 1.67</td>
<td>1.63</td>
<td>1.28</td>
</tr>
<tr>
<td>Fallow deer</td>
<td>1.73, 1.67</td>
<td>1.63</td>
<td>1.28</td>
</tr>
<tr>
<td>Sheep</td>
<td>1.73, 1.67</td>
<td>1.63</td>
<td>1.28</td>
</tr>
<tr>
<td>Donkey</td>
<td>1.24, 1.32</td>
<td>1.19, 1.28</td>
<td>1.94</td>
</tr>
<tr>
<td>Mean</td>
<td>1.59 ± 0.22</td>
<td>1.52 ± 0.33</td>
<td>1.27 ± 0.32</td>
</tr>
</tbody>
</table>

Similarly, we tested two sacrocaudalis tendons from the dolphin at frequencies from 0.22 to 5.5 Hz and found little or no effect of frequency on modulus. One gave a modulus of 1.39 GPa at 0.22 Hz and 1.46 GPa at 5.5 Hz, for peak stresses of 34 and 35 MPa. The other gave 1.66 GPa at 0.22 Hz and 1.78 GPa at 5.5 Hz, for peak stresses of 41 MPa in each case.

### Energy dissipation

Percentage energy dissipation is one of several alternative measures of the internal damping of materials (Ker, 1981). In each cycle of a dynamic tensile test, work $W_1$ is done stretching the specimen and $W_2$ is recovered in the subsequent elastic recoil. The percentage energy dissipation is $100 \left( \frac{W_1 - W_2}{W_1} \right)$. It can be calculated from the appropriate areas in load-extension records like Fig. 1a.

Experiments in which the extensometer was used gave consistently smaller percentage energy dissipations than ones in which extension was obtained from the displacements of the actuator. This is almost certainly due to energy losses in the parts of the tendon that are gripped by the clamps: these are excluded from the measurements when the extensometer is used. Small artefacts nevertheless occur when the extensometer is used, due to movement at the attachment of the extensometer to the tendon. Ker (1981) treated these as end effects and used a series of experiments, with the extensometer attached to different gauge lengths of the same tendon, to eliminate them from his results.

Table II shows percentage energy dissipations at 1-2.2 Hz, measured by means of the extensometer. The values for sheep plantaris are the lowest and also the most reliable: only they have been corrected for end effects. The other, uncorrected values are presumably all a little too high.

We made an attempt to measure energy dissipation without the extensometer, obtaining extensions from the displacements of the actuator. We selected a wallaby tail tendon, as an unusually long, slender tendon, for which end effects should be relatively small. It was held in the freezing clamps, and subjected
to a series of tests, using progressively shorter lengths of the tendon. Percentage energy dissipation, calculated as explained by Ker (1981) was 8.4.

Ker (1981) found that the percentage energy dissipation of sheep plantaris tendon was independent of frequency, over the range 0.22 Hz to 11 Hz. Similarly, we found little frequency dependence for dolphin tail tendons. Two tendons gave values of 4.1 and 7.7% at 0.22 Hz and 5.6 and 8.5% at 5.5 Hz (not corrected for end effects).

Our data show no apparent relationship between percentage energy dissipation and amplitude. For example, a dolphin tail tendon gave the following dissipations when cycled at 2.2 Hz between zero stress and the stated peak stresses: 8.1% for a peak stress of 8 MPa, 6.5% for 15 MPa, 7.8% for 27 MPa and 6.0% for 35 MPa.

**Ultimate tensile strength**

Most of the dynamic tests were repeated with successively higher amplitudes until the specimens broke, but the increments of amplitude were too large for the results to give a precise indication of ultimate strength. Peak stresses exceeding 60 MPa were occasionally reached without breaking the specimen (Fig. 3).

Table III summarizes the results of the experiments designed to measure ultimate strength. In experiments with ordinary (non-freezing) clamps, fracture nearly always occurred at the point of entry to one of the clamps. The tendon was severely distorted by the clamps and the resulting stress concentrations may have caused premature failure. Tendons are distorted less severely in the freezing clamps, because they are frozen before the clamp is fully tightened. When the freezing clamps were used, rupture often involved much pulling out of fibres, rather than a clean break, and it was difficult to determine whether the break had started at a clamp. Table III shows that higher values for ultimate strength were obtained when freezing clamps were used than when obtained with ordinary clamps. These higher values are presumably closer to the ultimate strength of tendon, but even they may be too low. We think it likely that the ultimate tensile strength of mature tendon is at least 100 MPa.

**Discussion**

Many of the data presented in this paper were obtained by dynamic tests at frequencies of the order of 2 Hz, involving peak stresses of over 30 MPa. It seems pertinent to enquire whether tendons commonly experience such stresses in life. Table IV shows peak stresses in tendons,
calculated for moderate to fast locomotion of various mammals. It appears that at least some tendons commonly experience stresses exceeding 30 MPa. The stride frequencies are similar in magnitude to the frequencies used in most of our tests. However, stride frequency is not strictly comparable to test frequency, because the tendons in question are stressed principally during the small fraction of the stride for which the foot is on the ground. In a sinusoidal dynamic test at 2 Hz, stress rises from zero to its peak value in 250 ms, if the tendon is just allowed to go completely slack, or less if it remains slack for an appreciable fraction of the test duration. During locomotion, stresses in the leg tendons referred to in Table IV rise from zero to their peak values in only 50-80 ms. It might have been preferable to have used frequencies appreciably higher than 2 Hz, in the dynamic tests. However, tests at frequencies ranging from 0.2 to 11 Hz showed little or no frequency dependence of modulus and energy dissipation.

The data of Table I and Figs 2 and 3 show that the tangent Young's modulus of tendon increases from low values at low stresses but is close to an asymptotic value of about 1.5 GPa at stresses above 30 MPa. They show no clear differences between species or between tendons from different anatomical sites. Donkey tendons may have exceptionally low moduli, but a systematic error may have been introduced by the difficulty of clamping such thick tendons.

Table V shows tangent moduli taken from the literature. Most of them are lower than our asymptotic values. In some cases, this is probably because the peak stresses, in the tests, were too low for the asymptotic values to be closely approached. Also, in some cases, the tendons had been stored in saline and may have been swollen (Rigby et al., 1959; Benedict et al., 1968): this would have increased their cross-sectional areas and so reduced the modulus. Most of the data refer to much lower rates of loading than were used in our tests.

Table II shows percentage energy dissipations, at physiologically relevant frequencies. Most of the values lie between 5.5 and 10.0%. The values for sheep plantaris (mean 6.4%) are the most reliable: the others have not been corrected for end effects, and are probably too high. Hubbard & Soutas-Little (1984) measured percentage energy dissipation in human tendon at various strain rates, and obtained values around 25%. They used short specimens, obtained extensions directly from actuator displacements, and made no corrections for end effects. We suspect that the losses they measured were dominated by artefacts due to clamping. Ker (1981) measured the rate of rise of temperature of one of his sheep plantaris tendons, during dynamic tests, and calculated
Working conditions of tendons in locomotion. Stresses are as calculated for various leg tendons, in the papers cited. Higher stresses given by Alexander (1974) and by Alexander & Vernon (1975) were based on calculations involving an incorrect value for tendon density: the values given here have been corrected (see Ker, Dimery & Alexander, 1986). Stride frequencies are from the cited papers or from films of the same species. 'Time to peak' is the time from initial contact of a hind foot with the ground to the maximum ground force (wallaby and dog) or half the period of contact of the foot with the ground (other species)

<table>
<thead>
<tr>
<th></th>
<th>Peak stress (MPa)</th>
<th>Stride frequency (Hz)</th>
<th>Time to peak (ms)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wallaby hopping</td>
<td>15-41</td>
<td>2.9</td>
<td>70</td>
<td>Alexander &amp; Vernon, 1975</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ker, Dimery &amp; Alexander, 1986</td>
</tr>
<tr>
<td>Dog jumping</td>
<td>84</td>
<td>—</td>
<td>50</td>
<td>Alexander, 1974</td>
</tr>
<tr>
<td>Camel pacing</td>
<td>18</td>
<td>1.6</td>
<td>70</td>
<td>Alexander et al., 1982</td>
</tr>
<tr>
<td>Fallow deer galloping</td>
<td>28-74</td>
<td>2.7</td>
<td>—</td>
<td>Dimery, Ker &amp; Alexander, 1986</td>
</tr>
<tr>
<td>Donkey trotting</td>
<td>22-44</td>
<td>2.3</td>
<td>80</td>
<td>Alexander &amp; Dimery, 1985</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Dimery &amp; Alexander, 1985</td>
</tr>
</tbody>
</table>

Tangent moduli for tendon from investigations by other authors. The peak stresses for the tests, in which the moduli were measured, are also given

<table>
<thead>
<tr>
<th>Modulus (GPa)</th>
<th>Peak stress (MPa)</th>
<th>References</th>
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<tbody>
<tr>
<td>Human leg tendons</td>
<td>1.2</td>
<td>Van Brocklin &amp; Ellis (1965)¹</td>
</tr>
<tr>
<td></td>
<td>1.0-1.5</td>
<td>Benedict et al. (1968)</td>
</tr>
<tr>
<td></td>
<td>1.05</td>
<td>Rack &amp; Ross (1984)</td>
</tr>
<tr>
<td>Cat leg tendons</td>
<td>1.21</td>
<td>Matthews &amp; Ellis (1968)</td>
</tr>
<tr>
<td>Pig leg tendons</td>
<td>0.9</td>
<td>Woo et al. (1980)²</td>
</tr>
<tr>
<td>Rat tail tendons</td>
<td>0.8</td>
<td>Rigby et al. (1959)</td>
</tr>
<tr>
<td></td>
<td>1.5</td>
<td>Svendsen &amp; Thomson (1984)³</td>
</tr>
</tbody>
</table>

¹ Data from their fig. 6, for the highest rate of loading
² Data calculated from their fig. 6, for exercised pigs
³ The published data were based on cross-sectional area after drying. The values for mature tendons have been divided by 1.2 (as suggested by the authors) to obtain values based on the cross-sectional area of moist tendon.

from it a percentage energy dissipation of 4%. This is probably too low, because heat losses could not be prevented, but it tends to confirm that the value of 6.4% obtained from the experiments with the extensometer (Table 11) is of the right order of magnitude.

Our values for ultimate strength may be too low, because of stress concentrations. They show that the ultimate tensile strength of tendon (at rates of strain of the order of 0.05 s⁻¹) is at least 100 MPa. Benedict et al. (1968) and Blanton & Biggs (1970) obtained ultimate tensile strengths of approximately 80 MPa, in their tests on human tendons, but their results were also presumably affected by stress concentrations. Svendsen & Thomson's (1984) values for mature rat tail tendons would be about the same if the cross-sectional area of the moist tendon had been used in their calculations, instead of the area after drying. Benedict et al. (1968) found that extensor tendons
had higher ultimate strength than flexor tendons, but it is not clear whether the difference was statistically significant.

All our tests were made on tendons from adult animals. Immature tendons may have lower moduli and strengths (Svendsen & Thomson, 1984).

One of the aims of this investigation was to discover whether tendons from different species and anatomical sites have different properties. No clear evidence for such differences has been found, but small differences may be masked by uncertainties due to sources of error that we have been unable to eliminate. Values for Young's modulus are affected by uncertain end effects and by variations in cross-sectional area due to varying degrees of hydration. Values for energy dissipation are likely to be too high by uncertain amounts, because of losses in the extensometer and its attachments. Values for ultimate strength are likely to be too low because of stress concentrations and are also affected by uncertainty about cross-sectional area. We can only conclude that differences in these properties, between species and between anatomical sites, are probably small compared to the errors involved in measuring them.

One further word of caution seems necessary. The tendons were not a random sample. We chose most of them for study because we thought they might function as strain energy stores in locomotion (Alexander, 1984). It is possible that other tendons with different functions may have different properties.

Summary

Tensile tests have been performed on various tendons from the legs and tails of adults of 10 species of mammal. Young's modulus increases from low values at low stresses to about 1.5 GPa at stresses exceeding 30 MPa. Percentage energy dissipations of 6-11% were measured for different species, but the lower values are probably the most reliable. Most of the measurements of modulus and energy dissipation were obtained in dynamic tests at 1.0-2.2 Hz, but little variation with frequency was found in the range 0.2-11 Hz. The tensile strength of tendon, at strain rates of the order of 0.05 s⁻¹, is at least 100 MPa. Any differences in the properties investigated, between tendons from different species or anatomical sites, are probably small compared to the errors involved in measuring them.

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