

# The Mechanical Properties of Rat Tail Tendon

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**ABSTRACT** The load-strain and stress-relaxation behavior of wet rat tail tendon has been examined with respect to the parameters strain, rate of straining, and temperature. It is found that this mechanical behavior is reproducible after resting the tendon for a few minutes after each extension so long as the strain does not exceed about 4 per cent. If this strain is exceeded, the tendon becomes progressively easier to extend but its length still returns to the original value after each extension. Extensions of over 35 per cent can be reached in this way. Temperature has no effect upon the mechanical behavior over the range 0–37°C. Just above this temperature, important changes take place in the mechanical properties of the tendon which may have biological significance. The application of the techniques used here to studies of connective tissue disorders is suggested. Some of the mechanical properties of tendon have been interpreted with a simple model.

## INTRODUCTION

Most studies of collagen have been concerned with its chemical nature and reactivity, and with electron microscope and x-ray diffraction examinations with a view to determining its macro and molecular structure (1–4). As yet there is no entirely satisfactory molecular model, and one major stumbling block appears to be the confusion over whether collagen is or is not capable of large extensions.

A number of measurements have been reported on the mechanical properties of such collagen-containing structures as tendons, ligaments, and fascia. There is no extensive review of the older work available. However, typical results may be found in references (5–7). Structures containing a high per cent of collagen were found difficult to stretch and usually broke before they elongated appreciably, while structures with a lower collagen content and a

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higher per cent of elastic fibers were much more extensible. Thus, although we have a general picture of the mechanical properties of collagen from previous work, no really detailed studies have been reported. This paper is an introductory study of the load-strain and stress-relaxation behavior of wet rat tail tendon with respect to the parameters temperature, amount of strain, and rate of straining.

### *Materials*

Unless otherwise specified, all the experiments reported here were carried out with tail tendons from 4 to 5 month old male albino rats of the Sprague-Dawley strain. The animals were killed with ether, and the tails were cut off at the base and carefully skinned. The skinned tail is somewhat square in cross-section with white glistening bands of tendon running longitudinally along the four corners. The tail was then severed at 10 to 12 vertebrae from the tip and the tip discarded. The tendons, which lie in sheaths through which they slide freely, were removed with fine-tipped forceps. A few of the tendons were attached in spots and could not be removed easily, but approximately twenty-two tendons 10 cm. long and 0.3 mm. in diameter could be obtained from a mature rat. The tendons were usually used just as removed from the rat since they were easy to handle and showed mechanical properties which fell nicely within the range of the measuring equipment described below. The tendons could be split lengthwise into fibers of smaller diameter if desired. A minimum of force was used in removing the tendons in order to avoid altering their properties. They were washed in normal saline (0.9 per cent NaCl) and then stored in the refrigerator at 2–3°C. in the same medium. Under such conditions the tendons did not show any change in properties for as long as 1 to 2 months. The tendons were never permitted to dry out. A few measurements were made on tendons stored in a deep-freeze at –35°C. These showed essentially the same properties as fresh material.

### *Methods*

The experimental arrangement for stretching the tendons and recording the loads involved is shown in Fig. 1. The motor, *M*, drives a rigid arm, *A* (which shows no deflection under the heaviest loads used in these experiments), through gears *G*. At the end of the arm a metal block holds the two ends of a looped tendon, which are jammed into a hole in the block by a bakelite plug, *P*. The looped end of the tendon passes over a hook, *H*, attached directly to a transducer, *T*, with the appropriate load range (model G1 transducer, manufactured by the Statham Instruments, Hato Rey, Puerto Rico). The transducer has a maximum displacement of 0.0015 inch which even at full load is negligible in these tests. It is calibrated by suspending known masses from the hook. The transducer output is recorded on a Brown  $\frac{1}{2}$  second 10 mv. strip-chart recorder, type 153X. The gears can be changed to allow a variety of speeds of arm movement and the motor is of a type which may be stopped abruptly by a switch, *S*, at any desired moment. Thus the rate of strain and the strain (per cent of elongation) of the tendon can be conveniently controlled. During measurements

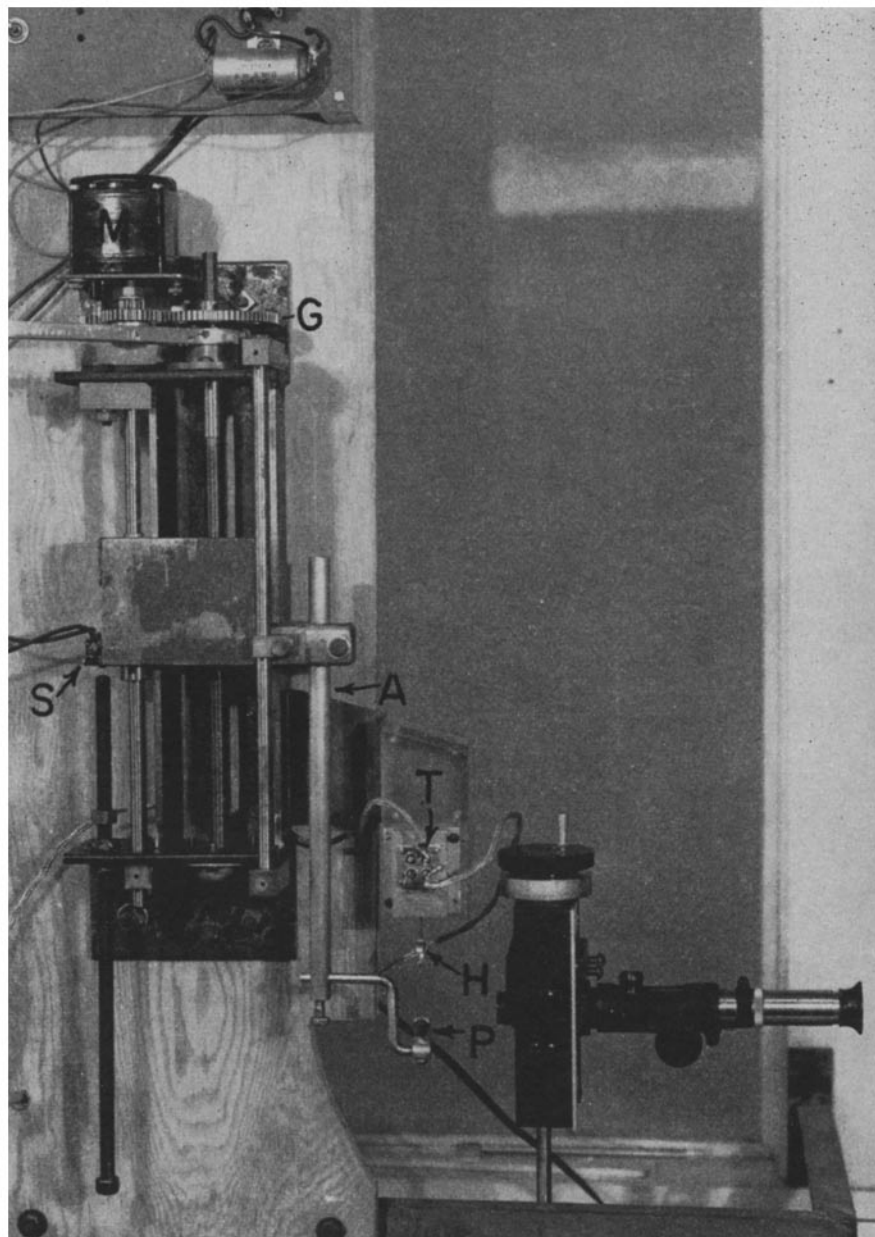


FIGURE 1. Experimental apparatus for obtaining load-strain and stress-relaxation data. The apparatus was built by H. Noffsinger, University of Utah. Please see the text for details.

the tendon is completely immersed in a bath of saline with the temperature maintained to within 0.1°C. Length changes in the tendon during stretching were measured with a Gaertner telemicroscope-micrometer slide combination. Tendon cross-sectional areas were calculated using the mean diameter of a slightly taut wet tendon as measured with a microscope provided with a calibrated eyepiece micrometer. A circular cross-section was assumed. The tendon was kept stretched during the measurement so that the wave pattern (see below) just disappeared. Measurements made in this way agreed with those taken from tendons hanging vertically in saline with just sufficient load added by the stretching machine to remove the wave pattern.

With the rates of straining usually employed (1 to 20 per cent/minute) and as long as the strain did not exceed approximately 4 per cent, the same tendon could be used for a series of ten or more stretches since its length and mechanical properties were entirely recovered after a rest period in the slack state of 10 minutes or less. It should be pointed out that the very first stretch of a new tendon, which we have termed a "conditioning stretch," produces a slight permanent elongation of about 0.6 per cent (the average of twenty experiments was  $0.6 \pm 0.2$  per cent) which is never recovered. After all subsequent stretches the tendon returns to this conditioned length, and so in the work to be reported here this first stretch will not be considered further. Tendon, of course, is not pure collagen, so this first stretch may involve the rupture of other components of the tendon (tendon cells, blood vessels, nerves, ground substance, etc.) which take no subsequent part in the mechanical behavior.

## RESULTS

When in its natural position in the tail of the rat, or when separated and placed in normal saline in a slack condition, the tendon shows a macroscopic banded or crinkly pattern. This pattern, on the basis of microscopic examination, was originally thought to indicate a wave structure in the tendon (as reviewed in reference 8), while more recent studies (8) indicate a helical microstructure. Our observations indicate that the tendon in reality shows a wave pattern, while the apparent helical structure is an illusion resulting from the angle and type of illumination. Fig. 2, a photograph taken by transmitted polarized light, shows the wave pattern impressed upon the "fibers" constituting the tendon and indicates how the apparent helical or band structure arises from the light and shadow on opposite sides of the waves. If the tendon is stretched slightly the wave pattern disappears as shown in Fig. 3. If the tendon actually had a helical structure of the type suggested in reference (8), a much greater degree of extension would be required to produce the parallel pattern shown in Fig. 3. The fact that the tendon can be halved lengthwise many times without any tendency to twist or snarl also supports our suggestion of a wave structure.<sup>1</sup> The tendon resembles very closely a lock of crimped

<sup>1</sup> After our experiments were completed, we became aware of unpublished data by G. S. Shields (B.S. Thesis, Massachusetts Institute of Technology, 1948) which agree with our findings. This thesis also contains information on the load-strain behavior of rat tail tendon.



FIGURE 2. A wet unstretched rat tail tendon photographed under polarized light.

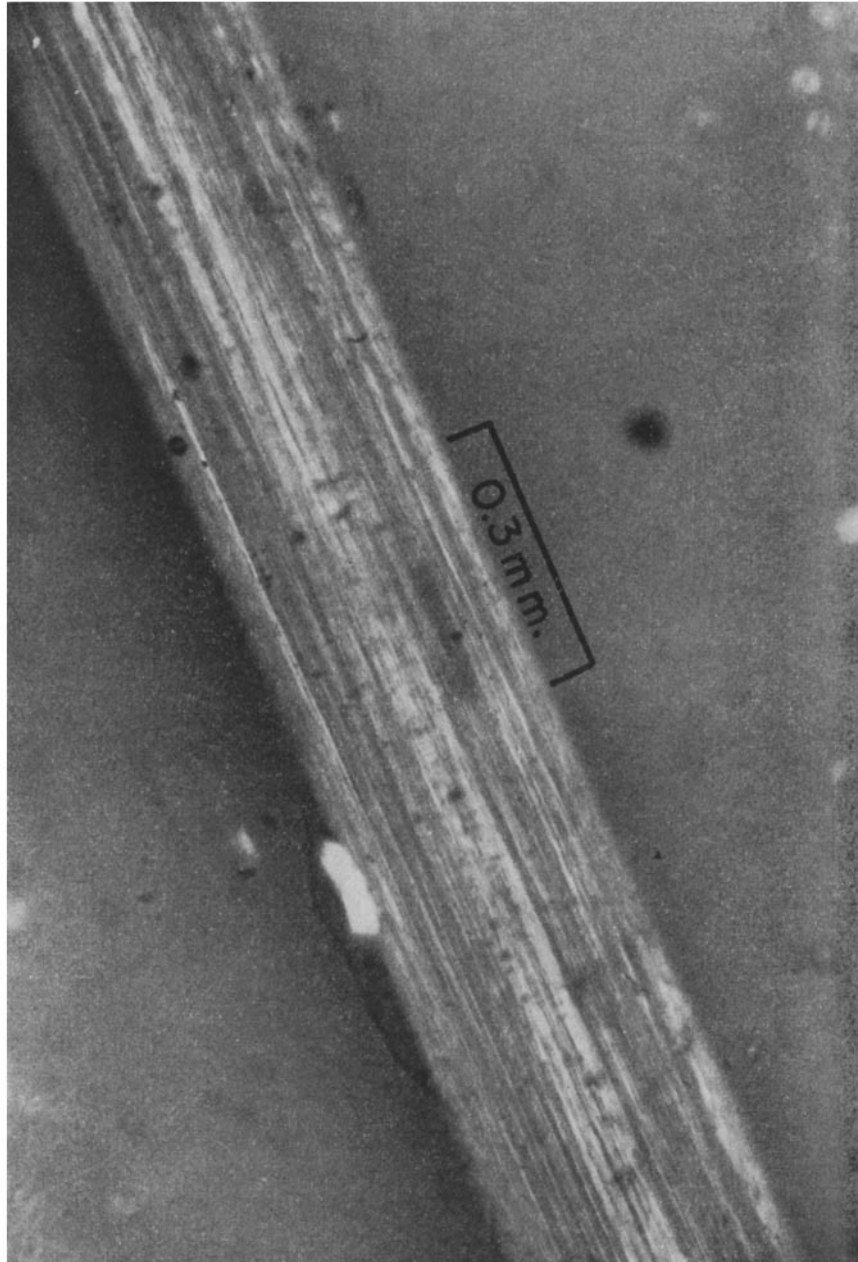


FIGURE 3. The same rat tail tendon as in Fig. 2 stretched slightly and photographed under polarized light. It will be noted that the wave pattern has disappeared. Upon unloading, this tendon will immediately revert to the condition shown in Fig. 2 provided it has not been stretched beyond 4 per cent.

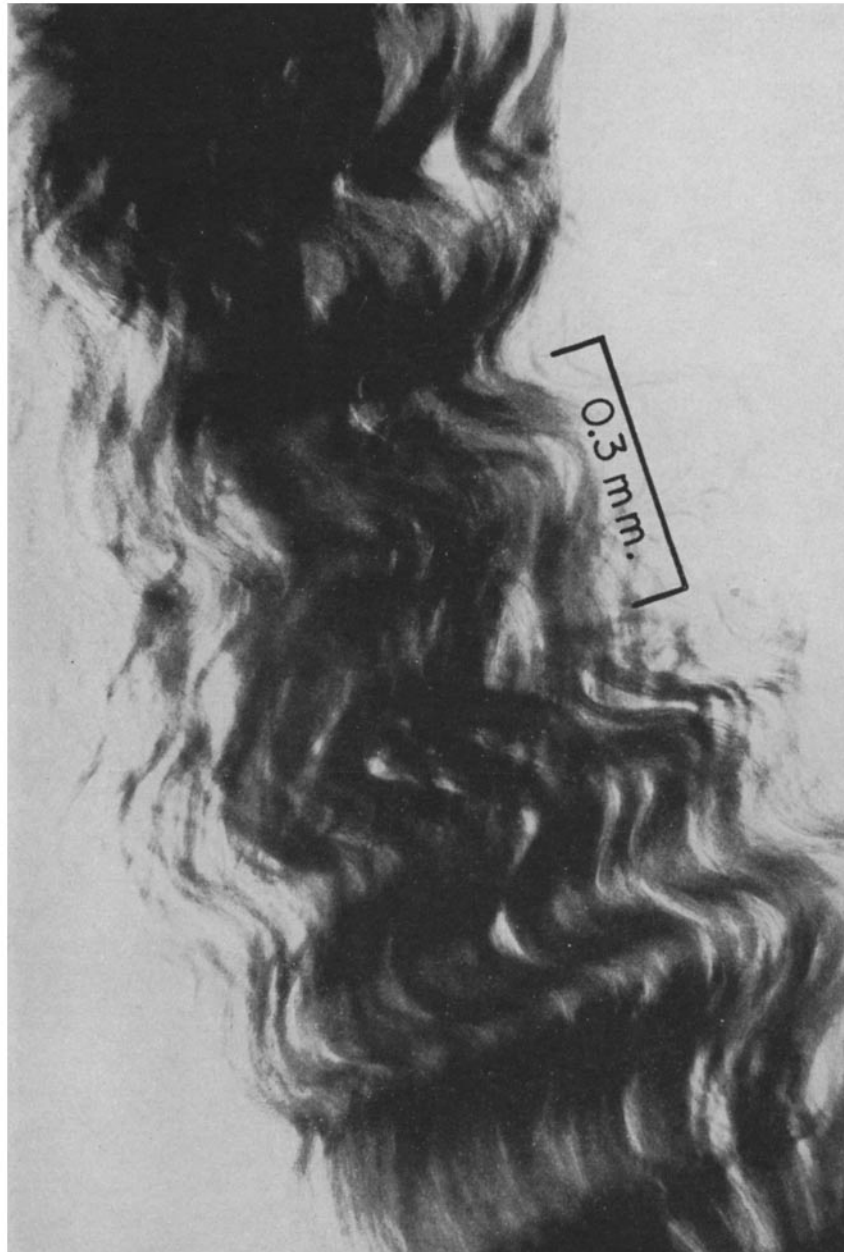


FIGURE 4. A wet rat tail tendon partially separated into subfibers in order to show the wave pattern more clearly.

wool, although it forms a much more compact and unified structure. However, under certain conditions it can be teased into "fibers" much like a clump of wool, as is shown in Fig. 4. An examination of other tendons of the rat showed this wavy structure to be of fairly general occurrence, although the pattern is usually much less regular than in tail tendon. Such a pattern also occurs in the tendons of other mammals.

### *Load-Strain Behavior*

We use load, with units of gram weight, when referring to stretching experiments since the cross-sectional area of the tendon does not remain constant, and the term stress, with units of dynes/cm<sup>2</sup>, would not be appropriate unless corrections were made at all strains. However, we will speak of stress-relaxation experiments later (although again we will measure loads for convenience), for here the strain and hence cross-sectional area remain constant. In a typical load-strain, stress-relaxation experiment a curve is obtained of the type shown diagrammatically in Fig. 5. The tendon is stretched at a predetermined rate to the desired strain, thus producing the load-strain curve shown at the left. The tendon is then maintained at this particular strain and measurements of the load are continued, resulting in the stress-relaxation curve shown at the right.

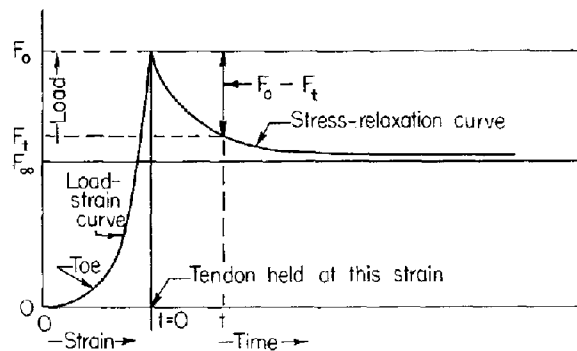


FIGURE 5. Schematic diagram of the curve obtained in a typical load-strain, stress relaxation experiment. The tendon is stretched at a predetermined rate to the desired strain, thus producing the load-strain curve shown at the left. The tendon is then maintained at this particular strain and measurements on the stress are continued, resulting in the stress-relaxation curve shown at the right.  $F_\infty$  would represent the stress when  $t \rightarrow \infty$ ; *i.e.*, the limiting stress.

Fig. 6 shows a characteristic sequence of tendon load-strain curves. All these were made with the same tendon. In each case the tendon was extended at the same constant rate but to different extensions. After each extension the tendon was unloaded and rested in a slack condition whereupon its



original length was fully recovered, except as noted below. This recovery process in all cases took no longer than 10 minutes. The sequence begins with curve A which represents a strain of only 2.5 per cent. After a rest the tendon was stretched again, and, as shown in curve B, the behavior exactly follows that of curve A. If the strain does not exceed approximately 4 per cent, this load-strain behavior is reproducible through an indefinite number of cycles. The third extension, as shown in curve C, does not follow curves A and B, even though the length of the tendon was recovered after extension B. Curve C is obviously representative of a slightly weaker tendon. Looking back, it can be seen that curve B departed slightly from linearity at its upper end. Such a departure from linearity indicates that the "safe limit" of extension was exceeded, and this is why curve C is displaced to the right. Curve C represents an extension well beyond the safe limit, and the next curve, D, is greatly

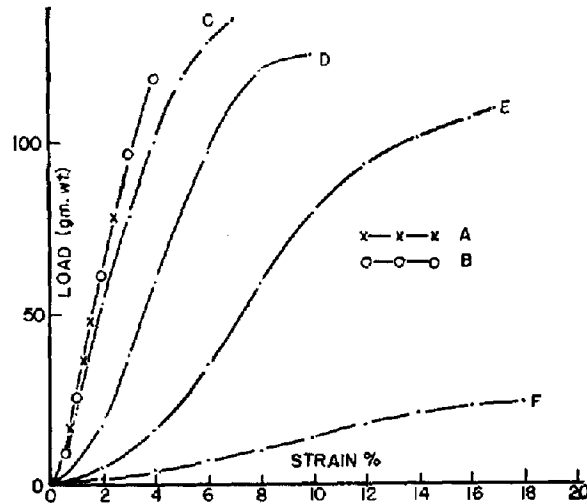


FIGURE 6. A typical set of load-strain curves showing the effect of a series of successive stretches on the behavior of the same rat tail tendon. The rate of straining was 2 per cent/minute, the temperature was 21°C., and the cross-sectional area of the tendon was  $8.2 \times 10^{-4}$  cm<sup>2</sup>. The first stretch, to a strain of 2.5 per cent, is shown in curve A. After a rest, the tendon returned to its original length and was stretched again as shown in curve B. The lower region of this curve is identical with curve A, but the tendon was extended slightly past the "safe limit" as shown by the slight bend at the top. The tendon was allowed to rest and then stretched again as shown in curve C. It is obvious that the tendon has become weaker as a result of the previous stretch. This effect becomes more pronounced with subsequent stretches as shown in curves D through F.

displaced. Curves E and F represent two more extensions in the sequence, and the marked progressive weakening of the tendon is clearly seen. It is important to note again that the length of the tendon was recovered each time before the next extension in the series was carried out.

If the first load-strain curve, A, is continued beyond the safe limit it turns over into a "yield" or "flow" region (where there is a relatively large extension for a small load increase), and if the rate of straining is sufficiently slow (less than 1 per cent/minute) extensions of up to 20 per cent can be reached.<sup>2</sup> However, when the tendon has been weakened by successive extensions to the state represented by curve F, strains of more than 35 per cent can be obtained even at rates of strain greater than 1 per cent/minute.

Another interesting observation connected with the load-strain studies is that the tendon wave pattern (as described in the previous section) always returns after each extension so long as the safe limit is not exceeded. Once this limit is passed, however, as in stretches C-F of Fig. 6, the wave disappears and never returns. Thus tendons stretched past the safe limit have a small permanent extension corresponding to the straightening of the wave pattern (this residual extension should not be confused with that resulting from the "conditioning stretch" described earlier). The excellent reproducibility of tendon mechanical behavior in the region below the safe limit should be stressed again as shown for load-strain in curves A and B of Fig. 6, and for stress-relaxation by the lower four curves in Fig. 10.

The wave pattern in the tendon, as seen in Figs. 2 and 4, suggests the mechanism responsible for the initial "toe" region of the load-strain curve. This toe is just discernible in curves A and B of Fig. 6, and is shown in exaggerated form in the diagram in Fig. 5. In fact, by observing the tendon through the telemicroscope while it is being stretched, the disappearance of the wave pattern is easily correlated with the toe portion. The wave pattern is entirely absent by the time the linear part of the load-strain curve is reached. It might be remarked that when the tail of a living rat is bent, the tendons on the outside of the bend are stretched until the wave pattern disappears.

An increase in the rate of straining does not significantly alter the shape of the reproducible region of the load-strain curve. The main effect is an increase in the load required to produce a given strain. An average of seven determinations (at a rate of straining of 10 per cent/minute) of the maximum slope of the load-strain curve yields a value for the Young's modulus of wet rat tail tendon of  $8 \pm 2 \times 10^9$  dynes/cm.<sup>2</sup>. This is approximately the same value as that reported by Gratz (5) for human fascia lata.

When the temperature is varied, two interesting results are observed. First, considering the reproducible portion of the load-strain diagram, there is no alteration in tendon behavior between 0 and 37°C. The average normal body temperature of the albino rat is 37.3°C., although the tail temperature is probably less than this. In other words, all the tendon mechanical properties mentioned above are temperature-independent as long as the temperature is

<sup>2</sup> In this paper the term "safe limit" will be used to indicate the strain of approximately 4 per cent beyond which the "yield" or "flow" region begins in which irreversible changes occur. The region below the safe limit will be termed the "reproducible region."

below approximately 37°C. Second, if the temperature exceeds this critical value by only a few degrees the properties of the tendon are changed in an abrupt irreversible manner. In most cases the tendon breaks at 3 to 4 per cent strain. However, there is no contraction of the tendon associated with this change. In common with most mammalian collagens, wet rat tail tendon does not contract until temperatures of 60–70°C. are reached. If the strain exceeds the safe limit, a temperature increase hastens the tendon breakdown no matter whether the temperature is above or below approximately 37°C. It is important to note that the transition temperature varies somewhat with different tendons. However, the transition has never been observed below 36°C., and has always occurred by approximately 40°C.

### *Stress-Relaxation Behavior*

The gradual decrease in stress when a tendon is held at a given extension (a phenomenon termed stress-relaxation) follows a definite behavior when

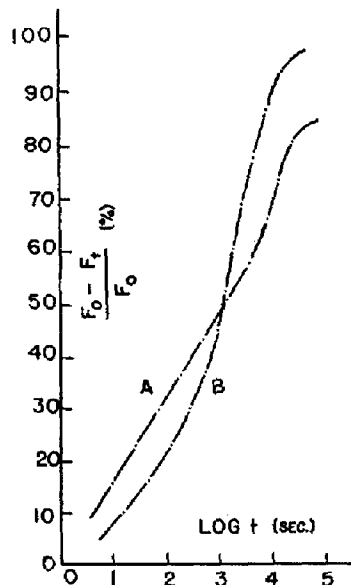


FIGURE 7. Typical examples of stress-relaxation curves for rat tail tendon plotted in the form  $(F_0 - F_t)/F_0$  (per cent) against the logarithm of  $t$  in which  $F_0$  is the initial stress and  $F_t$  is the stress at time  $t$  as described in Fig. 5. Curve A shows the stress-relaxation of a tendon held at 3.5 per cent strain (within the safe limit), while curve B shows relaxation from a strain of 7.5 per cent (in the flow region). The temperature in each case was 25°C.

the parameters strain and temperature are altered. Stress-relaxation behavior is very different with strains above and below the safe limit of about 4 per cent. The results of a typical experiment are shown in Fig. 7 in which the data are plotted in the form  $(F_0 - F_t)/F_0$  versus the logarithm of time. The quantity  $F_0 - F_t$ , in which  $F_0$  is the initial stress at the end of the period of elongation and  $F_t$  is the stress at time  $t$  after this, is used in this paper as a measure of the amount of stress-relaxation (see Fig. 5).

Curve A of Fig. 7 is for a tendon strained to only 3.5 per cent. It will be

seen that after approximately 24 hours the stress apparently decays to a limiting value of approximately 15 per cent of the initial value. It appears that two distinct regions of decay occur, both approximately linear with the logarithm of time. The second region begins after about 60 minutes. When stress decay has reached its apparent limiting value, it is found that an increase in temperature lowers the stress, while a decrease in temperature increases the stress. Both of these processes are reversible, and the variation in stress is approximately linear with temperature as shown in Fig. 8. It is also found in these experiments that prolonged strains (even within the reproducible region) are deleterious to the tendon if the time exceeds 60 minutes; *i.e.*, the time at which the second decay region begins in the relaxation phenomenon.

Referring to curve B in Fig. 7, which represents a tendon strained beyond the safe limit to 7.5 per cent, we note that the curve has an entirely different

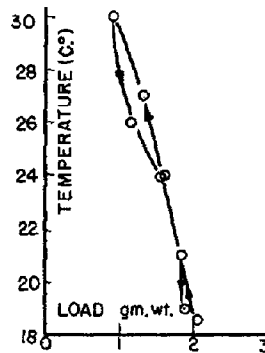


FIGURE 8. Figure showing the effect on stress of varying the temperature of a stretched tendon (same tendon as used to obtain curve A in Fig. 7) after the stress-relaxation had reached its limiting value  $F_{\infty}$  of approximately 84 per cent of  $F_0$ . As may be seen from the arrows on the curve, the temperature effect is essentially reversible over the range indicated.

shape compared with A, while in addition the stress decays almost to zero. If the temperature is increased by 3–4°C. while the stress is at this limiting value, the stress decreases irreversibly. This temperature response is in marked contrast to that of tendon which is not stretched beyond the safe limit as shown in Fig. 8.

If we examine the stress-relaxation process while working with strains of less than 4 per cent and with times of relaxation considerably less than 60 minutes (*i.e.*, under highly reversible conditions), we find that the relaxation behavior is entirely reproducible. When tendon is stretched slowly, the subsequent amount of stress-relaxation,  $F_0 - F_t$ , is fairly linear with the amount of strain as shown in curve A of Fig. 9 where the rate of straining was 3 per

cent/minute. A time  $t$  of 60 seconds was arbitrarily selected for presenting the data: however, choosing any other time (less than 60 minutes) does not alter the general nature of the results. There is a deviation from linearity in the plot below about 1 per cent strain which probably results from the effects of the wave pattern of the tendon on the mechanical properties in this region of strain. With high rates of straining the amount of stress-relaxation is increased at a given strain, especially as the strain approaches 3 per cent, as shown in curve B of Fig. 9 for a rate of straining of 20 per cent/minute.

It will be recalled from above that temperature had little effect on the load-strain behavior of rat tail tendon until a critical temperature of approximately 40°C. was reached. A similar relationship was found for stress-relaxation which is independent of temperature over the range 0°C. to approximately 37°C. when strains in the safe range are used. If, however, the temperature is raised above this range, the value of  $F_0 - F_t$  increases rapidly as shown in Fig. 10 where the data are plotted in the form  $F_0 - F_t$  against the logarithm of time. The lower group of curves represents a series

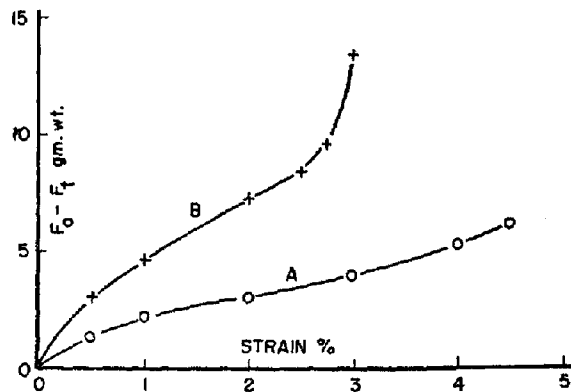


FIGURE 9. Curves showing the effect of strain and rate of straining on the stress-relaxation behavior of rat tail tendon. The amount of stress-relaxation,  $F_0 - F_t$ , was calculated for  $t$  equal 60 seconds. The temperature was 26°C. Curve A represents a rate of straining of 3 per cent/minute, while curve B represents a rate of 20 per cent/minute.

of tests made below 35°C. These are all parallel and can be made to coincide within experimental error by adjusting the values of stress-relaxation to a standard strain (which is difficult to reproduce exactly in a series of experiments). The upper curve which was obtained at 41°C. has not only a different slope, but also a magnitude about twice that of the lower curves. The lower curves show very nicely the linear relation between stress-relaxation and the logarithm of time as discussed previously.

Although we have not examined in detail the effect of the rat age on the

mechanical properties of tail tendon, a few observations should be reported here. Tendon from young (3 week old) rats is very weak and usually breaks at 1 to 2 per cent strain in its first extension. Tendon from old (20 month old) rats is stronger than the tendon from 4 to 5 month old rats upon which this paper is based. The tendon from old rats does not break as easily at temperatures over  $37^{\circ}\text{C}$ .; however, it appears to be more brittle and cannot be stretched through as many cycles as that from younger rats. In connection with these observations, it has been noted by Verzář (8) that (a) the extent of thermoelastic contraction and (b) the force exerted during the thermoelastic contraction of tail tendon both show a marked increase as the age of the rat increases. Although only a few experiments were carried out as a function of rat age, it is significant that all the tendons we examined from rats over 2 months of age showed the unexpected temperature effect at slightly over  $37^{\circ}\text{C}$ . as described above.

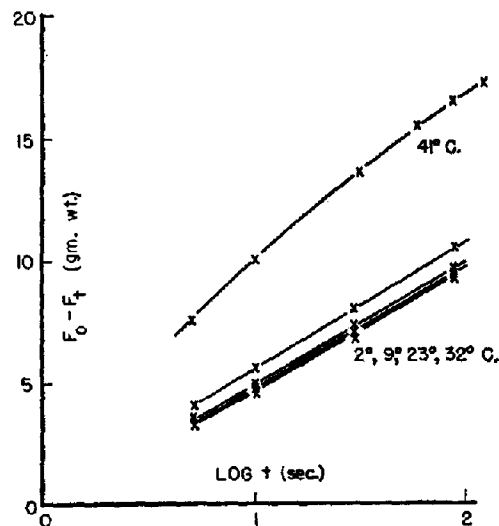


FIGURE 10. Curves showing the result of a typical experiment on the effect of temperature on the stress-relaxation behavior of rat tail tendon stretched to a final strain of 3 per cent. The bottom group of curves represents a number of tests made at lower temperatures. These are all parallel and can be made to coincide within experimental error if  $F_0 - F_t$  is adjusted to standardize the strain (which is difficult to reproduce exactly at each extension). The upper curve was measured at  $41^{\circ}\text{C}$ . It shows not only a different slope, but also an increase in amplitude by a factor of almost two. The rate of straining was 9 per cent/minute.

## DISCUSSION

Assuming that the use of normal saline solution as a medium in these experiments approximates the condition of the tendon *in vivo*, the results should

have some biological significance, at least for small strains when the material has recoverable properties. One might expect that during its normal operation tendon never experiences strains greater than the safe limit. We will first discuss the behavior of the tendon in general terms and then say a little concerning the biological implications of this behavior. The initial toe of the load-strain curve (Fig. 6) can be easily interpreted. In view of Figs. 2 and 3, and on the basis of observations during the stretching process, the toe region is clearly due to the straightening out of the wave pattern of the tendon. Of course, the structural basis for the wave pattern itself is not known, just as the reason for the crimp pattern in certain other fibrous proteins such as wool and hair is not known. Once this wave pattern is straightened out the tendon behaves like a stiff spring until a stress is reached at which certain chemical bonds or perhaps ground substance between the collagen fibers or other subunits, breaks. This might allow subfibers to move past one another. The other alternative, of course, is that some kind of unfolding process takes place. Our results lead to the view that it is an opening out or unwinding of subfibers since the length of the tendon is recoverable even after strains of greater than 35 per cent. However, since there is no tendency for the tendon to contract below its initial length after such elongation, we feel that the extension process does not involve a rupture of primary bonds or a disruption of the collagen molecules themselves. That is, the extension is not due to the unfolding of the collagen molecules, although, of course, a small part of the extension must be due to elastic stretching of these molecules.

To further examine this view, we have taken high angle x-ray diffraction pictures of unstretched tendon and of tendon stretched to a strain of about 20 per cent. On stretching, the basic x-ray pattern of the tendon remains unchanged except for a sharpening of the arcs which indicates an improvement in the orientation of the units responsible for the x-ray pattern. See reference (4) in this connection. A full account of this work will be given elsewhere.

Also, the fact that the tendon becomes progressively weaker with each extension (at strains beyond 4 per cent) suggests that ruptured secondary bonds (those adjoining adjacent molecular units) are not able to reform. This could indicate that the extension involves the unwinding of loops or folds of molecules during which procedure secondary bonds are irreversibly broken, since the groups on the amino acid residues responsible for the bond are separated and never come together again. Stress relaxation is due to the rupture of strained secondary bonds which, when broken, allow adjustments in position of molecular units. This movement allows local stresses to be relieved.

Considering the reversible extension now in more detail, we need to examine the indifference to temperature of both load-strain and stress-relaxation behavior at temperatures below 37°C. This lack of temperature response

implies that the cross-linking bonds and the flow units associated with them form a spring-like mesh with an entropy, but no energy of activation. This means that even though stress-relaxation (bond breaking) occurs below approximately 37°C., the rate of breaking is not temperature-dependent. This type of behavior in other systems has been termed "entropic flow" (9). A phase-like transition apparently sets in at a little above 37°C. The bonds break with temperature in a manner similar to the melting of an ice crystal; *i.e.*, they show no tendency to weaken until a critical temperature is reached at which time they begin to break rapidly. Continuing with this notion, we picture the basic units of the tendon as consisting of one or more (probably 3) polypeptide chains, strongly braced with hydrogen bonds, forming the collagen molecule. Groups of molecules are then weakly bonded by other hydrogen bonds, salt linkages, etc. into fibrils. Bundles of fibrils group into fibers and finally form tendons. Below temperatures of approximately 37°C. the entire system is stable and behaves like a crystal. Then at slightly above 37°C., the rate of breaking of bonds joining groups of molecules begins to increase rapidly, causing an increase in stress-relaxation (Fig. 10). However, the hydrogen bonds within the molecule are only partially disrupted and are still present in sufficient numbers to prevent the peptide chains from assuming a random structure which would result in the "thermoelastic contraction" which does not occur with rat tail tendon in aqueous media until temperatures of 60–70°C. are reached. A similar notion of "melting" is used by Flory (10) in discussing the abrupt onset of tendon contraction at 60–70°C. It is important to remember that the increase in bond breakage rates discussed above occurs only when the tendon is under tension whereas thermoelastic contraction will occur in tendon which is not under tension. For the relation of these views to recent ideas on the molecular structure of collagen see references (11 and 12).

With reference to non-reproducible behavior, curve A of Fig. 7 indicates that after about 60 minutes under strain the amount of rearrangement in the tendon becomes too great to be ever recovered, although subsequently the structure stabilizes again so that the tension reaches an equilibrium value. This is equivalent to saying that the spring-mesh has deteriorated and has lost much of its strength. However, curve B suggests that the spring-mesh structure has been entirely disrupted by straining beyond 4 per cent, and there is therefore no restraint to molecular movement during relaxation and the stress decays to zero.

Fig. 8, which shows the effect of temperature when the stress has decayed to its limiting value, supports this general picture. In this case it can be suggested that the spring-like mesh (although weakened) is in fact expanding and contracting with the temperature change, thus altering the stress.



In conclusion, we would like to mention some possible implications of this work. What, for example, is the functional significance of the wave pattern shown by the fibers of the tendon? It is tempting to suggest that this represents an adaptation to prevent overstretching of the tendon on the outside of a bend or joint, since our results indicate that the tendon properties are altered by strains of more than a few per cent. The wave pattern may also participate in a sort of shock absorber system. If the tendon, through which the muscle operates some part of the skeletal system, for example, were entirely rigid, the acceleration initially applied to the moving part would be enormous. The wave pattern can thus be conceived of as serving in much the same capacity as the elastic tow cables used for launching gliders, or the elastic shroud lines used on a parachute; *i.e.*, as a device to permit lower accelerations while transmitting forces.

The collagen of rats is chemically quite similar to that of other mammals including human beings (13, 14). If we assume that the temperature responses described above are typical of the behavior of collagen in the living organism, we might expect that body temperatures only slightly above normal in mammals could produce alterations in structures such as tendons, especially if they were stretched while at the elevated temperature. Temperatures of 104–105°F. (approximately 40°C.) are not uncommon in human beings during illness, especially in children. This approximates the range of the temperature effect reported here. One might speculate that with severe fever in human beings, the tendons in the heart which operate the valves might be altered to the point at which proper operation of the valves would be interfered with. It appears, for example (15), that the verrucae of cardiac valves characteristic of rheumatic endocarditis and of bacterial endocarditis are formed as a result of alterations of the collagen of the valves. The temperature effects discussed in this paper might play a role in such alterations. At the other extreme, many animals are still active even at temperatures approaching 0°C. Thus, it is probably of biological importance that lowering the temperature to this extent appears to have little effect on the mechanical behavior of tendon.

It is conceivable that the techniques described in this paper as applied to the study of tendon might have application in the study of certain pathological conditions of connective tissue in human beings. For example, some workers believe that fibrinoid degeneration in connective tissue is characterized, not primarily by alteration of the ground substance which cements the collagen fibrils together as proposed by many investigators, but by changes in the structure of the collagen fibrils themselves (16). The collagen fibrils in lesions of the major collagen-vascular diseases such as rheumatic fever, rheumatoid arthritis, etc. appear to swell, become irregular in outline, and degenerate.

Similar alterations occur at the site of hypersensitive reactions of the anaphylactic type. Recent electron microscopic studies of the skin of the rabbit at the site of a local anaphylactic reaction termed the Arthus phenomenon show the presence of characteristically altered collagen fibrils which do not occur in normal skin (17). The interesting observation was also made that in the manipulation involved in preparing the material for electron microscope examination the altered collagen fibrils fractured very readily, whereas the normal fibrils were very resistant to breakage.

Another interesting abnormality is the hereditary condition termed *cutis hyperelastica* (Ehlers-Danlos syndrome) observed in the "India rubber man" of the circus in which the skin, tendons, and other collagen-containing structures can be extended by much larger amounts than is normal (16). The skin in particular can be stretched enormously; however, after the force is released the skin returns to its original position. Some authors (16) suggest that this condition results from an alteration of the collagen fibrils which are responsible for most of the mechanical properties of the skin. From the above description we might suggest that the skin collagen in *cutis hyperelastica* is in a form comparable to that in the tendon which gave curve F in Fig. 6.

It might be suggested, then, that an examination be made of collagen-containing tissues from patients with pathological conditions such as those described above (especially skin and tendon) in terms of their mechanical properties as discussed for tendon in this paper. Such an approach might be of great utility in defining the relative roles of alteration in the ground substance, elastic fibers, and collagen fibrils in these important diseases or abnormalities.

#### REFERENCES

1. RANDALL, J. T., (editor), *The Nature and Structure of Collagen*, New York, Academic Press, 1953.
2. GUSTAVSON, K. H., *The Chemistry and Reactivity of Collagen*, New York, Academic Press, 1956.
3. BEAR, R. S., *Advances Protein Chem.*, 1952, **7**, 69.
4. COWAN, P. M., NORTH, A. C. T., and RANDALL, J. T., *Symp. Soc. Exp. Biol.*, 1955, **9**, 115.
5. GRATZ, C. M., *J. Bone and Joint Surg.*, 1931, **13**, 334.
6. HARDY, R. H., *J. Anat.*, 1951, **85**, 135.
7. SMITH, J. W., *J. Anat.*, 1954, **88**, 369.
8. VERZÁR, F., *Gerontologia*, 1957, **1**, 363.
9. HALSEY, G., WHITE, H. J., and EYRING, H., *Textile Research J.*, 1945, **15**, 295.
10. FLORY, P. J., *Science*, 1956, **124**, 53.
11. BEAR, R. S., *Symp. Soc. Exp. Biol.*, 1955, **9**, 97.

12. HUGGINS, M. L., *Proc. Nat. Acad. Sc.*, 1957, **43**, 209.
13. TRISTRAM, G. R., in *The Proteins*, (H. Neurath and K. Bailey, editors), New York, Academic Press, 1953, 1, pt. A, 181.
14. ESTOE, J. E., *Biochem. J.*, 1955, **61**, 589.
15. ALLEN, A. C., and SIROTA, J. H., *Am. J. Path.*, 1944, **20**, 1025.
16. ALLEN, A. C., *The Skin: A Clinicopathologic Treatise*, St. Louis, C. V. Mosby Company, 1954.
17. RICH, A. R., VOISIN, G. A., and BANG, F. B., *Bull. Johns Hopkins Hosp.*, 1953, **92**, 222.