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extremely well for long periods under experimental conditions. Curiously enough (Hartree & Liljestrand 1926), the recovery heat production, for a given initial heat production, occurs at nearly the same rate in a tortoise's muscle as in a frog's. Although the processes of contraction and relaxation are so much slower, in accordance with the needs and habits of the animal, those of recovery are about the same. This may be one of the reasons why the isolated muscles of the tortoise behave so well for long periods. It would be interesting to find out whether the chemical processes which take place after contraction, in the presence or absence of oxygen, occur no more slowly than in frog's muscle, in spite of the great difference in speed of contraction and relaxation.

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## The series elastic component of muscle

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The properties have been examined of the undamped elastic component which lies in series with the contractile component of muscle. At higher tensions the elasticity is normal; the form of the load-extension curve as a whole must be largely due to the statistical distribution of tendon length in different fibres. The mechanical (elastic) energy of a contracting muscle is expressed graphically as a function of its tension. Even under completely isometric conditions this elastic energy is a significant fraction of the heat production in a twitch.

An important factor in the mechanical behaviour of muscle is the passive elastic component in series with the active contractile one (see Hill 1949*a*). This acts as a buffer when a muscle passes abruptly from the resting to the active state, and it accumulates mechanical energy as the tension of the muscle rises. If the muscle is opposed, as in most ordinary movements, by the inertia of a limb or an external mass, this mechanical energy can be used in producing a final velocity greater than that at which the contractile component itself can shorten. This is important in such movements as jumping or throwing. For simplicity in description the series elastic component will be referred to as 'tendon', but no assumption is implied that other undamped series elastic elements do not exist within the fibres themselves; the evidence of its properties is derived from mechanical experiments with active muscle, not from histological observation.

Some muscles have long tendons, or their fibre groups have long tendon bundles, while others have short ones. In the frog's gastrocnemius, for example (Hill 1931), the fibres run, on the average, only half the full length of the muscle; the other half must be tendon. The toad's sartorius, on the other hand (see Hill 1949*b*), can shorten to about 30 % of its length in the body, which leaves little remainder for tendon. The former muscle is designed for rapid impulsive movements, the latter for slow crawling movements.

It is impossible to examine the properties of the series elastic component in a resting muscle; the contractile component at rest is so extensible that a load is taken almost entirely by the parallel elastic component, sarcolemma, etc. It is necessary to work with an actively contracting muscle, in a range of lengths within which the tension of the parallel elastic component can be neglected. Static experiments are impossible, because (*a*) a muscle fatigues too rapidly, and (*b*) because its active component shortens if the tension is lowered. It is necessary, therefore, to use a dynamic method, recording the tension as a function of length while shortening occurs at a speed greater than the maximum speed of the contractile component.

If a muscle is stretched while actively contracting a large part of the work done on it vanishes, that is to say, does not appear either as heat or as elastic mechanical energy; presumably it is used in driving some endothermic chemical process backwards. The muscle resists strongly and its tension rises to a high value during the stretch. In studying the time relations of this absorption of work it was necessary to know approximately how much of the work at any moment was still present as elastic energy in tendons and recording system—none was present after relaxation because the tension had fallen to zero. To avoid unnecessary complication it was advisable to make this elastic energy as small as possible, so that the tension recorder and its connexions to the muscle were made as inextensible as was consistent with a small enough inertia and a sufficient sensitivity, and a minimum of tendon and connecting thread was allowed at the end of the muscle. Nevertheless, substantial elastic energy was present in the system under the high tensions developed during the stretch of an actively contracting muscle. It was determined in the way described below. It should be noted that the results given here refer to two types of muscle only, the sartorii of the English frog and English toad, with a minimum of tendon at the tibial end. With other muscles the quantities found might be considerably larger; the methods described, however, are applicable to any muscle.

A Levin Wyman ergometer (Levin & Wyman 1927) constructed by Messrs C. F. Palmer was used. It had a magnetic release controlled by a key of a moving contact breaker, other keys of which determined the stimulus. To secure quicker attainment of the final velocity the driving weight was replaced by a powerful spring. Oil as the damping fluid was changed for silicone (D.C. fluid 200; 500 or 200 centistokes) which has a smaller temperature coefficient and is clean and reliable. The recording system consisted of a spring tension-lever carrying a vane of blackened aluminium foil which cast a shadow on a twin vacuum photocell. The output from this was transferred to an amplifier and recorded on one beam of a double beam cathode-ray tube; in the myothermic experiments the other beam was used for the heat. The tension lever, photocell and lamp were carried on the moving arm of the ergometer.

The start and end of the movement, after release, were recorded by contacts as slight flicks on the tension record. The tension lever was joined to the muscle by a light chain, which was adjusted to be exactly vertical in order to avoid sagging at low tensions.

A frog's sartorius was tetanized isometrically at 0° C with 5 maximal condenser discharges each way per second, and after 1.5 sec., when it had developed its full tension, it was released 5 mm. with the Levin Wyman ergometer at a speed of 42 to 46 mm./sec. The maximum velocity of shortening of the contractile component is about  $\frac{4}{3}$  times the length of the muscle per second (Hill 1938); the muscles usually being 26.5 to 28.5 mm. long, their maximum velocity would be 35.5 to 37 mm./sec., so that their tension fell to zero after about 3.5 mm. release. The initial length was less than the resting length in the body, so that the initial resting tension was very small; after 3.5 mm. shortening it was negligible.

The equation of motion of the ergometer accelerating after release is

$$s = v_0 \left\{ t - \frac{Mv_0}{F} (1 - e^{-tF/Mv_0}) \right\},$$

where  $s$  is the distance travelled,  $v_0$  the final velocity,  $t$  the time after release,  $M$  the mass, and  $F$  the driving force provided by the spring.  $M$ ,  $F$ ,  $s$  and  $v_0$  are expressed in equivalent values at the point of attachment of the chain from the muscle to the tension recording lever.  $F$  was large compared with the force exerted by the muscle and  $M/F$  was found to be about  $10^{-3}$  sec.<sup>2</sup> cm.<sup>-1</sup>. After acceleration was complete  $s$  became  $v_0(t - Mv_0/F)$ , so that a total distance lag of  $Mv_0^2/F$  finally occurred. With  $v_0 = 4.5$  cm./sec.,  $Mv_0^2/F = 2 \times 10^{-2}$  cm. or 0.2 mm. This is small, and could be allowed for by extrapolating the falling tension curve backwards, as soon as it became linear (which it did, see below), to the initial level of tension. It would be better to use lower velocities, so that  $Mv_0^2/F$  would be less; but this would permit a greater total contractile shortening of the active component of the muscle during the release. In order to reduce the contractile shortening it would be better to make  $v_0$  greater, but this would increase the lag during acceleration; and it had the further disadvantage of setting up more vibration in the instrument. If  $F$  could be increased the lag would be diminished, but it was already 2.2 kg., about as much as the ergometer and its release mechanism could safely stand. An ergometer could be designed which would have a considerably smaller  $M$ , but its construction would take time and effort better expended otherwise. The velocity of about 4.5 cm./sec. was chosen as the best compromise.

The recording system is extensible, consisting of thread, chain, tension lever, etc., and its contribution to the shortening observed in the muscle experiments was by no means negligible; indeed, if care was not taken it could make up a large part of it. It is easy, however, to allow for the extensibility of the recording system alone by a blank experiment without a muscle, the chain being joined to a fixed support in the usual muscle chamber by a thread of the same length as was used with a muscle. By adjusting the recording system with a screw, the tension was raised, and then the ergometer was released and a tension-shortening curve recorded exactly as in the muscle experiments. From this the shortening of the recording system and its connexions, between any two tensions, could be read off and subtracted from the shortening observed in the muscle experiments between those

tensions. In this way the true relation was determined between tension and shortening of the muscle itself, without any error due to the elasticity of the recording system and connexions.

The shortening of the muscle so determined is made up of two parts; (*a*) the shortening of the series elastic component, and (*b*) that of the contractile component. Of these, (*a*) is what we wish to determine, so that (*b*) must be allowed for. In principle, (*b*) could be eliminated by using a release so quick that the contractile shortening was negligible in the short time occupied by it. This would require a velocity of release much faster than that actually employed, and the equipment would not permit it. Even if special apparatus were constructed for the purpose, a further difficulty might arise from the natural viscosity of the series elastic elements. At the speeds actually used these elements are sufficiently nearly undamped; at much higher speeds even a small viscosity might diminish the force exerted externally during shortening. It was necessary, therefore, to allow for the contractile shortening.

According to the characteristic equation relating force and speed,

$$v = b(P_0 - P)/(P + a),$$

where  $P$  is the force exerted by the contractile component shortening at velocity  $v$ ,  $P_0$  is the isometric tension, and  $a$  and  $b$  are constants. Of these,  $P_0$  was the starting tension in each experiment, and  $a$  was taken as  $\frac{1}{4}P_0$ ,  $b$  as  $\frac{1}{3}l_0$  per sec., the mean values found for the frog's sartorius at  $0^\circ\text{C}$  (Hill 1938). To apply the equation, the force-shortening curve was divided into equal intervals of time  $\delta t$ , and  $P$  was taken as the mean force in each interval. Then the amount of contractile shortening in any interval,  $\delta s = v\delta t = b\delta t (P_0 - P)/(P + a)$ , was calculated and so the total amount of shortening from the start was obtained by addition.

This calculation could not be exact, because it was necessary to assume mean values of  $a$  and  $b$ ; it was not practicable to determine them directly in each experiment, for that is a fairly lengthy procedure and might alter the condition of the muscle for the subsequent observations. The error, however, cannot be large. The only way to avoid it completely would be to work with very quick releases, which might introduce (as suggested above) another and worse error.

The allowances having been calculated for (*a*) the extensibility of the chain and lever system and (*b*) the contractile shortening, these were added together and subtracted from the observed shortening. The result is shown in figure 1, for the mean of a number of records made on four muscle pairs freshly prepared from frogs in very good condition. Other experiments gave similar results. For generality, and so that the curve can be applied to any frog's sartorius at  $0^\circ\text{C}$  whatever its length and weight, the tension is expressed as  $Tl_0/M$ , which is very nearly the same as the force per sq.cm. of the muscle's cross-section (that is,  $\rho Tl_0/M$ , where  $\rho$  is the density of the muscle), and the shortening is expressed as a fraction of the resting length in the body.

At tensions above a  $Tl_0/M$  value of 600 a normal elasticity ( $\Delta$  extension  $\propto \Delta$  load) is shown in figure 1. The form of the curve below that must be due largely to statistical factors. In a large population of muscle fibres, each with its own tendon, it is very unlikely *a priori* that the lengths of these tendons would be the same. If  $x$  be

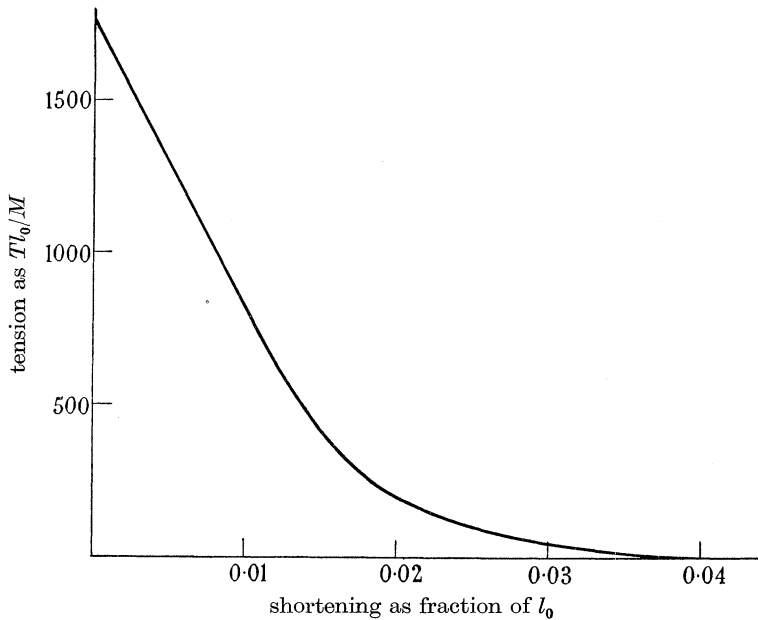


FIGURE 1. The relation between force and shortening during the rapid release of a frog's sartorius at 0° C during a maximal maintained contraction. Mean of a number of records obtained with four muscles. Allowance has been made (1) for the elastic shortening of the recording system and (2) for the contractile shortening of the active muscle. For generality, the tension is expressed as  $Tl_0/M$ , where  $M$  is the mass of the muscle, and the shortening as a fraction of the length  $l_0$  at rest in the body (see text).

In order to average the results, the shortening was measured, plus or minus, from the length at which  $Tl_0/M$  was 1000 in each case. It is not possible to define the length of zero tension and the maximum tension varied from muscle to muscle. The four muscle pairs of figure 1 were:

- (1) 28.5 mm. long, 185 mg.
- (2) 28.5 mm. long, 202 mg.
- (3) 27.5 mm. long, 202 mg.
- (4) 26.5 mm. long, 149 mg.

The units of shortening chosen were 0.0035  $l_0$  (about 0.1 mm.)

shortening units	0	1	2	3	4	5	6	7	8	9	10	11
$Tl_0/M$ muscle (1)	1530	1270	1000	740	481	250	159	97	54	31	15	0
$Tl_0/M$ muscle (2)	1610	1320	1000	660	378	217	129	74	31	13	0	0
$Tl_0/M$ muscle (3)	1670	1310	1000	685	389	245	163	95	55	29	10	0
$Tl_0/M$ muscle (4)	1840	1410	1000	598	364	242	155	98	66	44	27	12
Mean $Tl_0/M$	1660	1335	1000	671	403	238	151	91	21	29	13	3

It was very important that the muscles should be in good condition and uninjured. If one region were not contractile it would act as a series elastic body and the extensibility found would be much greater.

the stretched length and  $x_0$  the resting length of a tendon, then the total force exerted is  $\Sigma c(x - x_0)$ , where  $c$  is an elastic constant assumed for simplicity to be the same for each. If the length of the muscle as a whole be diminished by  $y$ , the force becomes  $\Sigma c(x - y - x_0)$ , so long as all the fibres remain tight. If some of them become slack when the length has been diminished by  $y$  the force is  $\Sigma c(x - y - x_0)$  for the remainder. Thus  $dT/dy = cn/N$ , where  $n/N$  is the fraction of fibres still taut

after shortening  $y$ . If we suppose  $n/N$  to follow the normal distribution shown by curve  $A$  of figure 2, then the value of  $T$  can be obtained by integration, being proportional to the area under the curve starting from the right. Curve  $B$  gives the result, and is obviously similar to the curve of figure 1. Conversely, by measuring the slope ( $-dT/dy$ ) at any point of the curve of figure 1 we can obtain the value of  $n/N$  at that point.

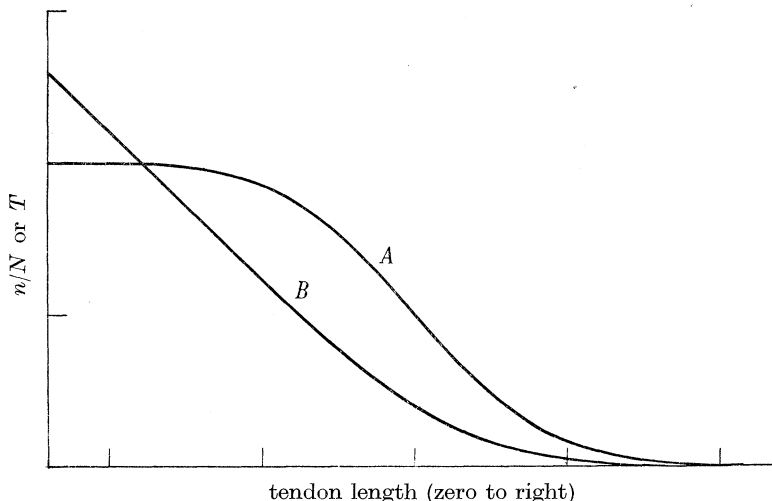


FIGURE 2. The statistical nature of the curve of figure 1. Curve  $A$ ,  $n/N$  the fraction of the fibre tendons which are just tight at any length, assumed to follow a normal (Gaussian) distribution. Curve  $B$ , the total tension exerted by all the fibres that are tight at any length (see text).

ery likely there are other factors affecting the form of the relation in figure 1, but it is difficult to imagine an assembly of several hundred fibres which did not have a statistical distribution of lengths of their tendons similar to that shown in curve  $A$ , figure 2, and this must necessarily produce a tension-extension curve of the type found.

The tension-extension curve of the series elastic component has not been directly determined before. In a recent paper (Hill 1949*a*) it was calculated from the form of the isometric contraction of a toad's sartorius, but the result necessarily included the extension of the connexions of the muscle to the tension lever and of the lever itself, which was not separately determined. It must be admitted that in the past sufficient attention was not paid to the extensibility of the recording system and its connexions to the muscle; so that the extensibility of the series elastic component of the muscle itself was overestimated. Experiments with abrupt releases from maximal tension appeared to show (Gasser & Hill 1924) that about 10% release was necessary to reduce the tension to zero, but control releases from the same tension, of the recording system alone without the muscle, were not made. If they had been, and if the muscles were in good condition contracting throughout their length, the amount of abrupt release required to reduce the tension of the muscle to zero would have been found considerably less.

The original purpose of the present experiments was to determine how much mechanical energy was present in a muscle and its mechanical recording system,

due to elastic stretch. The elastic energy in the muscle itself is obtained by integration from the curve of figure 1. It is shown as a function of tension in the curve (not the circles) of figure 3. For generality, the elastic energy  $W (= \int T dx)$  is expressed as  $W/M$ , where  $M$  is the mass of the muscle, and the tension as  $Tl_0/M$ , where  $l_0$  is the resting length in the body. The following example shows how figure 3 can be used. A sartorius 3 cm. long weighing 0.15 g. has developed a tension of 80 g., so  $Tl_0/M = 1600$ . From figure 3,  $W/M = 15.6$ , so that  $W = 2.34$  g.-cm. If this were transformed into heat in the muscle (e.g. in relaxation) the rise of temperature would be  $4.2 \times 10^{-4}^\circ \text{C}$ , which is about one-seventh of the rise of temperature in a single twitch.

When a muscle is stretched during contraction, the tension with which it resists the stretch may be considerably greater than that which it can exert isometrically. In estimating its elastic energy, therefore, it may be necessary to go beyond the

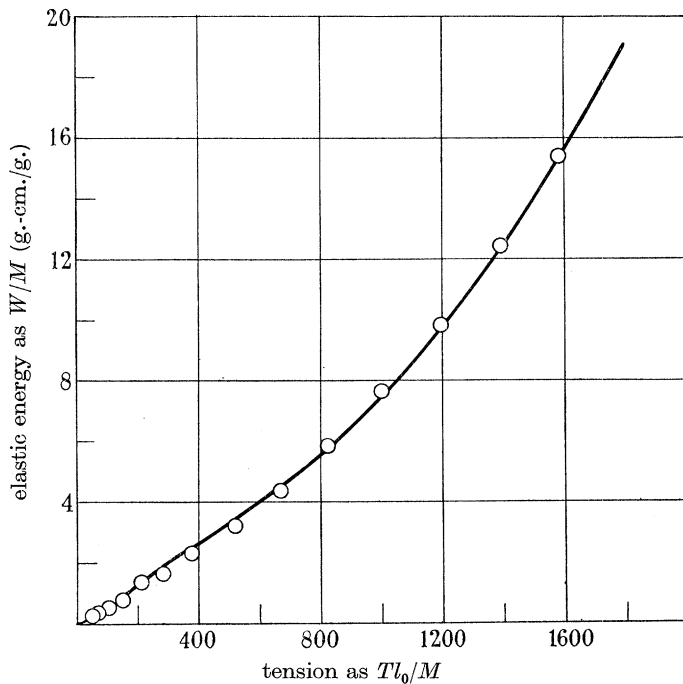


FIGURE 3. The elastic energy  $W$  of a muscle as a function of its tension. For generality the elastic energy is expressed as  $W/M$  (g.-cm. per g.) and the tension as  $Tl_0/M$ . The curve was calculated for frogs' sartorii from figure 1. The circles were calculated from similar measurements made on toads' sartorii.

range of figure 3. If we assume, as figure 1 strongly suggests, that the elasticity is normal above about  $Tl_0/M = 600$ , the curve from there onwards can be taken as  $W/M = 2.0 + 5.3 (Tl_0/M)^2$ .

In myothermic experiments it is necessary to have the muscle in a chamber in a thermostat rather far removed from the mechanical recording system outside. The connexion between them, 35 to 40 cm. long, is best made with a light chain. The chain must be light in order to avoid inertia, so is bound to be slightly extensible. With the best chain available (of the type formerly used with pince-nez) and



the present tension lever, the mechanical (elastic) energy present in the recording system was determined as a function of tension by the methods described above. The result was expressed in a graph similar to figure 3. The muscle referred to in the previous paragraph but one was supposed to have developed a force of 80 g. At this tension, from the graph, the mechanical energy in the recording system was 1.12 g.-cm., which is about one-half of that in the muscle itself. Together they make up 3.46 g.-cm., and if this were transformed into heat in the muscle the rise of temperature would be  $6.2 \times 10^{-4}$  °C, about one-fifth of that in a muscle twitch.

The recording system was a good one; a more ordinary tension lever and connexions to the muscle, being more extensible, might very well contain several times as much elastic energy under a given tension. If it contained 4 g.-cm. in the above example the total mechanical energy would be 6.34 g.-cm., which (transformed into heat in the muscle) would lead to a rise of temperature of  $1.14 \times 10^{-3}$  °C, nearly 40 % of the rise of temperature in an ordinary twitch. These quantities show the importance of the elastic energy developed by a muscle under supposedly 'isometric' conditions, and explain the relatively large amount of heat always found in relaxation after an 'isometric' contraction.

The measurements referred to hitherto were made on the sartorii of frogs (*Rana temporaria*). Three experiments, however, were performed in exactly the same manner and for the same purpose on the sartorii of toads (*Bufo bufo*), and the results are shown by the circles in figure 3. These muscles were:

- (1) 24.5 mm. long, 102 mg.
- (2) 23.2 mm. long, 64 mg.
- (3) 25.5 mm. long, 74 mg.

The speed of release of the ergometer was 35 mm./sec., which in relation to the maximum speed of contractile shortening of toads' muscles is relatively higher than in the frog experiments. The corrections for (a) elastic stretch of the chain and recording system and (b) contractile shortening during release, were made exactly as for frogs' muscles, with the only difference that  $b$  was taken as  $l_0/4.5$  per second instead of  $l_0/3$ , corresponding to the slower shortening of toads' muscles.

The agreement shown in figure 3 is good—indeed, the solid curve for frogs might have been drawn to fit the circles for toads. The toads' muscles were rather shorter and much smaller, and the agreement confirms the advantage of expressing the relation generally in terms of  $W/M$  and  $Tl_0/M$ . The experiments on frogs and toads were made independently and 5 months apart (the former in November, the latter in June), and the coincidence of the results would have been satisfactory even if they had been obtained on the same animal. The agreement between the different animals is striking.

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