LENGTH OF MUSCLE, AND THE HEAT AND TENSION DEVELOPED IN AN ISOMETRIC CONTRACTION.

BY A. V. HILL.

(*From the Department of Physiology, University College, London.*)

I. THE RELATION BETWEEN LENGTH AND HEAT PRODUCTION.

AN account of the older work upon this subject is given in O. Frank's review ((1), pp. 440, etc.). Heidenhain was the first to show that the extent of the heat production in a muscle is not determined once and for all by the stimulus, but depends also upon the mechanical conditions obtaining during contraction. This general statement of the matter has been fully substantiated since, especially by the work of Fenn(2). The simplest expression of Heidenhain's results is that, in a set of isometric contractions carried out at a series of different lengths, the heat production increases at first with increasing length, attains a maximum, and then decreases again as the length is still further increased. This conclusion was disputed by Blix, who believed that he had established the fact that the heat production goes on increasing indefinitely as the length in an isometric contraction is increased. Subsequent investigation, however, has shown that Heidenhain's conclusion was correct.

The matter was taken up again in 1914 by Evans and A. V. Hill(3). Their experiments made on frogs' sartorius muscles showed that, starting from a length not far from the resting unloaded length, an extension causes at first a rise in the heat production as well as in the force developed, while a further extension causes a fall in both. They found that the ratio of tension developed to heat produced is constant only for a certain range of extension of the muscle, the maximal value of T/H being reached at about the natural length of the muscle *in situ*.

A further investigation was undertaken by Doi(4), who showed, both in skeletal and in cardiac muscle, that the isometric mechanical response increases with extension up to a certain limit and then decreases as the extension is continued further. In his second paper Doi confirmed the statement that heat production in skeletal muscle reaches a maximum at a certain moderate extension, falling rather rapidly on both sides of this particular optimal length. Much recent work, especially that of Fenn(2), Azuma(5), Hartree (unpublished), etc., has incidentally confirmed this general statement of the variation, in an isometric contraction, of heat production with length.

Before the adoption of the shielded muscle chamber, which can be immersed in well stirred water in a constant temperature vessel, it was unsafe to allow muscles to shorten to any appreciable degree over the junctions of a thermopile, for fear of incurring errors due to bringing warmer or colder areas of the muscle upon those junctions. For this reason the experiments of Evans and Hill were made only at and beyond the resting length of the muscle. To investigate the heat production at shorter lengths, it is necessary to allow the muscle to shorten a certain distance over the thermopile on which it is stimulated, before holding it isometrically at the shorter length. With the muscle chambers now in use it is possible to secure such constancy of temperature within the chamber that no errors of this type are likely to arise; the relation, therefore, between heat production and length can now be investigated over the whole range of lengths, from the shortest to which the muscle will contract unloaded, on subjecting it to a tetanic stimulus, to the greatest to which it is safe to stretch it.

Methods. The myothermic chambers used were of the type described by Fenn. Several actual instruments have been employed, for all of which I am indebted to Mr A. C. Downing of this Department. They have been modified in various ways from Fenn's original design and two of them are shown in Figs. 1 and 2. Usually fixed electrodes have been employed, as shown in the figures; occasionally, however, the distal electrode has been brought into contact with the muscle just above its tendon, by means of a platinum loop soldered to a steel wire leading to the tension measuring apparatus. Some of the experiments have been performed in oxygen, in cases where it was necessary to obtain a measurement of the heat in absolute units: a calibration of the muscle is not possible in Ringer's solution. Several, however, of the relations established below do not demand an absolute calibration of the apparatus, and since the muscle lives longer and behaves better in

Ringer's solution, the experiments on frog's muscles have, where possible, been carried out in that medium.

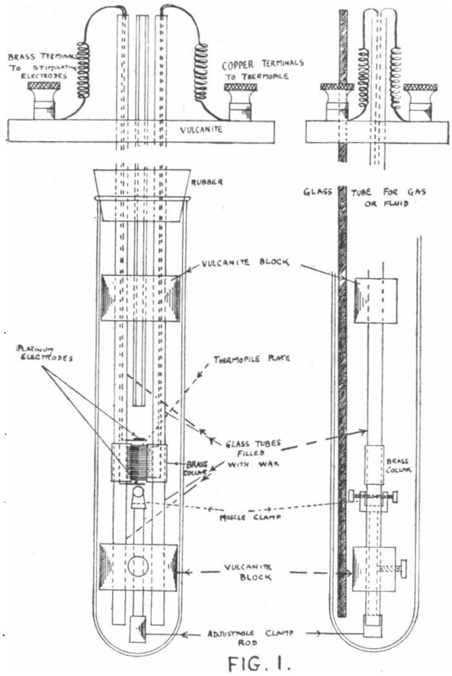

FIG. I.

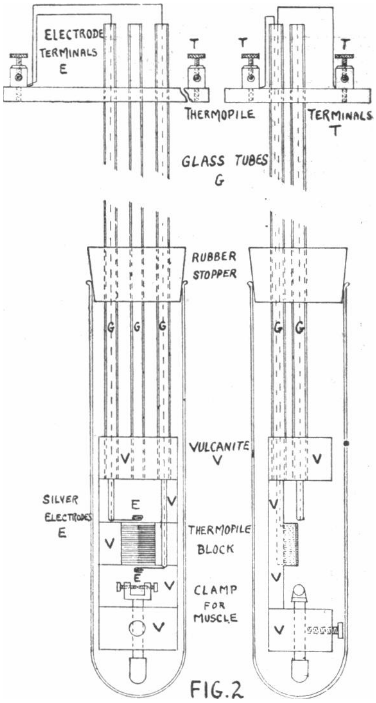

FIG. 2

Fig. 1. Thermopile and muscle-chamber, for pair of sartorius muscles. Front and side elevations. Thermopile made by silver-plating constantan wire wound spirally on a thin strip of ivory previously soaked in hot paraffin. Outer ("cold") junctions kept cool by being covered with brass collars. *N.B.* A sufficient distance must be allowed between the vulcanite plate at the top and the rubber stopper, to ensure that the chamber is fairly deeply immersed in well-stirred water.

Fig. 2. Thermopile and muscle-chamber for single muscle, *e.g.* biceps cruris of tortoise. Front and side elevations. Thermopile wound on a thick block of vulcanite, the "cold" junctions being at the back sunk in a groove in the vulcanite carrier *V*.

Two types of preparation have been employed: firstly, the usual double sartorius of the frog, and secondly, a single long straight leg muscle of the tortoise, the *biceps cruris* (see Bojanus (6)). The latter is usually about 50 mm. in length: it is thicker than the sartorius, and the single muscle employed (not a pair as with the frog's sartorius) usually weighs some 400 mgms. This muscle, the use of which will be further described elsewhere, contracts extremely slowly when compared with the frog's sartorius at the same temperature, and it would seem important that precisely similar results, qualitatively and quantitatively, have been obtained with two such different muscles.

When a calibration in absolute units of heat was required, this was carried out by a new method involving a "vacuo-junction," a delicate yet simple recorder of small alternating currents, supplied by the Cambridge Instrument Co.; the use of this will be described elsewhere. The method is simple and convenient to use, and gives results of considerable accuracy.

For stimulation a tetanus from a Porter coil was always used, its duration being adjusted by a Lucas revolving contact-breaker. For the calibration an alternator was employed, giving a single phase alternating current of about 100 cycles per second. A relatively high frequency is desirable for the calibration, to avoid polarisation at the electrodes. Such an alternating current, however, is not so suitable for stimulation, especially of a slow moving muscle such as that of the tortoise, where results analogous to a Wedensky inhibition appear to occur. Moreover, with a smooth alternating current of this type, if employed for stimulation, very large E.M.F.'s have to be used to secure a maximal response, and these are apt of themselves to liberate considerable quantities of heat in the live muscle. This is avoided by the use of the tetanising coil.

The muscle was connected to a set of levers as shown in Fig. 3.

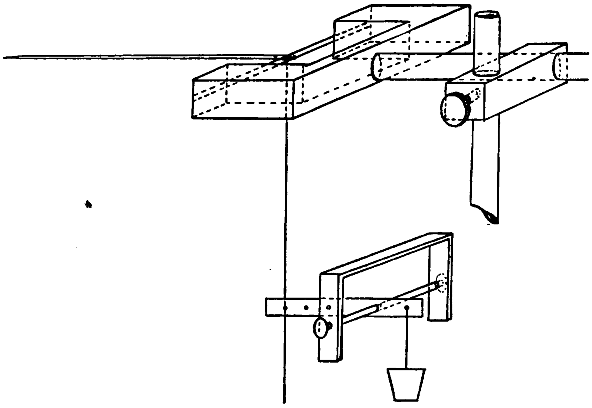

Fig. 3. Lever system, combined isometric and isotonic, with thread connecting. See text.

A strong piece of linen thread, or a steel wire, passed upwards from the muscle to an isotonic lever, loaded near its axis with a weight which put a tension of about 2 gms. constantly on the muscle. The resting unloaded length of the muscle—which is always somewhat arbitrary—is taken to be that corresponding to this small load. Vertically above the isotonic lever is an isometric one connected to it by a loose thread: this lever is of fairly short period and allows extremely little shortening. Both levers are mounted together upon the sliding portion of a Palmer stand, which can be adjusted vertically by a screw. A millimetre scale is provided to measure the amount of vertical movement. The resting unloaded length corresponds to a position of the stand in which the thread joining the two levers is just tight, so that the muscle comes up against the isometric lever directly it begins to shorten. Lengths greater than the unloaded one are obtained by screwing upwards by the required amount the stand which carries the two levers. The muscle is then stretched by the isometric lever by that amount. Lengths less than the resting one are similarly obtained by screwing the stand downwards through the required distance, so that the muscle can shorten freely under the small load of the isotonic lever, until the string joining the latter to the isometric lever becomes tight; then the rest of the contraction is carried out isometrically at the length determined by the position of the stand.

The experiments have usually been conducted at temperatures in the neighbourhood of 15° C., but they have been made also, in the case of frog's muscle, at temperatures as low as 0° C., and in the case of tortoise's muscle at temperatures as high as 25° C. Similar results, qualitatively and quantitatively, are obtained at all temperatures.

The tortoise muscle usually lasts so well and remains in such constant condition that it is unnecessary to make a "reverse" series. With a frog's muscle, in order to obtain results unaffected by on-coming fatigue, it is often desirable to take a reverse series, and to employ the average of the two readings made at any one length.

Apart from observations made at greater than the resting unloaded length, the maximum deflection of the galvanometer is always attained at a moment when the muscle has already relaxed into its original "unloaded" position. Thus over the lower range the heat may always be taken as being directly proportional to the number of scale divisions of galvanometer deflection. It is unnecessary then to make a new calibration for every position of the muscle during its contraction. When, however, the muscle is extended beyond its resting unloaded length, the conditions are different. In this case the whole contraction and relaxation occur, and the heat production is measured, at a length greater than the unloaded one. Consequently a smaller portion of muscle lies upon the junctions of the thermopile and the calibration number (*i.e.* the value of one scale division in ergs) is different. The variation of the calibration number with length depends upon the shape and thickness of the muscle, and upon the particular thermopile used. Theoretically, therefore, in order to measure the total amount of heat liberated in the whole muscle, it is necessary to make a calibration at every length considered. This would be laborious in practice and actually not essential. The method adopted has been to carry out a calibration on the dead muscle at two lengths, one as short as possible, approximating to the resting unloaded length, and the other at the greatest length at which observation has been made. A linear interpolation between these two gives, with sufficient accuracy, the calibration number for any intermediate length required.

This variation of the calibration number with length is an important factor in the technique, and it was never attended to in the older observations relating the heat production to length. It may have introduced serious and incalculable errors into the results both of Heidenhain and Blix. Its effect, with the thermopiles used by myself, is generally to make the apparent falling off of the heat production, with extension beyond the resting unloaded length, greater than the actual falling off. The explanation of the variation of calibration number with length is simple. With a sufficiently thin muscle the galvanometer deflection is approximately proportional to the total amount of heat liberated in the piece of muscle lying on the thermopile. If the muscle be extended the quantity of it actually lying on the thermopile is less: consequently the total heat liberated in the whole muscle, for a given amount of heat liberated in the portion lying on the thermopile, is greater. Since we are concerned with the heat liberated in the whole muscle, and not merely in the portion of it which happens to lie on the thermopile, this implies a greater calibration number for the whole muscle when it is in the extended condition. An example of the method of observation and calculation employed may make the argument clearer.

Exp. on pair of sartorii of Dutch *Rana esculenta*: weight, 0·228 grm.; length resting unloaded, 3·8 cm.; 0·5 sec. tetanus with Porter coil at 11 cm. employing 2 volt accumulator; with an extra 100 ohms in the galvanometer-thermopile circuit, as employed during observations (to reduce sensitivity) 4×10^{-6} volts gave 98 mm. deflection. Calibrated afterwards at lengths 40, 46 and 50·5 mm. Distance between (fixed) electrodes 23·0 mm. In the portion of muscle between the electrodes the value of 1 mm. deflection was observed to be 291 ergs, 286 ergs and 286 ergs respectively; so that in the whole muscle the value of 1 mm. deflection was $291 \times \frac{40}{23} = 505$ ergs, $286 \times \frac{46}{23} = 572$ ergs, $286 \times \frac{50 \cdot 5}{23} = 628$ ergs, respectively. Plotted against the corresponding lengths these calibration numbers follow a sensibly linear relation which allows values at intermediate lengths to be interpolated. The following observations were made on the live muscle:

Length, mm.	23	28	33	38	43	48	50½
Per cent.	60	74	87	100	113	126	133
Heat, mm.	292	598	796	805	620	494	469
Calibration no., ergs	485	485	485	485	538	597	628
Heat H, 10^3 ergs	142	290	385	390	333	295	294
Initial tension, 10^3 dynes	0	0	0	9	44	105	139
Tension developed T, 10^3 dynes	13	76	128	149	109	61	46
Tl_0/H	·34	1·00	1·27	1·45	1·24	·78	·595

Notes. (*a*) Here l_0 is the resting unloaded length, 3·8 cm.

(*b*) The calibration number for the first four lengths is the same, since for each the muscle relaxed to 3·8 cm. before the heat was measured.

This exp. is shown graphically as full circles in Fig. 8.

It will be seen from this experiment that a considerable error may be introduced by neglecting the variation of calibration number with length. Unless, therefore, proof be adduced to the contrary, it is always advisable to multiply the deflection of the galvanometer actually observed by a suitable calibration number: this must be determined at the length at which the muscle lay on the thermopile at the moment at which the maximum deflection of the galvanometer recording the heat production was measured. In none of the older investigations was this done, and it is impossible to say now how far the error so introduced may have affected the results. Moreover, since a calibration is impossible in the case of a muscle of non-uniform section, observations on such muscles are strictly comparable only if the muscle lie always in the same position on the thermopile, at the moment when the heat is recorded by the maximum deflection of the galvanometer.

In the example given above the calibration was carried out at three lengths, and the results show the relation between calibration number and length to be sensibly linear over the range considered. In other experiments this fact was assumed and the calibration number actually observed only at two lengths, the two points so obtained being plotted and joined by a straight line to allow interpolation. In this example the calibration was carried out by fixed electrodes. If the electrodes had not been fixed, but the distal one connected to the muscle near its tendon, the calibration number could have been read directly instead of being obtained by calculation from the length of the muscle. This procedure was adopted in some cases. The method described in the example makes it more obvious, however, why the calibration number varies with length, since it shows that for the piece of muscle lying between the electrodes the number is approximately constant, and therefore approximately proportional, in the case of the whole muscle, to its length.

In many of the experiments on frog's muscles, *e.g.* those shown in Fig. 4, the readings of heat production at lengths less than 100 p.c. were obtained simply in terms of scale divisions of galvanometer deflection. Since the sensitivity of the galvanometer may vary from time to time, this was tested at intervals throughout each experiment and the results all reduced to a constant sensitivity of the galvanometer.

In all the earlier experiments performed, which covered only the shorter range of lengths, observations were usually made in order of diminishing length, in or about the following positions: 110, 100, 95, 90, 80, 70, 60, 50. As shown in the figures, the maximum heat production occurs usually in the neighbourhood of relative length 95, so that an observation was interpolated between 100 and 90. In many experiments, including all those made upon tortoise's muscle, the observations were made not precisely at these stated lengths, but at certain neighbouring lengths chosen for convenience. In such cases, in order to obtain a curve representing the mean of several experiments, the observations of heat production were plotted against the relative lengths and a curve drawn through the plotted points. From the curve the heat production at certain standard relative lengths was read off, and reduced to a percentage of the maximum heat production. Since, in the first instance we are concerned only with the variation of heat production with length, these percentage values are all that is required for our immediate purpose. The stimuli were always maximal, and when a reverse series also was made, each point plotted represented the mean of the two observations at the length considered. Since chance variations occur from observation to observation and from muscle to muscle, it was desirable to make a mean curve from a number of observations on different muscles. A table therefore was constructed of the percentage heat production at each of the standard relative lengths, for a number of experiments on different muscles. The mean for each length was then calculated and plotted, and the mean curves resulting are those shown in Figs. 4, 5 and 6. The greater the care taken and the better the condition of the muscle, the more regularly is the same result obtained: qualitatively the results are always similar, quantitatively there are usually only slight differences from the means shown in the figures. The curves, therefore, represent with considerable accuracy the relation between heat production and length in a normal isolated muscle in good condition and unfatigued. To avoid fatigue an interval of 3½ to 5 minutes was allowed between successive observations.

Results.

The results can best be described with the aid of the figures. In Fig. 4 each full line represents the heat production from length 100

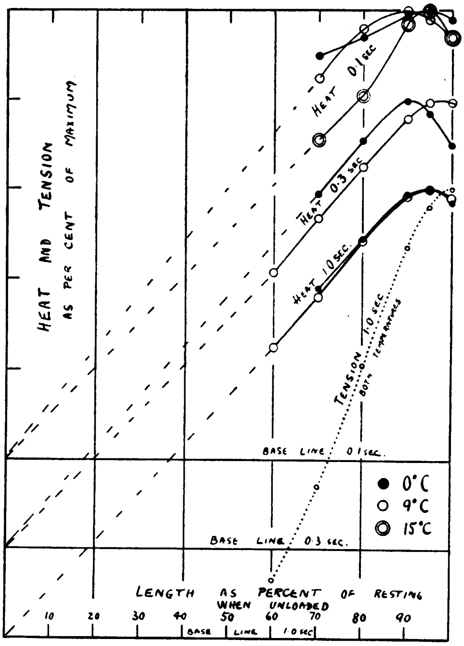

Fig. 4. Relation between heat production and length, at lengths up to that of the resting unloaded muscle; three durations of stimulus, three temperatures; mean results of a number of experiments. Sartorius muscles of *Rana temp.* [N.B. Three base lines.]

down to the smallest length to which the muscle will shorten. The experiments shown in this figure were performed in Ringer's solution, without a "reverse" and without calibration, at three temperatures and for three durations of stimulus. The observations at the highest temperature were made only for the shortest duration, since the muscle more readily fatigues at a high temperature. The experiments are shown plotted to three different base lines, in order to avoid confusion between the different curves. The broken lines to the left join the observed curves to the origin. The actual experimental observations were plotted, and interpolations carried out for lengths 100, 95, 90, 80, 70, 60, as described above. These interpolated quantities were then reduced to a common maximum of 100, and their average value for each length in a number of experiments is shown in the figure. A similar curve is shown for the tension exerted in a 1·0 sec. contraction at 0° and 9° C. This figure shows that, on the short side of the unloaded length, the same type of relation occurs at all temperatures and for all durations of stimulus.

In the shortest tetanic contraction, approximating to a single twitch, it is impossible to obtain results over so wide a range of lengths as it is with a more prolonged contraction; the muscle will not shorten so far in the less prolonged contraction. A certain characteristic and constantly recurring difference exists between the result of the very short stimulus, 0·1 sec., and that of the longer. Qualitatively the same relation is obtained, namely, a curve with a maximum heat production in the neighbourhood of 90 or 95 p.c. of the resting unloaded length. The curvature, however, is often not so pronounced as in the case of the longer stimulation. In all cases, but especially in that of the frog's muscle at a low temperature, or in that of the tortoise's muscle which contracts very slowly, a stimulus of 0·1 sec. is over, or practically over, before the shortening has been completed, so that the stimulus has been applied mainly at lengths greater than the final length at which the contraction is completed isometrically. Moreover, as Fenn(2) has shown, when a muscle shortens doing work it gives out more heat, corresponding to the work done. The only external load in these experiments was that of the isotonic lever, exerting a constant tension on the muscle of only 1 or 2 gms. The external work, therefore, is practically negligible. An active muscle, however, possesses, as Gasser and Hill have shown(7), a considerable degree of "viscosity," and in a rapid unloaded shortening an appreciable amount of mechanical work must be done by the muscle against its own internal viscous resistance. This work will entail—pursuing the argument of Fenn—a certain amount of extra heat, which in the contractions evoked by shorter stimuli must be relatively more important than in those evoked by longer ones. Hence, we might expect that in the contractions with shorter stimuli the heat production would not diminish with decreasing length relatively as much as in the contractions evoked by longer stimuli. The curvature of the relation would be less, as has actually been found. To study the relation between heat and length in its purest form it is advisable to consider chiefly the results of the longer stimulation.

Before discussing more fully the results shown in Fig. 4 we must consider those exhibited in Figs. 5 and 6. In Fig. 5 are shown three curves obtained by the methods of observation and calculation described above, on the biceps cruris muscle of the tortoise. Here again the observations were made, without reverse and without calibration, at lengths shorter than the resting unloaded length. Actually observations were continued to length 105, and the continuations of the curves are given. These continuations are shown in broken lines as, owing to the absence of a calibration, the observations beyond length 100 are not entirely reliable. In this figure also, to prevent confusion, the results for the three different durations of stimulus are shown plotted to three different base lines. The tension curves are presented in a similar way. It will be noted that the one second and the three seconds curves are practically identical, the former ending a little sooner than the latter, while the 0·1 sec. curve is appreciably different in form, and ends considerably sooner. The divergence of the 0·1 sec. curve is due presumably to the factors discussed above. Observations made at various temperatures are included in the means shown in Fig. 5: no difference was

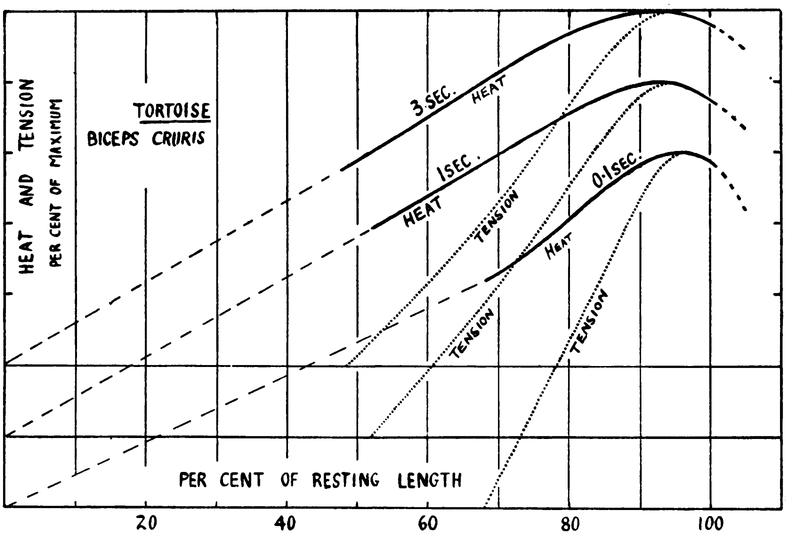

Fig. 5. Relation between heat production and length, at various lengths up to that of the resting unloaded muscle. Corresponding tensions also shown. Plotted to three different base lines to prevent overlapping. Mean curves from a number of experiments. Biceps cruris of tortoise. The dotted continuations to the right were observed but they may involve a slight error since no calibration was carried out for lengths greater than 100 p.c.

observed between the results obtained at different temperatures. The curves shown in Fig. 5 continue to a rather shorter length than those of Fig. 4 on frogs; the tortoise's muscle appears to be able to shorten relatively rather further than the frog's. The broken lines to the left join the origin to the commencements of the several curves. Here, again, we may say that the characteristic relation between heat and length, at lengths less than 100, is most clearly shown in the case of the longer stimuli. The tortoise's muscles of Fig. 5 were in air in the muscle chamber.

Fig. 6 is of a composite nature. The observations at lengths less than 100 were all made on English *Rana temporaria*, in Ringer's solution with reverse carefully carried through, in order if possible to eliminate the effects of on-coming fatigue. The observations of heat and tension were made actually at the relative lengths shown, and were not obtained by interpolation from other observations. In each experiment they were reduced to a maximum of 100, and the mean of the several experiments computed for each length. These mean values are shown in the figure. All experiments were carried out in the immediate neighbourhood of

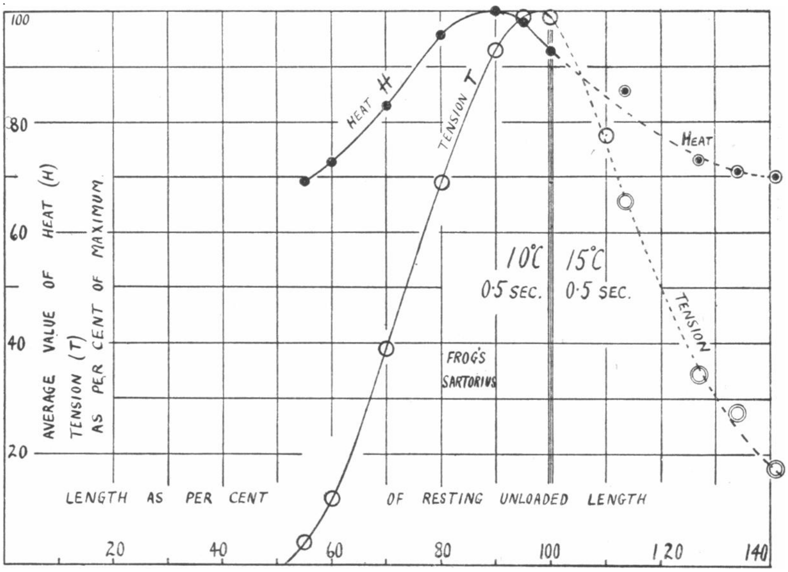

Fig. 6. Relation between heat and length, and tension and length, for frog's sartorius. All 0·5 sec. tetanus. Lengths less than 100 p.c., *Rana temp.* at 10° C. Lengths greater than 100 p.c., *Rana esc.* at 15° C. Curves made to join by adjusting the scale at 100 p.c. length. For details see text.

10° C., and all with a stimulus lasting for 0·5 sec. The observations in Figs. 4 and 5 having established the general relations, it was thought desirable to record them in a special series with all the accuracy possible. Since temperature has no effect on the relation, as shown by Fig. 4, and since the duration of stimulus has no effect, provided it be not too short, as shown by Figs. 4 and 5, a temperature and a duration of stimulus were chosen to give the greatest accuracy of observation, with as little fatigue as possible. These observations were continued only to lengths 100 on the long side, since it had not been realised at the time how important the higher range would prove. Subsequent experiments therefore were carried out to complete the investigation over the higher range of lengths. The experiments at the shorter lengths were on muscles in Ringer's solution, with reverse but without calibration: those to the right, at the greater lengths, were in oxygen, with calibration but without reverse. In the case of such severe stretching as that administered to these latter muscles a permanent extension of a few millimetres is always produced, and a reverse series is valueless. Each experiment over the higher range consisted of five observations only, starting from length 100 and going to length 140 approximately. After this the muscle was killed and a calibration carried out. The observations at the greater lengths were then fitted to those at the lesser lengths by adjusting the scale to make the values at length 100 coincide. To be precise, the mean values of the heat—five means obtained at five different degrees of extension—were reduced to a constant maximum of 93, in order to make the first point coincide with the end of the curve obtained from the previous observation. In the same way, the mean tensions were reduced to a constant maximum of 99, in order to make the end of their curve coincide with the end of the curve given by the previous observation. That this process is justifiable is shown by the fact that the mean value of the tension found at length 110 in the first set of observations comes fairly accurately on to the curve of the second observations so determined. It is unfortunate that the importance of making the observations over the whole range was not realised earlier in the investigation: later a few experiments were made over the whole range and the results of Fig. 6 entirely confirmed. In some ways it is an advantage to split up the observations into separate experiments, since this avoids the effect of fatigue or damage, which in the case of the stretch experiments, causes rapid deterioration of the muscle.

Table I includes the data from which the left-hand side of Fig. 6 was drawn.

TABLE I. Frog's sartorii at 10° C.: 0·5 sec. maximal tetanus; heat in galvanometer scale divisions reduced to a constant sensitivity of galvanometer, 4×10^{-6} volts = 100 mm.

	Length of muscle as p.c. of resting unloaded length.							
No.	110*	100	95	90	80	70	60	55
1	164	184	192	192	181	155	132	122
2	137	154	161	164	157	132	117	110
3	160	178	191	197	194	171	151	141
4	110	142	152	158	140	121	105	—
5	118	150	156	155	150	126	110	—
6	148	172	183	186	183	165	150	—
7	243	256	277	277	272	233	202	197
8	258	289	297	314	305	262	232	228
9	154	182	192	207	219	223	226	—
10	185	219	231	248	260	263	257	—

* The numbers in this column do not strictly represent the heat, because of the absence of a calibration at length 110.

The results, after averaging, are shown in Fig. 6. Nos. 9 and 10, made on the same muscle, are anomalous, and are not included in the average. They represent the only example found in the whole of this investigation of heat production increasing continually with decreasing length. No explanation can be offered of the anomalous behaviour of this particular muscle, but the possibility of such an occurrence is of interest.

The fact that the tension developed varies with length has long been known. On the short side of the resting unloaded length this diminution of tension with shortening would occasion no surprise, being a general property of an elastic body. At a length of about 50, which may be regarded as the "natural" length of the excited muscle, the tension exerted disappears: at lengths greater than 100 the tension developed diminishes with extension. This is true of such simple muscles as the frog's sartorius or the tortoise's biceps cruris, in which the fibres are straight and parallel, and not supported against a load by tendons or connective tissue. In the case of a complex muscle such as the gastrocnemius the relation is presumably not so simple. Fig. 6 shows the striking symmetry of the tension-length curve, about a relative length of approximately 98. There is indeed a tendency to spread out to the right, which, however, may well be accounted for by the permanent extension set up by straining the muscle beyond a relative length of about 125. The curve indicates that at an extension of 50 to 60 p.c.—if the muscle or its tendon does not break—no tension will be developed on stimulation. This is almost literally correct.

The same type of symmetry is shown by the relation between heat and length, although the maximum heat production seems always to occur at a length slightly less than that of the maximum tension. With the heat also there appears to be a tendency to spread out to the right, but this again can be accounted for by the permanent extension produced in the muscle by stretching it beyond a length of about 125. It is striking that the factors, whatever they be, which determine the amount of energy liberated in a contraction, are affected to an equal degree by an extension and a shortening. The same symmetry will be found again in the very extensive set of observations on T/H shown graphically in Fig. 7 below.

Another striking fact emphasised by the broken lines to the left of Figs. 4 and 5 is that in many experiments the heat production, as it diminishes with diminishing length on the short side of length 100, appears to be aiming at the origin. The relation settles down to a simple proportion between heat production and length. It is tempting to imagine that if the muscle were able to overcome its own lateral rigidity, or whatever stops it from shortening further, the heat production would continue to diminish, tending to vanish at length zero. The series of observations recorded in Fig. 6 is the only one which does not illustrate this proportionality: there the heat production diminishes rather less rapidly than does the length of the muscle. In general, however, there would seem, once the curve has passed its maximum and rounded the corner, to be a direct proportion between heat production and length, up to the stage when the curve ends, so to speak, in mid-air because the muscle is unable to shorten any further.

Whether this proportionality represents any fundamental fact it is impossible at present to say. At first sight it might have been thought to indicate that the heat production is determined by the area of some surface running the full length of the muscle fibre. It is difficult, however, to imagine any kind of surface in the muscle which will diminish in direct proportion to its length. For example, in the case of a long thin cylinder of constant volume, *e.g.* a muscle fibre or fibril, the area of the surface is proportional, not to the length but to the square root of the length: and a constant proportion between heat and square root of length is definitely not the relation suggested by Figs. 4 and 5. Moreover, if the heat were determined by the area of any such surface it would be difficult to explain why, as the length increases beyond 100, the heat production passes through a maximum and then decreases again. Some cause other than a simple proportionality to surface must be responsible for the relation between heat production and length.

That Heidenhain was correct in his statement that the heat production reaches a maximum at a certain length, beyond which any further extension results in a diminution of the heat, is very clearly shown by these experiments. The maximum heat production occurs at a relative length of about 95. It is realised that the "resting unloaded length" of a muscle is a very arbitrary quantity. It is defined here simply as the full length of the muscle substance, not including any of the tendons, when the muscle is extended by a load of 1 to 2 gms. It cannot, however, be far from the length which the muscle occupies in the body.

The effect of stretching is presumably not upon the mechanism by which chemical energy is transformed into mechanical energy, but rather upon those "governors," whatever they be, which regulate the amount of energy expended. As Hartree and Hill (8) showed, in their studies of the heat produced in contractions of various durations, there is a very distinct regulatory mechanism determining the amount of energy liberated in a maximal continuous tetanus. There is, so to speak, a channel along which energy or chemical transformation must pass, and the size of this channel is very largely affected by a change of temperature. The chemical reactions which determine activity in the muscle are limited in extent, and the speed at which chemical change can occur rises as the temperature rises. In the phenomena described here we have found an influence of mechanical, one might even say geometrical, conditions upon the mechanism by which the supply of energy is regulated. In discussing—as in the next section of this paper—the relation between heat produced and tension developed we are dealing with the mechanism by which chemical energy is transformed into mechanical energy and work. Hitherto, however, in discussing simply the magnitude of the heat (or the tension) developed in a maximal contraction under various conditions, we are dealing not with the mechanism by which energy is transformed from one form to another, but with that by which the amount of energy so transformed is regulated: we are dealing, to take an engineering analogy, not with the cylinder, the piston and the valves, but with the governor which determines the amount of steam which is let into the cylinder. It is necessary to make this distinction clear, since otherwise false deductions might be drawn. The relation between heat production and tension, which is what gives us information about the other part of the machinery, is dealt with separately below.

It is not proposed in this paper to discuss certain obvious applications of the variation of heat production with length: it is sufficient to indicate that the diminished energy liberation associated with a shortened muscle must have a considerable bearing upon the economy of muscular movement in general, and that it is striking how the maximum energy liberation for a given stimulus occurs nearly at the length at which the muscle lies in the body. If, as would seem probable, the same type of relation holds in the case of cardiac muscle, there are certain obvious applications to cardiology.

II. THE RELATION BETWEEN LENGTH, AND THE RATIO OF TENSION DEVELOPED TO HEAT PRODUCED.

In studying the actual mechanism of the muscular response the variation, with length, of T/H would seem to be of greater interest than that of H alone. If a muscle for any reason liberates more lactic acid when stimulated, we should expect it to give more heat and to develop more tension. In studying, therefore, the variation of H with length, we are never safe from the possibility that the effect observed, when the length is altered, is due to the "governor" mechanism discussed in the previous part of this paper. Moreover, in any kind of machine the most important factor in its working is that associated with its mechanical efficiency, the ratio of its mechanical output to the total energy it uses. In muscle for various reasons the maximum mechanical efficiency is difficult to determine. The simplest representation, however, of the response of muscle is the tension which it develops, and in many ways the most interesting and important criterion of a muscle's behaviour is the ratio of the tension developed to the heat produced. Since tension and heat are not quantities of the same dimensions, we must, if we wish to express T/H in absolute units, multiply the numerator by something of the dimension of length to make it of the same dimensions as the denominator. The obvious length to multiply it by is that of the resting unloaded muscle (l). The quantity Tl/H is one of considerable significance, being constant, in a twitch or a short tetanus, for variation of temperature and even for variation of the species from which the muscle is obtained. For such reasons, therefore, it was desirable to study the variation of T/H, or of Tl/H, with length.

The experimental method was identical with that described in the previous part and the results are shown in Figs. 7 and 8. Fig. 7 is a composite one, as was Fig. 6. The observations shown to the left were made on frog's muscle in Ringer's solution, uncalibrated, starting from length 100 and proceeding at intervals to the shortest length at which the muscle would develop any tension. Observations were made, as shown, at three temperatures and for three durations of stimulus. Many experiments were performed, the observations in each case when plotted lying upon a smooth curve. It was impossible, however, to draw all these curves in one diagram, and since it seemed desirable to show the degree of variation found in individual experiments, it was thought best to include in one figure all the observations made. These observations may appear rather scattered, but it should be realised that the individual curves, of one of which each observation forms a part, are themselves smooth, and that the "scatter" shown is not due to experimental error but to individual variation of the muscles. This variation seems to be a random one except in one respect, namely, that the observations made at the lowest temperature, especially in the case of the shortest stimulus, all lie below the curve passing through the mean of the other observations. This fact would seem to be due to the cause discussed above (p. 246). The muscle at a low temperature moves so slowly and has so high a viscosity that during a short stimulation it has no time to develop its full tension at anything but the length 100. Apart from this

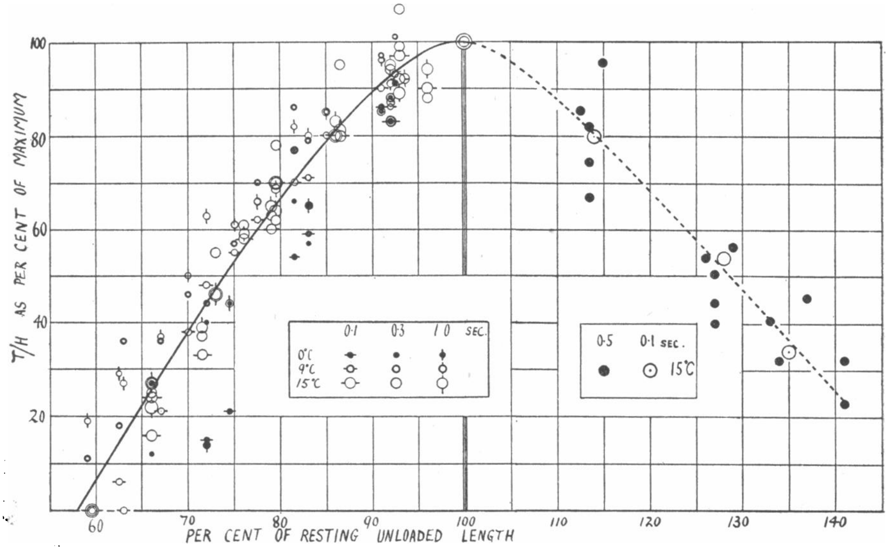

Fig. 7. Ratio of tension developed (T) to heat produced (H) as p.c. of maximum value of T/H, which in all except two of a very large number of cases was at 100 p.c. length. Observations to the left of the 100 p.c. length line made on *Rana temp.* at the temperatures and with the times of stimulation noted. The curves for the individual experiments were smooth, but since large numbers of curves cannot be shown in the same diagram, the observations only are given. Observations to the right of the 100 p.c. length line made on Dutch *Rana esc.* at 15° C., 0·5 and 0·1 sec. tetanus, with calibration to allow for the varying sensitivity of the thermo-electric apparatus with varying length and thickness of muscle. Curves made to meet at the 100 p.c. point.

consistent difference, the heavy line drawn through the middle of the observations would appear to represent, with considerable accuracy, the average relation between T/H and length on the short side of the resting unloaded condition.

The experiments shown to the right of length 100 required a calibration number at each length, and were made by the method described above. These observations were then fitted to those shown on the left by reducing them also to a constant maximum of 100 at the unloaded length. The double circle, therefore, which is shown at the point 100, represents one point in every set of observations made, whether to the right or to the left. In all series the value of T/H at length 100 is taken arbitrarily at this point. The observations to the right, that is those on the stretched muscle, were made at 15° C. and for 0·5 and 0·1 sec. of stimulation only. Since, however, the observations to the left show no difference between different temperatures and durations of stimulus, except for the one difference already mentioned, it is justifiable to continue the curve to the right by observations at one temperature only and with not so many durations of stimulation. The broken line drawn through the observations represents with fair accuracy the average relation between T/H and length for a stretched muscle.

Lest any error might arise in the construction of such a composite curve, a few experiments were carried out over the whole range on the muscles of Dutch *Rana esc.* in good condition. Fig. 8 represents two

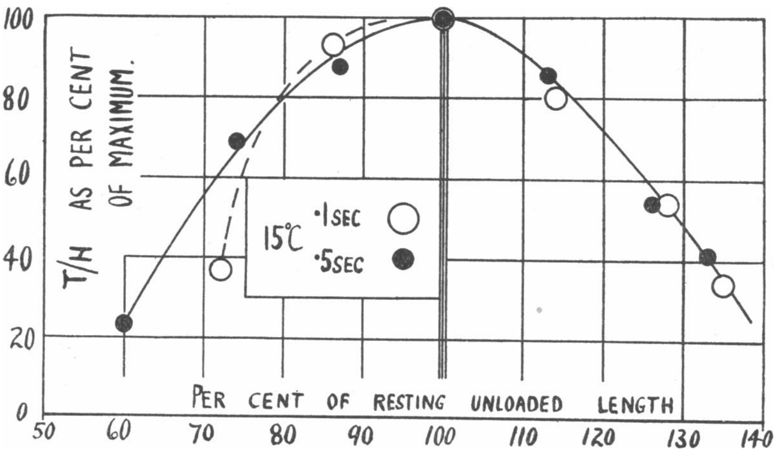

Fig. 8. Two individual experiments, the last experiments made, relating T/H to length. In each experiment observations began at the shortest length, and were continued with 5 mm. increments of length to the greatest. Note the similarity to Fig. 7.

such experiments. It is seen from Fig. 8 that individual muscles show identically the same kind of relation as that presented in the composite curve of Fig. 7 taken from a large number of different muscles. The symmetrical curve of Fig. 8, which is drawn through the full circles representing 0·5 sec. tetanus at 15° C., is exactly similar to the average curve of Fig. 7. The broken curve, drawn through the hollow circles, falls—on the left—below the full curve. In a contraction of such short duration the tension tends to be abolished by a smaller amount of shortening than in a contraction of greater duration. This fact we have already discussed, both here and in the preceding part. Details of one of the experiments shown in Fig. 8 are given in Part I above (p. 243).

There are several striking facts which emerge from Figs. 7 and 8. In the first place it is clear that the maximum value of T/H occurs almost exactly at what we have called here the "resting unloaded length." Only in two observations out of the very many shown in Fig. 7 was a greater value recorded than that at length 100. It is interesting to find that a muscle develops force with the greatest efficiency when at or near the length at which it lies at rest in the body.

A more striking fact, which we have discussed already in Part I in reference to other observations, is the almost exact symmetry of the curve. Here, as in Fig. 6, there is a tendency for the curve to spread out to the right at the greater extensions. This, however, can be explained if we remember that the large extensions leave a permanent mark on the muscle, so that it never returns precisely to the same resting unloaded length. A permanent stretch of 2 or 3 mm. is always found, and if this be allowed for it will make the curve almost exactly symmetrical. The shape of the curves indicates that at an extension of about 50 p.c. the value of T/H will fall to zero.

What the explanation of this relation can be it is impossible at present to say. It would seem, however, that this considerable variation of T/H with length, together with the symmetry of the relation and the fact that the maximum is at length 100, is a base line from which any theory of the mechanism of muscle must start.

It is not proposed to discuss here any possible application of these facts. It is sufficient to deduce that muscles, either extended or shortened from their natural unloaded length in the body, produce and maintain a tension with less economy than at that length. At extreme extensions or shortenings the economy becomes very poor indeed. Perhaps in the body this is, to some degree, counterbalanced by the greater mechanical advantage obtaining when a limb is partially flexed.

III. THE MECHANICAL EFFICIENCY OF THE MUSCLE REGARDED AS AN ELASTIC BODY.

The observations recorded here emphasise a difficulty which has been growing during the last few years in regarding the muscle as an elastic body whose elastic properties change as the result of stimulation. In Fig. 9 is shown the relation between the tension developed and the length, in an isometric contraction of a frog's sartorius muscle stimulated for 0·1 sec. Six experiments were performed, three at 9° C. and three at 15° C., and the results were plotted and averaged as described above for the heat production. The muscles were in excellent condition, in oxygenated Ringer's solution, and the results of the six experiments were in good agreement. Experiments were made also at 0° C., but these differ from the others at the shorter lengths, presumably owing to the fact that muscle, because of its viscosity, never has time to attain the shorter length before its tension has begun to pass off. The actual means are not plotted, since they lie exactly on the curve shown. All the observations were reduced to a maximum of 100 before averaging, and, as before, it is seen that the maximum tension occurs at a relative length of about 98. At this length, therefore, the tension developed is taken arbitrarily to be 100. Now if the muscle could be regarded simply as an elastic body, the area of the curve would undoubtedly represent the maximum work which it could do. Even if the muscle in actual practice

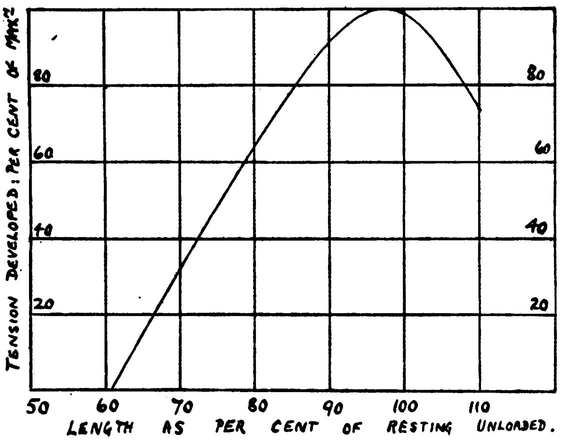

Fig. 9. Relation between tension developed and length for the case of a short tetanus, 0·1 sec. Mean of six experiments at 9° and 15° C. Muscle in excellent condition in oxygenated Ringer. For calculation of the theoretical maximum work see text.

could not perform this work, it might still be possible to argue that, owing to its internal viscosity, it could not shorten rapidly enough along the curve in time for the whole work to be done, before relaxation had caused the disappearance of its active state. Up to the time of Fenn's work (2) this view was indeed very generally accepted, and in 1913 I recorded experiments (9) in which the theoretical maximum work calculated from such a diagram was compared with the actual heat liberated by the muscle when subjected to a short stimulation. In this way a theoretical maximum for the mechanical efficiency of the initial process was determined, which reached the rather astonishing value of about 100 p.c. Such a value was of course possible, especially in view of the fact that the process considered was only part of the whole cycle, recovery providing an amount of heat somewhat larger than that liberated in the whole of the initial process. The experimental facts, however, which have been made available in the last few years, and especially the observations recorded in this paper on the variation of heat production with length, make it necessary to reopen the discussion.

From the diagram the area corresponding to the theoretical maximum work has been calculated at various lengths of the muscle, and the following values found:

Relative length	Ratio, $W/T_{100}l_{100}$
80	·063
90	·144
100	·244
110	·333

Here W implies the theoretical maximum work in a complete shortening from the length considered, and T_{100} the tension developed by the muscle at length l_{100}, the resting unloaded length. Now it is possible to pass directly from $T_{100}l_{100}$ to the initial heat production, and so to find W/H in absolute units. The maximum value of Tl/H occurs, according to Figs. 7 and 8, at length 100. Here, according to a number of experiments made by Hartree and Hill (8) confirmed by many recent observations both on frog's sartorius and tortoise's biceps cruris, the value of Tl/H in a twitch, or a very short tetanus, is uniformly about 5. Thus we may write $H_{100} = 0{\cdot}2\ T_{100}l_{100}$, from which

$$W_{100}/H_{100} = 1{\cdot}22.$$

In 1913 I found the theoretical maximum work to be about equal to the initial heat: the more accurate data now available make it on the average somewhat larger. Such a value as 1·22 for the ratio is not, in itself, impossible, since in the complete cycle the heat liberated in recovery must be added, and this is 1·5 times the initial heat, so reducing the theoretical maximum efficiency to 0·49. It is instructive to repeat the calculation for length 110. Here we find

$$W_{110}/H_{100}=1{\cdot}66.$$

From Fig. 6 we find $H_{110}/H_{100}=84\tfrac{1}{2}/93={\cdot}91,$
so that $W_{110}/H_{110}=1{\cdot}82.$

This value again is not in itself impossible, since for the whole cycle, including recovery, the theoretical maximum efficiency works out to 0·73. Moreover, if we could imagine the muscle shortening reversibly through the whole cycle it would have to pass through the various intervening lengths, and we might well suppose the heat liberated to be not H_{110} but the maximum heat, say H_{90} (Fig. 6). This would give

$W_{100}/H_{90}=1{\cdot}13$ (whole cycle 0·45),
$W_{110}/H_{90}=1{\cdot}54$ (whole cycle 0·62).

Even if we took the whole area, up to extreme extensions, of the tension-length curve, which from Fig. 6 is about double (actually rather less than double) that up to length 100, we should still find

$W_{\text{total}}/H_{90}=2{\cdot}26$ (whole cycle 0·90),

which again is not an impossible value. The free energy of the oxidation of carbohydrate, on which muscular contraction is based, is almost certainly great enough to allow such values as 90 p.c. for the theoretical mechanical efficiency of the whole cycle. Hence physical chemistry does not prohibit, even in the extreme case, the use of the tension-length diagram as an indicator of the theoretical maximum work.

It is obvious nevertheless that the variation of heat production with length does introduce a very serious complication into the elastic body theory, just as do Fenn's results (2) on the extra heat production associated with mechanical work. In view of the demonstrable viscosity of the excited muscle it is not surprising that the actual work can never —even approximately—attain, within the finite time occupied by a twitch, the theoretical value calculable from the tension-length curve. If, however, we could imagine the active state "fixed" without continual stimulation, or if we could suppose the viscosity eliminated, might we even then believe the active muscle capable of passing, like an elastic body, through the whole cycle of its tension-length curve? In a state of tetanus it undoubtedly can, as Fick showed (10) long ago with his "Winkelhebel": with that device, as also with his "Schwunghebel" though to a less degree, he was able to obtain actual external work not far short of the area of the tension-length curve: the same fact may be shown for human muscles with the inertia ergometer, as used by Lupton (11), Lindhard (12), and myself (13). In such experiments, however, the heat production is much greater, owing to the maintenance of the contraction: while the muscle, owing to its slow movement, can "adapt itself" to each new length as it arrives at it. It may well be the case that the fully tetanised muscle behaves simply as an elastic body possessing viscosity, though in it also the rate of energy expenditure required to maintain a contraction varies with the length. The muscle, however, which has been subjected to a short tetanus, or a single shock, possesses such a complex set of energy relations, as described by Fenn (2), Azuma (5), and in this paper, that we may well be forced to leave unanswered the question proposed above, can we even imagine the muscle stimulated with a single induction shock to be capable of passing through the whole cycle of its tension-length curve? If we can, then we are left with a series of perplexing questions: which heat ought we to compare with the work so obtained? the heat at the length of stimulation? the maximum heat at length 90 or thereabouts? the average heat over the whole range of shortening? and might we expect extra heat to be liberated, in accordance with the work done, as found by Fenn? Such questions can be answered only when we have a greater knowledge of the actual mechanism of contraction, a knowledge which perhaps may be afforded by the development of the theory which W. E. Garner describes elsewhere (14).

IV. A POSSIBLE MECHANISM OF THE FENN EFFECT.

While, in many respects, the muscle behaves as an elastic body, there is obviously some mechanism in it adapting the amount of energy liberated to the work performed. The following thermodynamic conception may help perhaps to reconcile the two points of view.

Imagine a set of electrical accumulators providing current for a motor driving a heavy flywheel: allow the motor to do external work: disconnect the load, and then by suitable electrical connections, cause the kinetic energy of the flywheel to drive the motor as a dynamo and so to recharge the accumulators. Part, then, of the energy liberated by the discharge of the accumulators, the part not used up for doing mechanical work, is restored to them afterwards. In such a system there will be an extra total liberation of energy when work is done, since there will be correspondingly less kinetic energy to employ after work in recharging the accumulators.

When a muscle contracts, glycogen disappears and lactate is liberated. The lactate is re-formed to glycogen afterwards, in the "recovery process," by means of free energy provided by the oxidation of carbohydrate or of lactic acid. The essential thermodynamic factor in recovery is the introduction of free energy, provided by oxidation, into a reaction, in order to drive it in the reverse direction from that in which it naturally goes. Thermodynamically speaking it is not necessary that this free energy should be derived from any special source: an electric current, whatever its origin, can liberate oxygen and hydrogen from water. Now in an actively contracting muscle there is a store of free energy, liberated in response to the stimulus, viz. the potential energy of the muscle as an elastic body. There may be some dispute as to the magnitude of this potential energy: there can be no doubt of its existence. The common view is that, in relaxation, the whole of this mechanical potential energy, if not previously employed in doing work, is dissipated into heat. Such a view, however, is not necessary, and one might well be led to look for a way in which the organism could avoid such an obviously uneconomical procedure. It would seem possible that part, at any rate, of the free energy of the muscle, while in a state of active tension, is used in commencing to carry out the recovery process which has later to be completed by oxidation.

The presence of such a mechanism would explain why extra energy is liberated, in shortening under a load, in proportion to the work done. The energy used to do external work is not available to assist recovery during relaxation, and the total breakdown is greater. It would explain also the converse phenomenon, viz. that less energy is liberated by the muscle when stretched during contraction: the extra potential energy provided by the stretch can cause a greater restoration during relaxation, and the total breakdown is smaller. It should not be impossible to devise an experimental test of this hypothesis.

SUMMARY.

1. Experiments are described by which the relation between heat production and length of muscle was determined, over a range of lengths from about 50 to 140 p.c. of that of the resting unloaded muscle. The same effects are found for all temperatures and for all durations of stimulus. The heat production is at a maximum, for a given duration of stimulus, at a relative length of about 90 p.c. On either side of this position it falls off considerably, along a curve which is approximately symmetrical about the vertical line through its maximum. In many

experiments, on the short side of the maximum, the heat production over a considerable range fell off in direct proportion to the length of the muscle. The relation is described also between tension developed and length. This relation also follows a symmetrical curve, with its maximum at a relative length of about 98 p.c. These positions of the maxima of heat production and tension, although near one another, are definitely not the same. At high initial extensions, of the order of 50 p.c. of the unloaded length, the heat is about 60 to 70 p.c. of its maximum value, while the tension has practically disappeared.

2. The variation is discussed of the relation between tension developed and heat produced, when the length of the muscle is varied. The ratio T/H has a maximum almost precisely at the resting unloaded length of the muscle, and falls on either side of that length along a symmetrical curve which reaches zero at about 40 to 50 p.c. of shortening or extension.

3. It is pointed out that the variation of heat production with length is determined by what may be called a "governor" mechanism in the muscle, which regulates the amount of energy liberated in response to a stimulus; while the variation of T/H with length depends upon the nature of the mechanism by which chemical energy is transformed into mechanical energy in the muscle.

4. The question is reopened of the validity of using the area of the tension-length curve, for a muscle stimulated with a shock or a short tetanus, as an indicator of the theoretical maximum work which the muscle could perform. Calling W the theoretical maximum work calculated from the T-l diagram, and H the heat production, W/H has at the resting unloaded length of the muscle and on the average a value of about 1·22. Starting from lengths greater than 100 p.c. still higher values of W/H are obtained.

5. The question is discussed, but left undecided, as to whether, in a muscle twitch, the area of the T-l curve is really an indicator of the maximum work which, in theory, the muscle might perform.

6. A mechanism is suggested of the Fenn effect, *i.e.* of the fact that more energy is liberated by a muscle when it does external work.

I am greatly indebted to Mr J. L. Parkinson for the skill and accuracy with which he has carried out the majority of the experiments described above; to the Scientific and Industrial Research Department for making Mr Parkinson's services available; and to the Royal Society for a grant to cover the expenses of the investigation.

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