

**STUDIES ON THE RELATION OF WORK AND HEAT
IN TORTOISE MUSCLE. BY JEFFRIES WYMAN, JR.**

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I. *The Problem.* Several observers recently have studied the relation of tension and work to shortening or stretching, at various speeds, in the case of voluntary muscle. A. V. Hill⁽¹⁾ and Lupton⁽²⁾ have shown that the work obtainable from human arm muscles accelerating an inertia wheel varies with the moment of inertia of the wheel, that is, with the time occupied by the shortening of the muscles. The results of their experiments could be quantitatively explained by assuming a certain maximum value for the work, corresponding to infinitely slow shortening, and by supposing that the difference between this value and that obtained in any actual shortening of finite duration was proportional to the speed of shortening. Gasser and Hill⁽³⁾ have found that the sudden release of an isolated frog's muscle during stimulation is accompanied by a fall of tension below the isometric value for the new length. The fall is followed by a re-development. They also found that stretching a muscle may lead to a temporary rise of tension above the isometric value for the new length. These workers have all suggested that these effects are to be ascribed to the "viscous" properties of the muscle, which resists a change of shape. Thus, when a muscle contracts and shortens, a certain amount of its potential energy is wasted in overcoming the resistance of the muscle substance itself, and appears as heat in the muscle instead of as external work. If the same muscle be stretched, the work done is greater than that required to overcome the elastic forces of the muscle by an amount due to the viscous and frictional resistance to deformation.

Long ago Fick⁽⁴⁾ remarked the same phenomenon in isolated frog muscle. He showed that greater tensions existed in a tetanised muscle which was being stretched than in the same muscle when shortening. He, however, ascribed the discrepancy to a greater responsiveness in the muscle being stretched. He assumed that stretching, although itself

incapable of exciting a muscle, could nevertheless increase the response to a given stimulus.

In the following paper certain aspects of the question, those relating to work, are re-opened, and an effort is made to provide evidence for a decision between the two views, that of Fick and that of the other observers mentioned above. The experiments carried out for this purpose serve also to suggest a view as to the relation between different forms of energy in the muscle system, which is discussed at the end of the paper.

II. *Method—theoretical.* It is of course obvious that there must be an element of truth in the view of Hill and his colleagues. The irreversible nature of all actual processes demands the appearance of a certain amount of heat in the shortening or stretching. The best of springs is not wholly free from viscosity and hysteresis. A muscle, different as it is from a spring, and possessed of a complex colloidal structure, suggests the possibility of very considerable irreversible effects. The question, therefore, is whether the view of Fick is to be retained in addition to that of A. V. Hill: whether the supposed physiological consequence of a stretch is to be invoked in addition to its undeniable physical effect, in order to explain the results. Our chief interest lies therefore in finding and measuring some property of stimulated muscle which may be taken as a measure of its physiological response to the stimulus. We can then measure this property of a muscle while it is (*a*) at rest, or (*b*) in process of shortening, or (*c*) being stretched, and compare the results of the measurements in the several cases. If they are the same, or if the result is greater in the case of shortening than in the case of stretching, we conclude that Fick's interpretation is disproved; otherwise it is substantiated.

One such quantity is the heat liberated by the muscle. This heat is a measure of the magnitude of the chemical changes set off in the muscle by the stimulus, and the extent of these chemical changes may reasonably be taken as what we mean by the size of the physiological response. In order therefore to test Fick's hypothesis on the basis of this criterion we have alternately to stretch and release a tetanised muscle and to compare the heats produced in the two cases. These heats, however, cannot be taken as they stand. In the case of a stretch work is done *on* the muscle by the external, stretching force; in the case of a release work is done *by* the shortening muscle on the external system to which it is attached. These amounts of work must affect the measured heat. Consider the case of a stretch where the muscle is drawn out from length (2) to length (1), work ${}_2W_1$ being done upon it. Some of this work,

namely, that done against the frictional and viscous resistance of the muscle to change of shape, will appear directly as heat. The remaining part will be used in increasing the mechanical potential energy of the muscle *qua* elastic body. This mechanical potential energy, however, may be assumed to be converted into heat at the moment of its disappearance in relaxation (an assumption to be discussed in detail at the end of the paper). In order, therefore, to obtain the true heat produced by the muscle itself during the operation we must subtract from the measured heat the work ${}_2W_1$. Similar considerations apply to the case of a release. Here the muscle shortens with a loss of potential energy, so that less heat is liberated in relaxation than would have appeared at the greater length (according to the assumption just mentioned). Part of this lost potential energy is used in overcoming the resistance of the muscle to change of shape, as in the case of a stretch, and appears directly as heat. The remaining part appears as the external work ${}_1W_2$ done by the muscle in shortening, and is lost to the muscle system. Accordingly, to obtain the corrected heat we add to the measured heat an amount of work ${}_1W_2$.

III. *Method—technical.* The muscle employed for these experiments was the *biceps cruris* of the tortoise. This is a long, uniform muscle running from the pelvis to the ankle. It serves both for locomotion and to hold the hind leg drawn in when the animal is frightened. It is chiefly useful in such an investigation as this because of its slowness of action. It may be tetanised for about 10 seconds without showing signs of fatigue. This capacity to maintain tension for such long intervals, even in the isolated condition, is to be explained no doubt in part by the extreme general slowness of the tortoise, and in part by the function of the muscle in maintaining the legs in a flexed position for long periods of time when the animal is frightened and in danger. The muscle is also useful in showing no harmful effects from even very quick stretches (2–3 cm. per sec.). In this respect it stands in marked contrast to the muscles of the frog, with which indeed it would have been impossible to carry out these experiments at all.

The measurements of heat are made according to the general methods developed by A. V. Hill, which need not be here described. The thermopile employed is of the type shown in (5), Fig. 2, p. 239. The muscle is supported by the bone attachment at the pelvic end in a glass clamp fixed to the thermopile and bearing one electrode. The flat face of the muscle lies over one set of junctions of the thermopile. Its free end is secured to a wire rod bearing the top electrode and connecting it with

the device for measuring work. The electrodes are used both for the stimulating and calibrating currents; thus the calibrating current passes through the full length of the muscle. The whole rigid structure bearing muscle and thermopile is contained in a moist chamber filled with oxygen and kept at very constant temperature inside the usual Dewar flask. The wire connecting the free end of the muscle with the device for measuring work passes out of the moist chamber through a long, narrow glass tube, as in previous cases where heat and tension have been measured together. In this way simultaneous measurements of heat and work can be made.

The device referred to for measuring work produces a continuous tension-length curve for the muscle throughout a stretch or release. It is analogous, but not similar in design, to the Blix Myograph figured in Fick's book (4), p. 23). It gives, in curvilinear coordinates, an "indicator

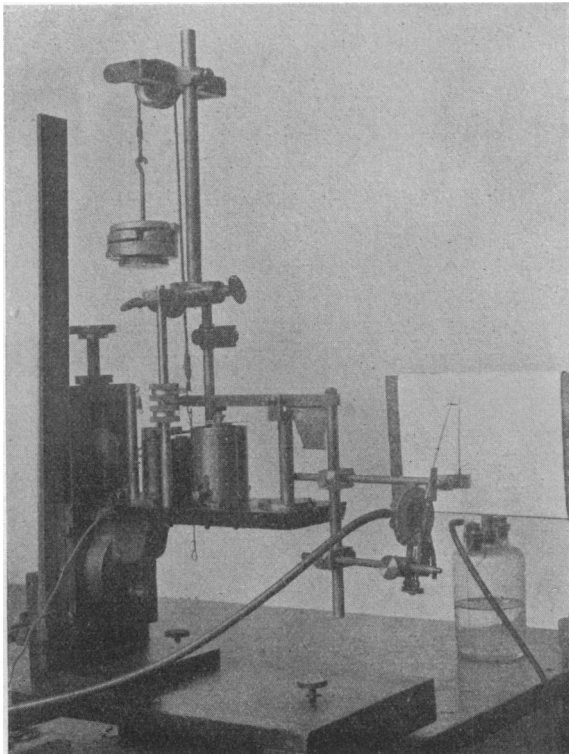


Fig. 1. Photograph of device used for writing continuous tension-length curves of muscle during shortening or stretching.

diagram" for the working muscle. In this diagram ordinates give displacements of the free end of the muscle, abscissæ tensions, and consequently the area of the diagram is a measure of the work done on or by the muscle. It is best explained with reference to the accompanying diagram (Fig. 1 *a*). The photograph (Fig. 1) will also serve to make the

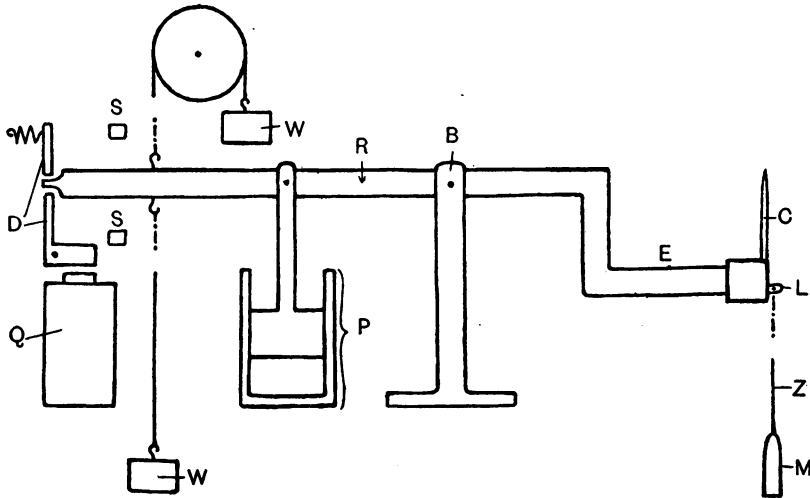


Fig. 1 *a*. Diagram of device shown in Fig. 1.

matter clearer. *L* is an isometric lever to which the free end of the muscle *M* is attached by the wire *Z*. The lever *L* is rigidly fixed, by an L-shaped metal connection *E*, to a brass rod *R*, which may be rotated about an axis *B*, perpendicular to the plane of the diagram, by suitably suspended weights *W*. The angle of rotation is controlled by adjustable stops *S*. *R* is held in an initial horizontal position, until the moment of release, by a catch *D* controlled by an electromagnet *Q*. The speed of rotation is constant, due to nearly instantaneous critical damping by the dash-pot *P*; it may be adjusted at will by the weights employed, and by a tap belonging to the dash-pot. The lever *L* is equipped with a writing pointer *C*, which is perpendicular to *R* (in the plane of the figure) when the lever is not under tension. The tip of *C* lies in the line of *R* (produced). Thus, when *R* is rotated from its resting horizontal position through a small angle, the tip of *C* describes what is very nearly a straight vertical line, provided the lever is not under tension. If, on the other hand, the tip of *C* is displaced from the position of zero tension, *R* remaining stationary, it will describe an arc of a circle of radius equal to the length of *C*, cutting this vertical line at right angles. When the

stimulated muscle under tension is stretched, or is allowed to shorten, the tip of C will thus receive both horizontal and vertical displacements, and will describe a curve like that shown in Fig. 2. Actual curves, traced by the pointer on smoked paper, are given in Fig. 3.

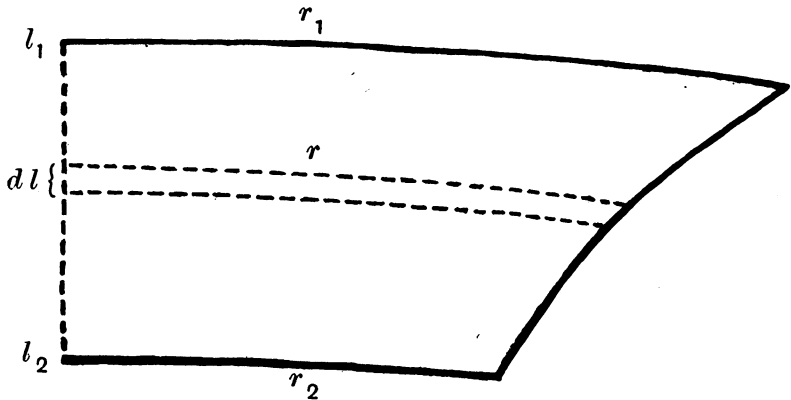


Fig. 2. Diagram of a tension-length curve: horizontally tension; vertically length of muscle.

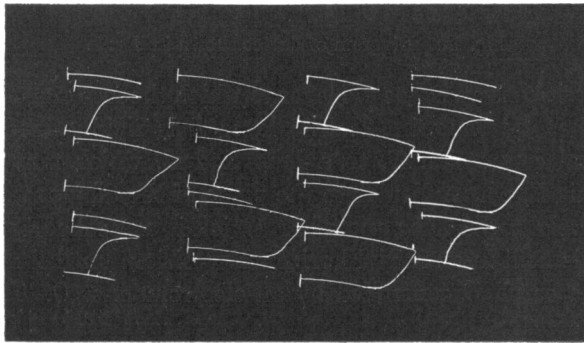


Fig. 3. Tension-length curves recorded for *biceps cruris*. Small curves are for releases; large curves for stretches. Isolated lines represent isometric contractions in the "long" or "short" positions.

That the curves really serve to measure the work may be shown as follows. Since the arcs of horizontal displacement are small, not differing sensibly from the chords for cases covered by the experiments, and since they all cut the vertical line of zero tension at right angles, they may be taken as parallel without appreciable error, and the area of the curve, closed by the line of zero tension, may be taken as nearly equal to $\int_{l_2}^{l_1} r dl$. Here dl (see Fig. 2) denotes an element of vertical displacement at any length l , and r the corresponding horizontal displacement. But dl can be shown as follows to be equal to the vertical displacement

of the free end of the muscle. Let B , C and L in Fig. 4 refer respectively to the axis of rotation of the bar, the tip of the pointer in the position of zero tension, and the long axis

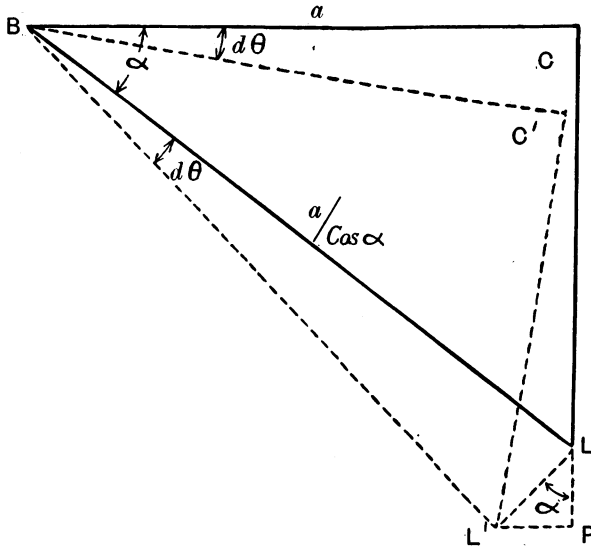


Fig. 4. Diagram of small displacement of lever.

of the spring of the lever. Let $BC = a$, and $\angle CBL = \alpha$. The triangle CBL is rigid, and moves as a whole (e.g. to $C'BL'$) when the bar R is rotated. Suppose now that R is rotated through an angle $d\theta$. Then C traces a vertical element $dl = ad\theta$, and at the same time L traces an element $LL' = \frac{ad\theta}{\cos \alpha}$. This element makes an angle α with the vertical, and has a vertical component $LP = LL' \cos \alpha = ad\theta = dl$. The free end of the muscle, being attached to L , is thus given a vertical displacement dl . Furthermore, returning to Fig. 2, r is proportional to the tension exerted by the muscle, the spring being so chosen that over the range of forces exerted by the muscle $f = Kr$, where f denotes force and K is a constant. Consequently

$$\int_{l_2}^{l_1} r dl = \int_{l_2}^{l_1} \frac{f}{K} dl = \frac{2W_1}{K},$$

where $2W_1$ is the work done by, or on, the muscle when its length changes from l_2 to l_1 .

By calibrating the spring we may determine K . Now we have seen that $\int_{l_2}^{l_1} r dl$ is sensibly equal to the area of the curve written by the tip of C , completed by the line of zero tension. Consequently by measuring this area with a planimeter and multiplying by K we obtain directly the work done by, or on, the muscle. It may be remarked that, since the length of the wire joining the muscle to the lever is great, the horizontal displacement of L will give rise to only a very slight horizontal displacement of the free end of the muscle.

In practice a light isotonic lever, as used by A. V. Hill (5), Fig. 3, p. 240) in recent measurements of heat production, was interposed between the muscle and the isometric lever, being fixed to the bar R . This was to ensure that the heat was measured (by the maximum

deflection of the galvanometer after the moment of relaxation) at the greater length of the muscle, the length at which the calibration was later carried out. Since this lever performed a complete cycle between the beginning of the stimulus and the maximum deflection of the galvanometer it introduced no additional corrections.

In an actual experiment the muscle is set up on the thermopile, as previously described, and attached to the lever *L* by the wire *Z*. It is adjusted so that its stretched length is just greater than its resting unloaded length. When this is the case the isometric heat at the greater length is nearly equal to that at the shorter length (about 7 mm. less). The existence of this approximate equality is essential to the argument. When the system has attained thermal equilibrium the point of the writing arm *C* is brought into contact with a plane surface of smoked paper on which it writes freely. At a given moment a tetanic stimulus is applied by the breaking of a short-circuit by one of the arms of a Lucas revolving contact breaker. After a fixed interval of time sufficient to allow development of maximum tension the circuit containing the electromagnet *Q* is broken by a second arm of the contact breaker, and the muscle is allowed to shorten, or is stretched, under tension and at a constant speed determined by the weights and the adjustment of the dash-pot. After the lapse of an interval great enough to allow completion of the movement the stimulus is removed by the breaking of the primary circuit of the induction coil by the third arm of the contact breaker. The reading of the galvanometer is then taken, the properties of thermopile and galvanometer being so chosen as to ensure that maximum deflection occurs only after relaxation is complete, without danger of heat having been lost by the thermopile in the interval¹.

In the meantime the pointer *C* has written the curve from which the work done by, or on, the muscle can be later calculated. Stretches and releases, as well as isometric "long" and "short" heat measurements, are made in this way in a definite order of rotation, each experiment having at least three cycles. It is of course essential to insure that the stretches and releases should always take place between the same lengths of the muscle. To allow of this the whole instrument for measuring work is mounted on a stand which can be raised and lowered by a screw adjustment. At the conclusion of the experiment the muscle

¹ The fulfilment of this condition may be tested at the end of the experiment by heating the dead muscle for various times, up to that occupied by the actual stretches and releases, by a constant alternating current. In this case the deflection of the galvanometer should be proportional to the duration of the heating up to the limit considered.

is calibrated in the usual way to allow for conversion of galvanometer readings into ergs.

An objection may be raised, based on the contention that the system of the wire and lever (Z and L) is not truly isometric, so that the curves written by the pointer do not give the works actually done by or on the muscle. Beyond doubt the lever-wire system is extensible; indeed, it may be shown by carrying out a complete cycle with it that it behaves like a very stiff spring possessed of negligible hysteresis. But precisely for this reason it follows that the errors in the measurements of work cancel one another, though the areas of the curves taken alone require corrections. Consider the case of a shortening muscle. Before release the muscle develops tension "isometrically" and does work not recorded on the diagram, since the pointer simply moves to the right. During the shortening the tension falls and the pointer moves back towards the left. At the same time the lever-wire system, relieved of a certain amount of tension, must shorten. For this reason the vertical displacement on the tension-length curve is greater than the true shortening of the muscle, and the work recorded is correspondingly too large. On relaxation the lever-wire system shortens still further, actually doing work on the muscle not recorded at all. But since the lever-wire system possesses no appreciable hysteresis, the excess work registered on the diagram and the work done on the muscle at relaxation together exactly nullify the unrecorded work done by the muscle "isometrically" before release. Similar considerations apply to the case of a stretch. The objection is thus seen to be groundless.

IV. *Experimental results.* The experiments carried out fall into two classes, those done in the spring of 1925 and those done in the following autumn. During the intervening summer the tortoises obtainable were found to be in bad condition and unsuitable for the experiments. The two sets of observations were alike in showing that the heats, measured and corrected according to the procedure described above, were unequal, the heats for the releases being clearly greater than those for the stretches. The size of the difference varied from experiment to experiment and was of the order of 30–40 p.c. for the mean values. The "isometric long" and the "isometric short" heats lay in general between the two. The data of a single typical experiment are given in Table I.

TABLE I. Results of Exp. 5, Set II.

Operation	Gross heat (10^8 ergs)	Work (10^8 ergs)	Net heat (10^8 ergs)
Shortening	107	37	144
Stretch	204	118	86
Isometric long	103	—	103
" short	123	—	123
Shortening	101	40	141
Stretch	222	120	102
Isometric long	110	—	110
" short	129	—	129
Shortening	107	36	143
Stretch	221	113	108
Isometric long	109	—	109
" short	129	—	129
Shortening	115	39	157
Stretch	224	116	108

It was thought desirable, since the muscles varied considerably according to their size and condition in the amounts of heat which they produced, to "reduce" the results so as to make them more strictly comparable. For this purpose the heats for stretch, release, "isometric long" and "isometric short" were averaged for each experiment, and the averages were then multiplied by a scale factor so chosen as to reduce the average value of the "isometric long" heat to 100,000 ergs. The results of the two sets of experiments, so treated, are given in Table II. It is easily seen that the two sets of experiments are very similar, though there is considerable variation among the individual experiments comprising each set. In order to get representative values of the different heats for the two sets, in view of the fact that the experiments of each set appeared, in the judgment of the observer, to be of various degrees of reliability, weights were assigned to each experiment, and weighted

TABLE II. Summary of experiments.

		SET I.					
		Work (10^3 ergs)		Heat, corrected (10^3 ergs)			
Exp.	Weight	Stretch	Short- ening	Isometric long	Isometric short	Stretch	Shortening
1	2	68	24	84	86	73	108
2	2	98	56	254	256	254	289
3	1	179	95	374	409	383	465
4	2	174	67	190	220	174	263
5	1	68	29	200	226	209	234
Same, reduced to 100,000 ergs for isometric long.							
1	2	81	29	100	103	87	124
2	2	39	22	100	101	100	114
3	1	48	25	100	109	102	124
4	2	92	35	100	116	92	139
5	1	34	15	100	113	104	117
Weighted mean		63	27	100	108	95	124
		SET II.					
1	2	206	62	464	435	452	495
2	5	169	78	275	311	291	383
3	5	210	118	404	441	446	525
4	3	178	87	389	389	378	470
5	5	117	38	107	124	101	146
6	5	166	62	195	225	174	281
7	5	114	47	105	110	80	153
Same, reduced to 100,000 ergs for isometric long.							
1	2	44	13	100	94	98	107
2	5	61	38	100	113	106	139
3	5	47	27	100	109	111	130
4	3	46	22	100	100	97	121
5	5	109	36	100	116	94	136
6	5	61	46	100	115	89	144
7	5	109	45	100	105	76	146
Weighted mean		72	36	100	107	96	135

means for the different heats for each set were obtained. These, together with the weights, are also given in Table II.

V. *Discussion.* It is at once evident that just the reverse of what would be expected from Fick's hypothesis is in fact the case: the test appears to be fatal to the hypothesis. To be sure it is observed that the "isometric long" and "isometric short" heats are not quite the same: the mean values for the "isometric short" heats are 7 p.c. or 8 p.c. greater than those for the "isometric long" heats. This, however, cannot possibly explain the much larger differences between the heats of "stretch" and "shortening"; so we are left with the conclusion that the physiological response, as measured by heat production, is less for a stretch than for a shortening, whereas the work, recorded by the diagram, is greater. Consequently, the difference between the works (*a*) for a stretch, and (*b*) for a release cannot be ascribed to a difference in physiological response of the muscle in the two cases; and we are constrained to fall back on the explanation offered by Hill and his co-workers, unless at least some third alternative is offered.

So much as regards work. But how are we to account for the phenomena in the case of the heats? We have just seen that the heats of shortening are always considerably greater than those of stretching. Are we to make a new assumption just contrary to Fick's assumption? We might indeed suppose that there is a regulatory mechanism in the muscle, which cuts down its response when it is being stretched and work is being done on it, and which increases its response when it is actively shortening and itself doing work. Such a supposition, however, while giving an *ad hoc* explanation of the discrepancy of the heats, is not favoured by the results in regard to the works. It is moreover unnecessary: it is easy to show that without making any such hypothesis it is possible to explain the inequality of the heats by a simple modification of our initial assumption that the mechanical potential energy appears quantitatively as heat in relaxation.

Let us suppose that when the muscle relaxes only a fraction of its mechanical potential energy is transformed into heat, the rest appearing in some other guise, *e.g.* as chemical energy (see A. V. Hill⁽⁵⁾, Garner⁽⁶⁾). Then it is clear that if we stretch a muscle a fraction only of the work done on it in increasing its potential energy will appear as heat in relaxation. Consequently, in applying our corrections to the heats for the stretches, we are subtracting too much from the observed values. Similarly, in the case of the releases we are adding too much; and we

should expect what in fact we find, that the corrected heat in the stretches is less than the corrected heat in the releases, even though the physiological response of the muscle is the same for both cases. It cannot be denied that by modifying our fundamental assumption in this way we weaken our case against Fick: we open a possible loophole of escape. Yet the matter is not serious. If we do not make this modification we are forced not only to reject Fick's view, but to accept the direct opposite. By introducing it we are enabled to explain the results without supposing that the physiological response of the muscle differs for stretches and releases; and we might conceivably go further still and insist on Fick's hypothesis. Yet such procedure not only appears highly gratuitous, but would demand, as will appear presently, an unexpectedly small value for the fraction of potential energy passing into heat at relaxation.

It is instructive to formulate the matter algebraically. For this purpose some discussion is necessary. If we stimulate a muscle isometrically for different times and plot total heat production (which here needs no correction) as ordinate against the corresponding duration of stimulus as abscissa, we get a curve which is approximately a straight

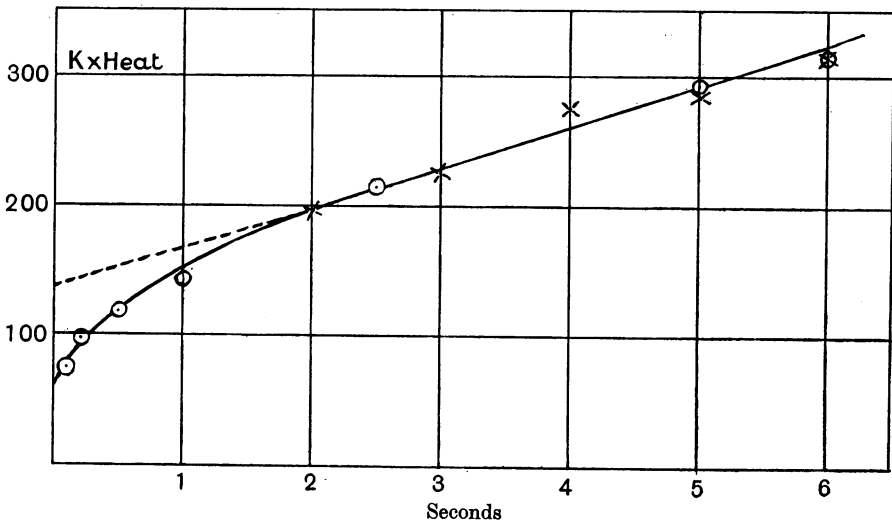


Fig. 5. Curve showing relation of total heat produced (isometrically) to duration of stimulus for *biceps cruris* at about 12° C. \odot = muscle A; \times = muscle B.

line of positive slope. Such an experimental curve for *biceps cruris* is given in Fig. 5. The equation of this line may be written $Q = A + Bt$.

Here Q is to be interpreted as the total heat produced by the muscle, A as the heat corresponding to a very short stimulus (just sufficient fully to excite the muscle), and B as the excess heat produced per unit time for a stimulus of finite duration. B is also equal to the slope of the line. Now Hill and Hartree's analyses have shown that the heat produced in a single twitch may be divided into two parts, of which one is the initial burst of heat and the other the heat given out on relaxation. We will therefore regard A as the sum of two terms like the above, and we will further identify the heat of relaxation with the disappearance of the mechanical potential energy of the contracting muscle. Thus, letting H denote the initial burst of heat, P the potential energy of the contracting muscle, and α the fraction of this energy appearing as heat at the moment of relaxation, we can write for the heat produced isometrically during a tetanus at any length l ,

$$Q = H + \alpha P + Bt.$$

Over the range of lengths used in these experiments, B (giving the slope of the curve discussed above) may be taken as independent of the length of the muscle. Its effect is in any case not predominant. Consequently if l_1 is the greater, l_2 the shorter, length of the muscle, we may write for the isometric long and isometric short heats respectively

$$Q_1 = H_1 + \alpha P_1 + Bt$$

and

$$Q_2 = H_2 + \alpha P_2 + Bt.$$

For the work of a stretch we write ${}_2W_1$, and for the work of a shortening ${}_1W_2$. These works, as recorded by our indicator diagrams, are not equal: ${}_2W_1$ is greater, ${}_1W_2$ less, than the thermodynamic work $P_1 - P_2$. In making our corrections it is the quantities ${}_1W_2$ and ${}_2W_1$ that we actually employ. Nevertheless, since the differences between the actual works and the thermodynamic work appear either in our galvanometer readings or in our work curves, and since in all our experiments the true isometric value of the tension for the final length (whether after a stretch or shortening) is always attained before relaxation, reflection will show that the effect of the corrections may be expressed in terms of the P 's. The corrected heat for a stretch then becomes

$$Q_{\text{stretch}} = H_2 + \alpha P_1 + Bt - (P_1 - P_2)$$

and that for a shortening

$$Q_{\text{shortening}} = H_1 + \alpha P_2 + Bt + (P_1 - P_2).$$

But since isometric long and isometric short heats are nearly equal,

i.e. $Q_1 \cong Q_2$, we have $H_1 - H_2 \cong -\alpha (P_1 - P_2)$. Consequently the difference ($Q_{\text{shortening}} - Q_{\text{stretch}}$) is equal to

$$2(1 - \alpha)(P_1 - P_2).$$

This quantity is positive since α is by hypothesis a fraction, and P_1 is necessarily greater than P_2 (as has been found by the experiments described above). This simple hypothesis, therefore, regarding the fate of the mechanical potential energy of the muscle in relaxation serves quite as well to explain our results as any assumption of a "governor mechanism" in the muscle.

If we know $(P_1 - P_2)$, that is, the thermodynamic work for change of length of the muscle from l_1 to l_2 , it is obviously possible to calculate $(1 - \alpha)$, *i.e.* the fraction of the mechanical energy of the excited muscle available in relaxation for chemical synthesis, etc. But, since the stretches and releases were made at nearly the same speed, we shall not incur a very large error if we take $(P_1 - P_2)$ as the mean of ${}_1W_2$ and ${}_2W_1$. Making use of these values for $(P_1 - P_2)$ we get for $(1 - \alpha)$ the results shown in Table III.

TABLE III. Values of $(1 - \alpha)$ for the various experiments.

SET I		SET II	
No. of experiment	$(1 - \alpha)$	No. of experiment	$(1 - \alpha)$
1	.34	1	.16
2	.23	2	.33
3	.30	3	.24
4	.27	4	.35
5	.26	5	.29
Weighted mean = .32 (weights as in Table II)		6	.51
		7	.49
		Weighted mean = .36 (weights as in Table II)	

It is worth noting that such a reabsorption of part of the muscular potential energy during relaxation would be of very great value to the animal. This would be particularly the case for animals like the frog, whose locomotion is effected by twitches of the leg muscles rather than by any considerable shortening. Indeed very seldom can muscles at work in the animal be supposed to shorten to the point where the isometric tension falls to zero; there must accordingly be a very considerable waste when, on relaxation, the potential energy of the contracted muscle passes over into heat. Any provision for the utilisation of even part of this energy would be valuable.

It is interesting to compare the magnitude of such a restoration—assuming its existence—with that due to aerobic recovery as estimated by

Hill and Meyerhof. The total mechanical potential energy of a tortoise muscle at the resting unloaded length, reckoned from the work diagrams obtained in these experiments, is approximately equal (within about 10 p.c.) to the isometric heat for this length. This is in accord with previous observations on the relation between anaerobic heat and theoretical work. Thus, at the resting length of the muscle the amount of mechanical potential energy available for re-synthesis of breakdown products during relaxation is about 33 p.c. of the anaerobic heat production. Now Hill and Meyerhof⁽⁷⁾ have shown that in aerobic recovery, of every 1 grm. of lactic acid set free in the initial phases of contraction, about 0.8 grm. is restored to its initial condition, the remainder being oxidised; so that the energy absorbed in aerobic recovery is about 80 p.c. of that given out in the preceding anaerobic breakdown. Consequently, the effect of the restoration discussed above would be, at the resting length of the muscle, between one-half and one-third of that described by A. V. Hill and Meyerhof, between one-third and one-quarter of the whole.

According to the above calculations about 36 p.c. of the potential energy of the contracting muscle is restored as chemical energy during relaxation: it is perhaps pertinent to note that of the energy liberated by oxidation in recovery about $\frac{80}{80+150}$, i.e. 35 p.c., is stored as chemical energy in the re-synthesis of lactate into glycogen.

SUMMARY.

1. A maximally tetanised skeletal muscle exerts a greater force while being stretched, a smaller force while shortening, than during an isometric contraction. This phenomenon has been attributed by A. V. Hill and his co-workers to irreversible physical factors such as viscosity; by Fick, however, who was familiar with the same fact, it was ascribed to a change in the "physiological response of the muscle" evoked by the actual process of stretch or release. Experiments have been undertaken and are here described to decide between these alternative views. These experiments employ as the criterion of the "physiological response" the total energy liberated by the muscle.

2. When the *biceps cruris* muscle of the tortoise, undergoing a 4-6 seconds tetanus, is allowed to shorten, or is stretched, between two lengths, the work done on it during the stretching is considerably greater than that done by it when it shortens, to an extent depending on the speed of movement. The corresponding total energies, on the other hand (heat - work and heat + work respectively), bear just the opposite relation, the energy liberated during a stretch being 30-40 p.c. less than

that liberated during a release. Fick's hypothesis is consequently discredited: the greater work is not associated with a greater liberation of energy—rather in fact the reverse. We are left with the necessity of finding a physical explanation of the phenomenon.

3. In carrying out the test described above it was assumed that the potential energy undeniably existing in the contracting muscle is degraded quantitatively into heat during relaxation. This assumption is not necessary: if we suppose that about one-third of this energy is reabsorbed during relaxation in helping to effect those chemical re-syntheses which are completed in oxidative recovery, then we are able quantitatively to explain the phenomena without having recourse to any hypothetical "governor mechanism" in the muscle.

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