

The effect of load on the heat of shortening of muscle

BY A. V. HILL, F.R.S.

Department of Physiology, University College London

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During the process of shortening against a load a muscle liberates extra energy as work and as heat. The methods used in measuring the extra heat due to shortening have been critically examined and are described in some detail.

The constant α of the heat of shortening depends on P , the load lifted, according to an average linear relation for frog sartorii at 0 °C,

$$\alpha/P_0 = 0.16(\pm 0.015) + 0.18(\pm 0.027)P/P_0,$$

P_0 is the maximum force developed at constant length.

The constant α of the heat of shortening can no longer be regarded as the same quantity as the constant a of the characteristic equation $(P+a)v = b(P_0-P)$, relating velocity (v) of shortening to load; but α/P_0 and a/P_0 , being always of the same order of size, are almost certainly connected in some way. The original (Hill 1938) conclusion that α and a were the same was probably due to a persistent error in the measurement of α , making it about 30% too great.

In the original (Hill 1938) hypothesis the rate of extra energy liberation $(P+\alpha)v$ during shortening was taken to be proportional to (P_0-P) , i.e. to the gap between the maximum force a muscle could exert and the actual load it had to lift. In its simple form this idea must be abandoned; but a modification is suggested which still provides the characteristic equation and supplies a connexion between α and a .

The assumptions made in calculating the heat of shortening are examined; to regard it simply as a change, produced by shortening, in the maintenance heat would make little difference. Further advances in the chemistry of contraction may allow the facts to be expressed in more concrete terms.

INTRODUCTION

In the original description (Hill 1938) of the heat of shortening of muscle, during after-loaded isotonic contractions produced by a tetanic stimulus, table 4 (p. 175) showed a slight tendency for the extra heat produced by shortening through a given distance to be somewhat greater with greater loads. But with the accuracy possible at that time the difference was hardly significant and the general conclusion was drawn that 'as a first approximation at least we may conclude that the heat for shortening is independent of the load, the speed and the work'. It was added, however, 'it may be that the difference... is genuine but in any case it is very small when compared with the great difference in respect of mechanical work'. It is not in fact so small, as the present experiments have shown.

The same conclusion was drawn 11 years later (Hill 1949) for the case of single maximal twitches. In the experiments then described the whole of the work which the muscles could do was taken out of them by a special ergometer, and return to the initial length occurred under a small constant load. A fixed amount of shortening was allowed and in spite of considerable variation of the work performed (with different loads) the heat produced was constant. But 4 years later still, when the case of a single twitch was re-examined (Hill 1953*b*), it was found that with a constant amount of shortening the performance of more work was accompanied by the production of more heat. The work was varied by altering

the speed of a Levin-Wyman ergometer, and again all the work the muscles could do was taken out of them; as in 1949 they returned to their original length under a small load; there was no relaxation heat. The extra heat due to the performance of extra work was about 25% of the work.

Again Aubert (1952; 1956, p. 248), working with tetanic contractions and an ergometer rather similar to that of Levin & Wyman (1927), found that at lower speeds the extra heat produced by shortening a given distance was greater than at higher speeds. With an isotonic lever the load is the independent variable, with the ergometer the speed of shortening is; a lower speed corresponds to a higher load, and with either more work is performed. Thus Aubert's experiments in 1952 confirmed the indication of mine in 1938, but appeared more decisive. It seemed likely, therefore, that the constant of the heat of shortening does vary with the load, or with the speed of shortening. Finally, Abbott & Lowy in a short note (1956) stated that in the muscles of *Mytilus* and *Helix* the constant of the heat of shortening (under a small load?) was not the same as the constant a of the force-velocity relation.

In none of these experiments, however, was the information detailed or accurate enough to justify a quantitative statement of how the constant of the heat of shortening varies—if it does—with load or speed. The question was important because the constant a of the characteristic equation between load P and velocity of shortening v , in isotonic contractions, appeared in the 1938 experiments to be the same as the constant a of the heat of shortening as measured by thermal methods. Indeed the existence of the relation $(P+a)v = (P_0-P)b$ was originally noticed during experiments (Hill 1938, p. 176) in each of which a was first 'determined by thermal measurements, and with v read off directly from the mechanical records $(P+a)v$ was plotted against P ' and shown to give a straight line. It came, therefore, to be believed that the constant a of the heat of shortening measured thermally was the same as the constant a derived from mechanical measurements by means of the characteristic equation.

It was obvious, however, that the equation could yield only a single value of a ; if thermal measurements showed that a varied with the load the two constants could not be the same. That was the origin of the present investigation. It is best introduced by a critical discussion of a single simple experiment.

In order to save confusion, in what follows the constant of the heat of shortening obtained by thermal measurements will be called α ; while the constant derived from mechanical measurements, via the characteristic equation, will be called a . Although α and a are not the same thing they are always of the same order of size and this led to an attempt to find some relation between them, as described below under 'Discussion'.

ARGUMENT

In figures 1 and 2 are the results of an experiment made at 0 °C on a pair of sartorii of a frog (*Rana temporaria*). Contractions were isotonic with an initial load of 2 g and after-loads of 0, 16.1, 33.8, 51.4 and 69.3 g, respectively. A final contraction was isometric at the same initial length. Details of the muscles were: $l_0 = 3.1$ cm, $M = 0.199$ g. The amount of shortening permitted in the isotonic

contractions was 0.7 cm, from about 0.2 cm above to 0.5 cm below l_0 . The muscles were in a nearly steady state; contractions were at regular intervals of about 13 min and those illustrated in figure 2 were the continuation of a sequence which started 90 min earlier. Each stimulus consisted of alternating condenser discharges, $12\frac{1}{2}$ /s each way, and lasted beyond the end of the curves shown.

Each record of heat production was analysed fully throughout, to allow for time-lag due to thermopile and galvanometer. Heat and shortening were recorded on the same photographic paper by a double-beam cathode-ray tube. Fuller details are given below under 'Method'.

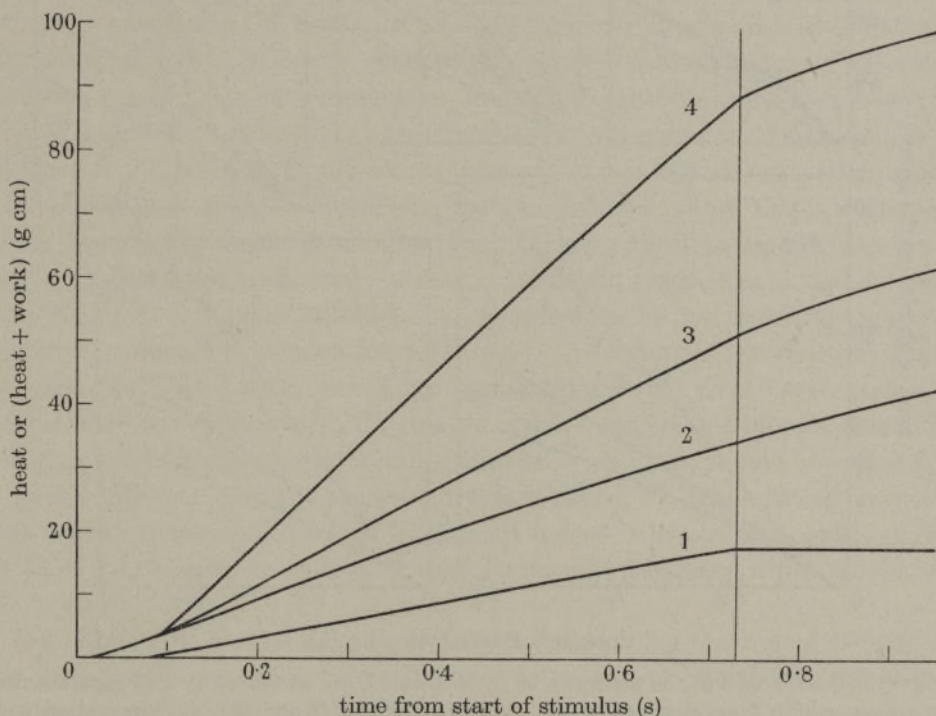


FIGURE 1. Comparison of the heat, or (heat + work), produced in an isotonic contraction with 7 mm shortening, with the heat produced in an isometric contraction. (1) shortening, (2) heat in isometric contraction, (3) heat in contraction with shortening, (4) (heat + work) in the contraction with shortening. The vertical line at 0.736 s shows the moment when shortening ended. Load 53.4 g. Details are given in the text.

In figure 1, on a larger scale than figure 2 in order to provide more detail, the bottom line (1) shows 7 mm shortening of the muscles under a total load of 53.4 g. Curve (2) gives the heat in an isometric contraction in the 'long' position. Curve (3) gives the heat during the contraction with shortening. Curve (4) gives the total energy (heat + work) during the shortening; it was obtained by adding the work calculated from line (1) to the heat in curve (3). The curves involve no assumptions, they merely record what happened.

Figure 2 allows a comparison of the results obtained in five isotonic contractions, all of 7 mm from the same initial length, of the same pair of muscles under different loads. For simplicity the curves of shortening are omitted; but arrows show the

beginning and end of shortening, which was nearly linear as in figure 1. From below upwards the curves in each picture represent in order (*a*) the heat in the isometric contraction, (*b*) the heat when shortening was permitted, and (*c*) the (heat + work) in the latter case. Under the smallest load the work was very small, so the two upper curves nearly coincide; but they both differ considerably from the curve for an isometric contraction. The scales of energy, and of time, are the same for all the curves. These curves represent the 'Fenn effect' in its simplest

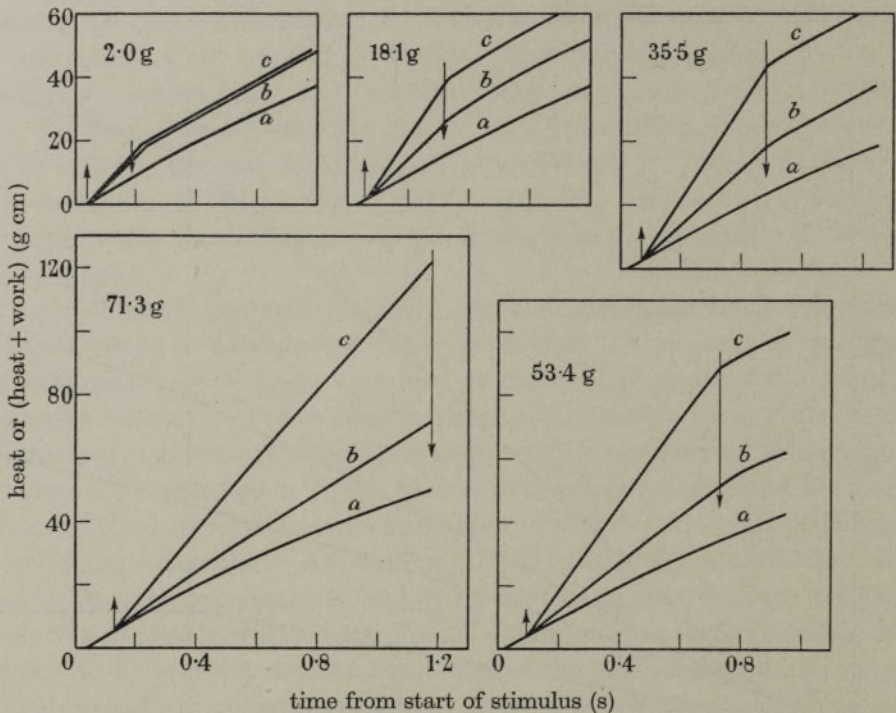


FIGURE 2. Comparison of the heat, (*b*), or (heat + work), (*c*), produced in five separate contractions with 7 mm shortening, with the heat produced in an isometric contraction (*a*) at the same initial length. 2.0 g initial load, various after-loads, total load shown in each diagram. The scales of energy and time are the same in all. The beginning of shortening is indicated by an arrow pointing up, its end by an arrow pointing down.

form during an isotonic shortening, without the complications which Fenn (1923) had to face in the days when the only way of measuring the heat was as the maximum deflexion obtained after contraction and relaxation were complete.

The curves of figures 1 and 2 show qualitatively, beyond doubt, that a shortening muscle gives out extra energy, both as work and as heat. When the load is small, the work also is small and nearly all the extra energy appears as heat. With large loads the greater part of the extra energy appears as work. But unfortunately the simple procedure of this experiment does not lend itself to an unambiguous estimate of the extra heat due to shortening. 'Extra' compared with what? With that in the isometric contraction? But it is known that during an isometric contraction the rate of heat production falls off, rapidly at first and then more slowly as stimulation continues, finally dropping to a constant level but only after several seconds (5 to

7 s in frog sartorii at 0 °C: Hill & Woledge 1962, p. 320; Aubert 1956; Abbott 1951). Can this changing rate be regarded as that associated with the maintenance of activity, and can it be supposed to persist unaltered when the muscles are allowed to shorten? Or should the constant rate finally attained after several seconds be regarded as the 'base line' from which the heat rate due to shortening itself can be calculated? This appears to be Aubert's conclusion (1956, p. 248) expressed in his words: 'L'effet thermique du raccourcissement paraît donc bien se greffer sur la production "stable" de chaleur de maintien, sans intéresser la fraction labile de la thermogénèse.' If so, the heat production during the earlier stages of an isometric contraction, as in figures 1 and 2, would provide quite an unsuitable 'base-line' for use in calculating the heat of shortening proper from the observed heat with shortening. Its rate at first is considerably greater than that during the stable condition reached several seconds later. Subtracting it from the rate of heat production during the contractions with shortening would leave too small a residue for the heat of shortening. Should some intermediate rate be assumed? Then what?

Such ambiguities are so formidable that, in order to reduce them, the experiments were better made in another way, namely, by allowing the muscles to shorten only after a preliminary period of isometric contraction, long enough to allow the tension to reach its full value. In principle the best procedure might be to allow the muscles to shorten only after (say) 7 s of stimulation at constant length, by when the final steady rate of heat production would have been reached (if fatigue were not coming on). But the purpose of the present inquiry demanded that a number of isotonic contractions, with different loads, should be undertaken in each experiment; and if every contraction lasted 7 s, with various isometric contractions thrown in, it would be difficult indeed to maintain a constant condition of the muscles throughout. A compromise was necessary, which is described below under 'Method'.

The effect, however, of these difficulties in interpreting the curves of figures 1 and 2 should not be exaggerated; it is not so great as to invalidate the general conclusions to be drawn from experiments made in this way. The following calculation illustrates this. In each of the five diagrams of figure 2 the difference between heat with shortening and heat isometric was read off at a moment 0.2 s after the end of shortening, by when the difference had become nearly constant. This heat difference (in g cm) was divided by the distance shortened (0.7 cm) to give the constant α of the heat of shortening. The results are shown in table 1. If α/P_0 is plotted against P/P_0 (where P was the load and $P_0 = 110$ g was the full isometric tension) quite a good linear relation is obtained, namely $\alpha/P_0 = 0.105 + 0.33 P/P_0$. This illustrates, perhaps in rather exaggerated form, the dependence of α on the load P . The constants of the equation are not, in fact, very different from those found in one of the experiments, used later to provide a mean relation between α/P_0 and P/P_0 ; and these experiments were made by a more sophisticated method. The values of α in table 1 cannot well be too great, for it is hard to suppose that the 'true' maintenance heat rate was *greater* than the heat rate during the early stages of an isometric contraction. It is pretty safe to regard them as minimum values for the muscles used.

There are other difficulties of experimental procedure and calculation, particularly those due to variation of the isometric heat rate with muscle length. These are considered under 'Method' below. They are not as important as the fundamental one of what to choose as a 'base line'.

TABLE 1. CALCULATIONS FROM FIGURE 2

For definitions and details see text.

load P (g)	2.0	18.1	35.8	53.4	71.3
P/P_0	0.018	0.164	0.325	0.485	0.648
heat difference (g cm)	7.6	12.9	16.7	19.3	[23.8]
α (g)	10.9	18.4	23.9	27.6	[34.0]
α/P_0	0.099	0.167	0.217	0.251	[0.309]

(In the contraction under 71.3 g the stimulus ended shortly after the moment when shortening ended, and the curve was not continued; the heat difference therefore was read at the end of shortening and 2.3 g cm was added, which is the increment after 0.2 s inferred from the heat increment under 53.4 g load.)

METHOD

The methods used were those normally employed, but with special precautions to ensure accuracy.

Muscles

The sartorii of *Rana temporaria* were used, from a single batch of frogs delivered early in November. They were kept in glass jars in grass and earth, in a cold store at about 4 °C; they remained completely quiet and showed no wasting for 3 months. This is much better than putting them in a tank with running water, which keeps them unnecessarily active, even at 4 °C. The muscles were exceptionally strong and usually maintained their performance throughout a long experiment; the frogs must have been well fed and treated before delivery, since their muscles showed the unusually high solid content (dry weight) of about 20.5 to 21.5%. Their 'standard length' l_0 was generally about 3.1 cm and the weight of a pair was usually 0.18 to 0.25 g; the average thickness of each in the region on the thermopile was 0.7 to 0.8 mm.

Temperature

The temperature was always 0 °C, maintained in a large vacuum flask filled up to the top with a mixture of water and small lumps of ice, strongly stirred with a stream of bubbles. Trial with a sensitive thermometer showed that the temperature was constant throughout the mixture to within 0.001 degC.

Stimulus

The stimulus consisted of alternating condenser discharges, usually 15 V 0.1 μ F, delivered at the electrodes e_1 , e_2 shown in figure 3 below. It was well above maximal. The period of the complete cycle (one shock each way) was either 0.08 or 0.12 s; the frequency was 'locked' to the mains. All records were made with 50 c/s dots, obtained by modulating the beams of the cathode-ray tube; the individual shocks occurred at every second or third dot. The stimulus was continued for a few tenths of a second after shortening was complete.

Ringer's fluid

The Ringer's fluid contained (mM): NaCl 115.5, KCl 2.5, CaCl₂ 1.8, phosphate 3 or 4; its pH was about 7.1. When the muscles had been mounted on the thermopile the metal cover of the latter was put on and 120 ml. of Ringer's fluid was introduced. Low on the outside of the cover was attached a glass chamber into which the solution fell. Oxygen was turned on and forced the fluid up around the muscles. They were left in the solution with the oxygen running for some time before stimulation and recording began. When the oxygen was stopped the solution fell and left the muscles in moist oxygen.

All recording was done with the muscles in oxygen; but as soon as a record had been made the oxygen was turned on again and drove the Ringer's fluid back. Some 6 or 7 min before the next stimulus the oxygen was stopped and the fluid ran out. This periodic washing with Ringer's fluid helped to maintain a constant performance of the muscles, particularly if stimulation was done at regular intervals so that the muscles got into a nearly steady state.

Mechanical recording

The shortening was recorded by means of a very fine rheostat (a 'displacement transducer' by Langham Thompson & Co) which operated one beam of a cathode-ray tube. The rheostat was driven either by an isotonic lever or by the main arm of a Levin-Wyman ergometer. With the ergometer a little 'indicator diagram' (force against distance, see figure 7 below) could be made by a very stiff lever writing on a smoked plate. From this the tensions developed before and after shortening could be read, and the work done could be calculated.

For reasons given in the preceding section, it was not possible without ambiguity to measure the heat of shortening, and its variation with load, when the muscles were allowed to shorten freely from the start. It was necessary to release them later, after the tension in an isometric contraction had developed. For this purpose a quick release mechanism was required. With the Levin-Wyman ergometer this is standard equipment. With the isotonic lever an electromagnet was used, the armature of which prevented the lever from moving until the current was broken by the opening of a key. The armature was then dragged down by a strong spring. The elastic energy developed in the undamped series-elastic component of the muscles, and in the connecting chain, during the isometric contraction which preceded release, was absorbed in accelerating the armature; it was not transferred to the muscles. But the contractile component of the muscles had too low a maximum speed of shortening to do any appreciable work on the rapidly moving armature. The work it did later was used in lifting the load on the lever.

Galvanometer

The galvanometer which recorded the current produced in the thermopile by temperature changes in the muscles was of the usual rapid type, with photoelectric amplification which operated one of the beams of the cathode-ray tube. In order to allow for delay due to inertia and damping, the shape of its deflexion

was determined for a current rising uniformly to its full value in a time equal to the interval taken for analysis. This was then embodied in a set of 'factors' for use with a calculating machine.

Thermopile

The accuracy of the experiments described in this paper depends critically on the characteristics of the thermopile. It is necessary, therefore, to set out the rather stringent requirements and to discuss whether the present instruments meet them.

The essential conditions for making accurate measurements, and an accurate resolution in time, of the heat produced when muscles are allowed to shorten, are as follows.

(1) There must be no significant temperature gradient along the frame which carries the thermopile.

(2) The active part of the thermopile must be fully 'protected', so that no parts of the muscles come on to it, during shortening, which were not subjected previously to exactly the same thermal conditions (heat loss, etc.) as the parts already on it (see Hill 1937, p. 126).

(3) The thermopile must be very thin, so that the muscles share their heat with it rapidly.

(4) The thermopile must be smooth, so that the muscles can shorten without friction.

(5) The thermopile must be flat, so that pools of liquid do not exist between it and the muscles.

(6) The thermopile must be well insulated, so that no significant current (due to differences of electrode potential) flows between its metallic elements along the muscles; otherwise movement might cause changes of current in the galvanometer.

The thermopile (D1) used throughout this work was constructed by A. C. Downing and was described by Abbott, Aubert & Hill (1951). It is shown in figure 3, with a pair of muscles in position. It has two similar parts, 'pelvic' and 'tibial', which can be used separately or together as required; in the present investigation only the 'pelvic' thermopile was used, the first active couple of which is *c*, the last *d*. These are connected to the galvanometer by the wires *g*. To the right of *c* are two dummies to help to provide thermal 'protection'. The 'tibial' thermopile to the left of *d*, including its two dummies, provided ample thermal 'protection' (see below). The muscles were fixed by holding the pelvic bone in a clamp with two screws pressing on either side into the acetabulum (*a*). A thread (shown to the left) joined the tibial tendon to the chain going to the mechanical recorder. The 'pelvic' thermopile gave (at 0°C) a thermo-e.m.f. of 877 $\mu\text{V}/\text{degC}$.

The central electrode described in 1951 was not used, it was insulated; stimulation was between the flat platinum electrodes e_1 , e_2 at the ends. A thin platinum wire *w* had been inserted between the side arms in the plane of the thermopile plate, about 2.7 mm below (i.e. to the right) of electrode e_2 . This was originally used to lead in a heating current, when a measurement of the coefficient of heat loss was required; but it was found also to serve as a useful guide in setting the muscles accurately.

The length of muscle lying on the active thermo-elements from c to d was about 8.5 mm; this is the most uniform region of the muscles. The sheet of tendon joining the muscles to the pelvic bone is shown shaded in figure 3. The length of muscle capable of shortening, between the tendon and the last active thermocouple d , was about 11.5 mm. The length of the protecting region from d upwards (i.e. to the left) was 11.5 mm.

With the arrangement shown in figure 3, with a pair of muscles 32 mm long shortening 7 mm at their tibial ends, the contractile 11.5 mm to the right of the last active couple d would shorten to 9 mm, so bringing 2.5 mm of the thermopile into contact with muscle coming from the left of d . Before contraction this 2.5 mm of muscle was 3.2 mm long and 3.2 mm is only 28% of the length of the protecting region; so the protection seems perfect.

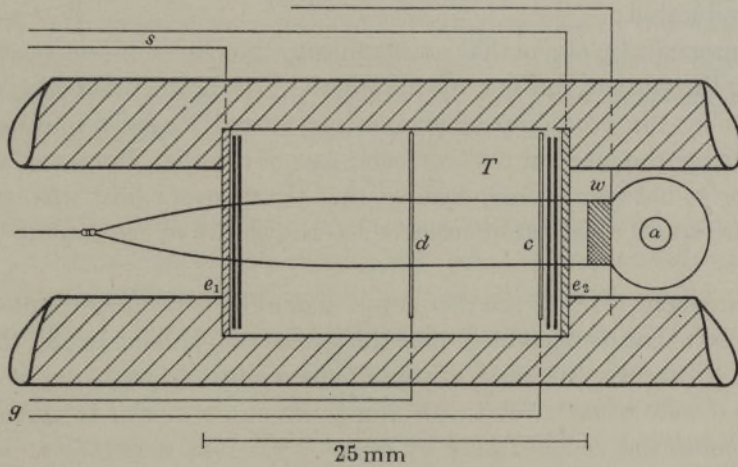


FIGURE 3. The thermopile as used with a pair of sartorii 32 mm long from tendon to tendon. The pelvic tendon is shown shaded, the tibial tendon was connected to a thread which joined a chain going to the mechanical recorder. The active thermopile, with 20 thermocouples, is T ; its first and last thermocouples are c and d , which are connected to the galvanometer by the wires g . The 'protecting' region is from d to the last 'dummy' thermocouple shown on the left. The stimulating electrodes e_1 and e_2 are flat strips of platinum in the plane of the thermopile plate; they are connected by the wires s to the stimulator. The platinum wire w was used as a guide in adjusting the muscles; it lay in contact with the pelvic bone between the tendons. The bone was held by a clamp, not shown, with screws going into the acetabulum a . Two dummy couples are just to the left of electrode e_2 .

The velocity of shortening at the last active couple d , calculated from the dimensions, was initially 36% of that at the tibial tendon, at the first active couple c less than 10%. So the average velocity on the active thermopile was only 23% of the velocity measured externally. In the present experiments the greatest and least velocities of shortening recorded were about 5.0 and 0.6 cm/s, respectively, which correspond to average velocities on the active thermopile of 11 and 1.4 mm/s.

The requirement (1) above that no significant temperature gradient should exist along the frame of the thermopile was tested by fixing thermo-junctions

5.5 cm apart, above and below the thermopile proper. The cover was put on and the instrument was sunk in the thermostat, well stirred in the usual way. A steady state was finally attained with the top junction 1.1×10^{-3} °C warmer than the bottom. This was about 2×10^{-4} °C/cm, so during 7 mm shortening the last (left hand) 2.5 mm of the active thermopile might have had a portion of muscle coming on to it about 3.2×10^{-5} °C hotter, on the average, than what was originally there. The extra heat due to shortening 7 mm produces a rise of temperature of the order of 2×10^{-3} °C, so the error due to a standing gradient of temperature in the frame was negligible. The observed gradient was presumably due to a small leak of heat along the wires and metal tube connecting the instrument to the room which was at a temperature 20 °C higher. These wires and tube also were immersed in the ice/water mixture, but a small leak of heat might still occur. If it were large enough to matter it could be reduced by using thinner wires and a tube of low thermal conductivity.

The requirement (2) above that no significant differences of temperature should occur along the muscles was met by the length of the protecting region referred to above; also by the procedure of introducing stirred Ringer's solution into the chamber during the interval between each pair of records. Moreover, an interval of 13 min or so between stimuli ensured that the recovery heat was largely completed before a new contraction occurred, so any source of heat on the thermopile was small.

The requirement (3) that the thermopile should be extremely thin was already met by the fact that its equivalent half-thickness is only about $15 \mu\text{m}$; that is, each muscle has to warm a thickness of thermopile equivalent to $15 \mu\text{m}$ of itself. The muscles used were usually 700 to 800 μm thick, so the rise of temperature when they contracted was reduced only by about 2%. It is true that an epimysium exists on the surface of the muscles, which is roughly $5 \mu\text{m}$ thick, and there might be 1 or 2 μm of Ringer's solution between the epimysium and the thermopile. The total thickness therefore to be warmed by each muscle might be equivalent to 21 or 22 μm of itself, which was less than 3%.

The requirement (4) that the thermopile should be smooth is met by the fact that each face is covered with a continuous sheet of mica. It has been suggested that rapid movement of a muscle over the mica could waste a lot of mechanical energy in overcoming the viscosity of the intervening layer of Ringer's solution. The viscosity of Ringer's solution at 0 °C is about 0.018 poise, and it can be calculated that the work dissipated in overcoming the viscosity of a layer of Ringer's fluid 1 μm thick between muscles and mica is very small. With the highest velocity of shortening recorded in the present experiments (5 cm/s at the tibial tendon), and with 7 mm shortening there, the work dissipated in the region of the thermopile came to only 24 ergs, or 0.024 g cm. From the mean relation, referred to below, between the heat of shortening and the load, a typical value of the extra heat associated with shortening 7 mm against a small load would be about 18 g cm. In the 8.5 mm of the shortened muscle lying on the active thermopile the extra heat would be about 8.5/25 of the whole, or 6 g cm. This is 250 times as great as the heat just calculated as due to viscosity. Moreover, an extreme example has

been taken. With a lower velocity of shortening under a greater load the heat due to viscosity would be proportionally less, while the heat of shortening would be greater.

The requirement (5) that the thermopile must be flat was met long ago by Downing in its construction (Hill 1937, Appendix III by Downing). No pools of liquid could exist between the mica and the muscles, unless the latter were very carelessly dissected and had chunks of loose tissue on them. The danger (6) of galvanic effects is obviated by the very high insulation resistance, usually 100 M Ω or more, between muscles and thermopile.

Analysis of records

All the results given here were derived by numerical analysis of photographic records, to allow for time-lag in galvanometer and thermopile. This analysis was seldom done in the past, it involves a lot of numerical labour; but it sharpens the pictures obtained and improves the accuracy, particularly when changes are rapid as in shortening under small loads. It ensures that heat, shortening and work really correspond in time.

The 'base-line'

The measurement of the heat of shortening necessarily involves the use of a 'base-line'; by definition, the shortening heat is the difference between the heat produced when shortening occurs and that produced in a *similar* contraction without shortening. In the section entitled 'Argument' above, with isotonic contractions in which shortening occurred early, i.e. as soon as the muscles could lift the after-load, it was shown that the early phase of an isometric contraction could not properly be regarded as 'similar'. For that reason it was better to employ a quick release from a previously isometric contraction, the muscles being released only at a time by when their tension had been fully developed. The continuation of that isometric contraction, obtained by another stimulus, provided the 'base-line' for the contraction with shortening.

The effect of muscle length

The rate of heat production during a maintained isometric contraction varies with the length of the muscle. In the neighbourhood, however, of the standard length l_0 the variation is small. According to Abbott (1951, figures 2, 3) the rate is practically constant over a range of lengths from 10% above l_0 to 15% below. An examination of the numbers in table 16 of Aubert (1956) yields about the same result. In the experiments reported in this paper the shortening was usually 7 mm, sometimes less, in muscles with l_0 about 31 mm. In each experiment, records of the heat in isometric contractions were made at several lengths, and the initial length l was usually successfully chosen so that the heat production was nearly the same at the various lengths through which the muscles passed during shortening. The heat produced in an isometric contraction at length l could then be taken as 'base-line' for the contractions with shortening from l as initial length.

Calculation

In long experiments, such as these necessarily were, the response of the muscles usually altered somewhat during their course, in size rather than in character. In a contraction with release at (say) 0.6 s the first 0.6 s was isometric. When the ordinates of the curve of heat production during this 0.6 s were not quite the same as those of the chosen isometric contraction, the ordinates of the latter could be multiplied by a factor which made them equal over the period before shortening began. This factor was applied throughout to the ordinates of the curve of isometric heat production.

The ordinates of the curve, so adjusted, were then subtracted from those of the curve with shortening, and the difference was analysed in the usual way.

The characteristic equation

If the constant α of the heat of shortening had proved to be the same with different loads it would have been necessary to compare it with the constant a of the equation $(P+a)v = (P_0-P)b$ relating speed of shortening to load. Since, as will be shown under 'Results', α varied considerably with load, such a comparison was unnecessary. Moreover, in order to obtain the value of a accurately a number of extra records would have had to be made in the upper range of loads; and these would have put an additional strain on the constancy of performance of the muscles. Of course P_0 was measured, usually several times, in each experiment, and the results were expressed in terms of α/P_0 .

The range of loads

The procedure adopted depends on the relations shown in figure 4. There the broken line gives the velocity of shortening as a function of load calculated from the equation $v/b = (P_0-P)/(P+a)$, with $a/P_0 = 0.25$, a usual value. The full line shows the ratio (rate of shortening heat)/(rate of maintenance heat) calculated from the quantities and equations given in the following paper (Hill 1964*a*). For this also a/P_0 was taken as 0.25; but the curve was found to be nearly the same with other values of a/P_0 .

The weakest link in the argument and calculations by which the heat of shortening is derived lies in the choice of a suitable 'base line'. When the rate of the shortening heat was large compared with that of the maintenance heat (as with smaller loads and higher velocities of shortening) an error in choosing the 'base line' would have a small effect. When the rate of the shortening heat was small compared with that of the maintenance heat (as with greater loads and lower velocities) a false choice of the 'base line' or its variation with time or muscle length would have a large effect. More accurate results therefore were likely to be obtained in the lower range of loads. (There is one reservation to this: with the smallest loads and therefore the highest velocities the technical problem of analysing the records becomes more difficult and the results are not so certain.)

This was realized already in the earliest work on the heat of shortening. In Hill (1938, table 3) it was noted 'for the determination of a [now α], the load lifted

was usually small'. If the constant α of the heat of shortening had been independent of the load (as was then thought) it would have been easier and more accurate to work in the lower range of loads, say $P/P_0 = 0.1$ to 0.2 . But since α was found to vary considerably with the load, it was necessary in the present experiments to use greater loads as well as smaller ones, in order to study the variation. Nevertheless, the load adopted was never so large, nor the speed of shortening so low, that shortening took more than 0.8 s. This gave a sufficient range, and reduced the possible error due to uncertainty of the 'base line'.

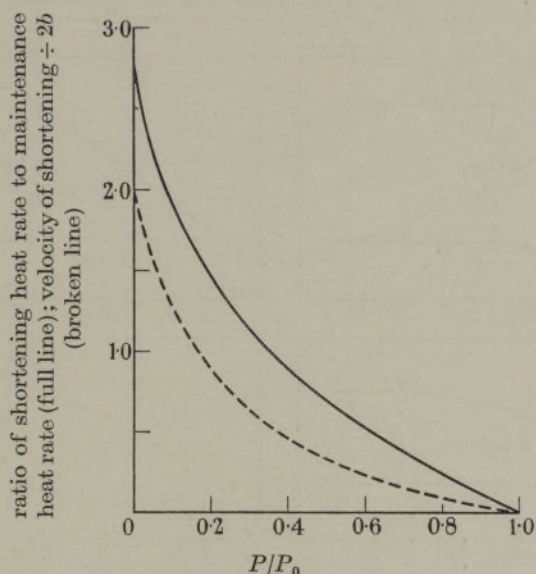


FIGURE 4. To show: (full line) the ratio of the shortening heat rate to the maintenance heat rate, during isotonic contractions with loads from $P = 0$ to $P = P_0$; (broken line) the velocity of shortening for the same loads. Calculated as described in the text.

RESULTS

The four upper curves of figure 5 give the extra heat produced during 7 mm isotonic shortening under various loads given by the numbers in the several diagrams. The four lower curves give the shortening. The extra heats were respectively 18.4 g cm, 21.0 g cm, 24.2 g cm and 26.4 g cm, so the values of α (obtained by dividing these by 0.7 cm) were 26.3, 30.0, 34.6 and 37.7 g. The standard length of the muscles was $l_0 = 3.45$ cm, their weight was $M = 0.25$ g, and their maximum tension in an isometric contraction was $P_0 = 180$ g; the initial load was 6.5 g. A quick release occurred at 0.45 s after the start of the stimulus, by when the tension developed had reached its maximum. The arrows indicate the moments at which shortening ended. The curve of heat production in an isometric contraction at the initial length was identical with that at a length 3.5 mm less; and the nearly horizontal run of the analysed heat difference after shortening ended showed that the curve of heat production at constant length after 7 mm shortening must have been closely enough the same. The procedure was described above under 'Method', the heat difference between a contraction

with shortening and the isometric contraction being analysed. The results of the analysis are shown by the small dots on the curves.

After a sudden release to isotonic conditions it was always found that the analysed curve of the heat difference showed an immediate jump up. This is almost certainly due to the thermoelastic rise of temperature caused by the sudden drop of tension (Hill 1953*a*; Woledge 1961, 1963). Another effect of the fall of tension would be to allow the series-elastic component of the muscles to shorten a certain amount; so, up to the moment when the external shortening was arrested (at the arrow), the contractile component had not shortened the full amount

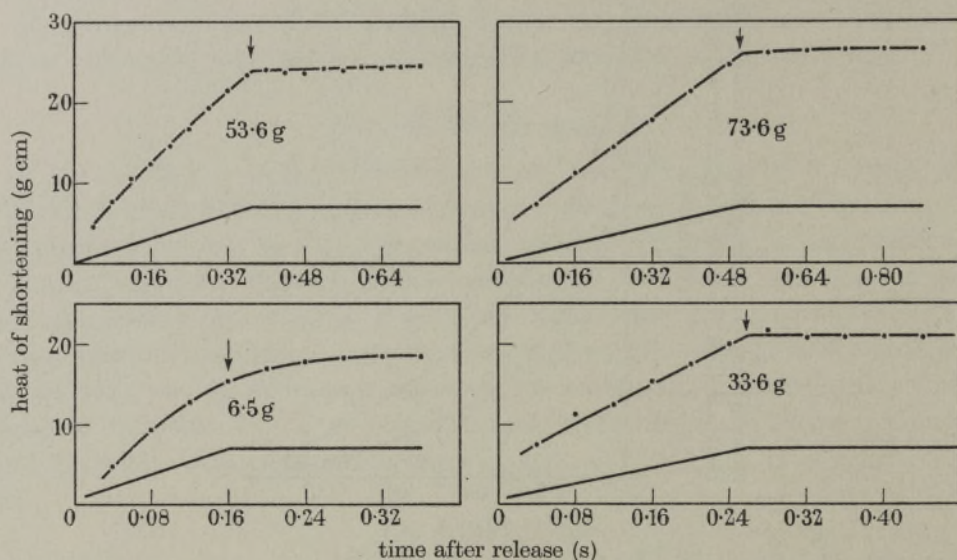


FIGURE 5. To show the heat of shortening (upper curves) as a function of time after release, during four isotonic contractions under different loads; the load is given in each diagram. The lower curves give the course of the shortening (7 mm). Release occurred at time zero (about 0.45 s after the start of the stimulus); the arrow indicates the end of shortening. The small dots give the actual results of the analysis. The relation between α/P_0 and P/P_0 is shown as line (1) in figure 6. See text for further details.

assumed (in this experiment 7 mm). This would make the heat of shortening measured at the arrow rather too small. As soon as arrest occurred the tension rose rapidly again and both these effects would be reversed; the thermoelastic heat would now be negative and the balance of the heat of shortening positive.

These effects would be less when the tension to which the muscles were released was greater. It would, however, be useless to try to allow for them, for too many unknown quantities are involved. But if the tension changes were reversed in a few tenths of a second after release, the final value of the heat of shortening would be that reached at the nearly steady level then attained. In every experiment, therefore, the analysis was continued for a few tenths of a second after shortening ended, and the level of the curve then reached was assumed to give the heat of shortening.

The constant α of the heat of shortening has been expressed throughout in terms of α/P_0 ; this is a dimensionless number and so allows a direct comparison between

different muscles, large or small, weak or strong. The present investigation has shown that α/P_0 is not constant for any one muscle, but increases linearly with the load. The relation between α/P_0 and P/P_0 , in this particular experiment, is given by line (1) in figure 6; it has the equation $\alpha/P_0 = 0.141 + 0.165P/P_0$. In another similar experiment, with release at 0.78 s, the relation was that of line (2) in figure 6, with the equation $\alpha/P_0 = 0.180 + 0.148P/P_0$. Later a 'mean' relation, so far as a mean is justifiable, will be considered.

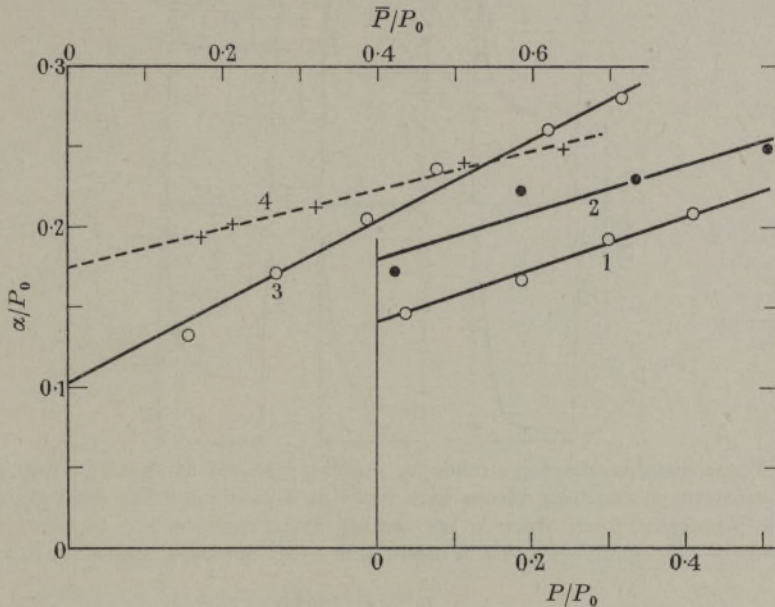


FIGURE 6. To show the relation of α/P_0 to P/P_0 ((1) and (2), isotonic contractions), or to \bar{P}/P_0 ((3) and (4), contractions at constant speed). α is the constant of the heat of shortening, P_0 the maximum isometric tension, P the load (isotonic), \bar{P} the mean tension exerted (constant speed). Four separate experiments. Details of (1) are given in figure 5, of (3) in figures 7 and 8; (2) and (4) are referred to in the text.

An abrupt release from an isometric to an isotonic contraction produces certain complications, such as the rapid appearance, discussed above, of thermoelastic heat; moreover, it makes the early analysis of the records more difficult. A few experiments, therefore, were made by another method, in which the muscles were permitted to shorten at a constant speed by means of a Levin-Wyman ergometer. Shortening began during a previously isometric contraction, about 0.7 s after the start of the stimulus. The ergometer allows a force-distance diagram to be traced on a smoked surface at the same time as the distance-time curve is recorded on the second beam of the cathode-ray tube. A good deal of further information was thus obtained which was useful in interpreting the results. The six curves of figure 7 were made in this way, distance shortened being shown horizontally from right to left, force exerted by the muscles vertically. The co-ordinates are necessarily curvilinear, but this provides no difficulty (see Wyman 1926; Levin & Wyman 1927; Hartree & Hill 1928*a, b*; Hill 1939).

The procedure was as follows. The muscles ($l_0 = 3.2$ cm, $M = 0.232$ g, $P_0 = 155$ g) were stimulated isometrically and the tension rose to its full height.

Then at 0.67 s the ergometer was released so that the muscles could shorten 5.0 mm in the times given in table 2. The heat record was made as usual. When shortening ended the tension rose again, not necessarily quite to the full isometric tension since the stimulus was not continued very long. The work (g cm) was calculated from the area of the force-distance curve and this, divided by the distance shortened (0.5 cm), gave the mean tension \bar{P} . The heat of shortening was

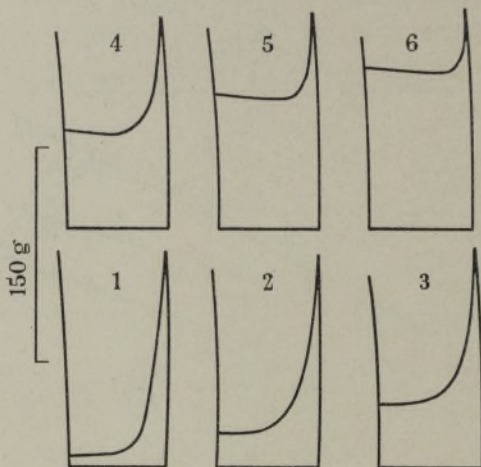


FIGURE 7. Force-distance diagrams made by muscles released to shorten 5 mm at six different constant speeds; the release took place at a moment 0.67 s after the start of a tetanus. Vertically, force exerted; horizontally from right to left, distance shortened. The heats of shortening are given in figure 6, line (3); classified results are in table 2.

TABLE 2. CALCULATED RESULTS FROM FIGURES 7 AND 8

contraction	1	2	3	4	5	6
shortening duration (sec)	0.10	0.16	0.24	0.34	0.54	0.78
work (g cm)	12	21	30	37	48	55.5
mean tension, \bar{P} (g)	24	42	60	74	96	111
\bar{P}/P_0	0.155	0.271	0.387	0.477	0.619	0.715
heat of shortening (g cm)	10.2	13.3	15.9	18.3	20.2	21.7
α (g)	20.4	26.6	31.8	36.6	40.4	43.4
α/P_0	0.132	0.171	0.205	0.236	0.260	0.280

obtained as before by measurement and analysis, and the analysed results are given in figure 8. From these the heat of shortening, and the values of α and α/P_0 , were calculated. The complete results are given in table 2.

As before quite a good linear relation was found between α/P_0 and \bar{P}/P_0 , as is shown by line (3) in figure 6; its equation is $\alpha/P_0 = 0.103 + 0.252\bar{P}/P_0$. Another similar experiment gave line (4) in figure 6, the equation of which is

$$\alpha/P_0 = 0.174 + 0.123\bar{P}/P_0.$$

The curves of figure 7 show that after external shortening ended the tension rose again to near its original maximum; so any effects due to thermoelastic heat, and to shortening of the series elastic component, would be neutralized if the shortening heat were read from the curves of figure 8 a few tenths of a second after shortening was arrested.

Altogether seven acceptable experiments were made, by which the linearity of the relation between α/P_0 and P/P_0 could be tested, and its constants measured. Several more experiments failed, for various reasons, to satisfy the criteria

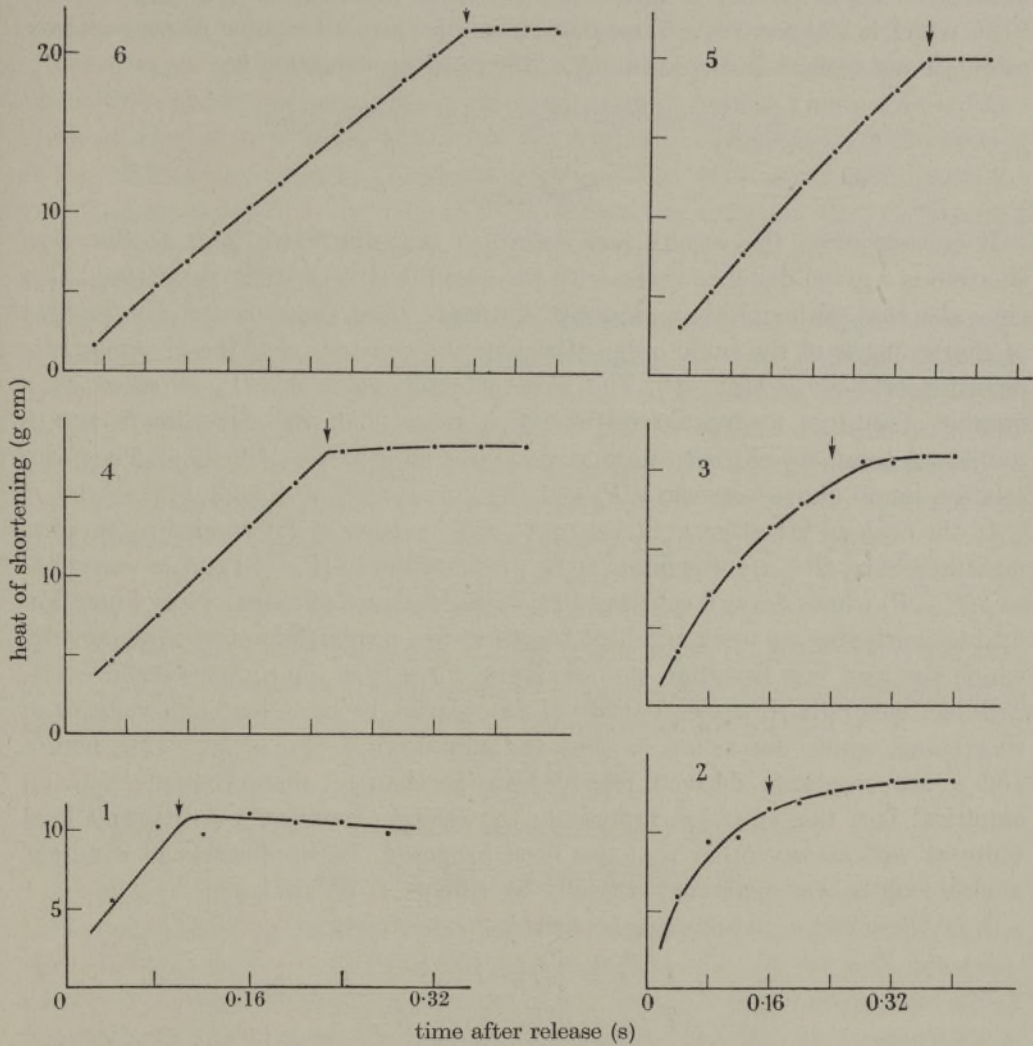


FIGURE 8. To show the heat of shortening (5 mm) as a function of time after release, in six contractions at constant speed. The force-distance diagrams of these, with corresponding numbers, are given in figure 7. The relation between α/P_0 and \bar{P}/P_0 is shown as line (3) in figure 6; classified results are in table 2. The small dots give the actual results of the analysis of the records. The diagrams are drawn with the same scale of heat vertically, but with different scales of time horizontally; though the time marks along the axis are all at intervals of 0.08 s. See text for further details.

described above as necessary for accuracy. Within the limits of error of such measurements, in all the seven experiments the relation obtained was linear. If it be expressed by the general equation $\alpha/P_0 = p + qP/P_0$, a 'mean' relation can be found by taking the average values of p and q . The result is

$$\alpha/P_0 = 0.16 + 0.18P/P_0.$$

It is hardly possible that the rather wide variation observed in the values of p and q could be caused entirely, or even mainly, by experimental error; at least a substantial part of it was probably due to natural differences between the muscles. They were all, in fact, in excellent condition, the average value of $P_0 l_0 / M$ being 2160, which is high for 0 °C. If one dare, from such a small number of experiments, calculate a standard error of the mean, the resulting equation is

$$\alpha/P_0 = 0.16(\pm 0.015) + 0.18(\pm 0.027)P/P_0.$$

DISCUSSION

It is clear from the results just described that the extra heat produced in shortening a given distance varies with the load lifted or the tension exerted. It is clear also that, although they cannot be the same thing, the constant α of the heat of shortening is of the same order of size as the constant a of the characteristic equation $(P+a)v = b(P_0-P)$. The most common value of a/P_0 obtained by a number of authors, for frog sartorii at 0 °C, is about 0.25, with variation from 0.18 to 0.33. A summary of their results is given in a later paper (Hill 1963). The mean relation found above between α/P_0 and P/P_0 gives $\alpha/P_0 = 0.25$ at $P/P_0 = 0.5$.

In the original investigation (Hill 1938), with α (then a) determined by thermal measurements, $(P+\alpha)v$ was found to be proportional to (P_0-P) and so was equal to $\beta(P_0-P)$ where β was a constant. In words, the rate of extra energy liberation during shortening, as work and heat together, was proportional to the amount by which the load was less than the maximum force that the muscles could exert. This led, naturally, to a closer study of the relation between load and velocity of shortening, which was found to obey the equation $(P+a)v = b(P_0-P)$; here a and b are constants derived purely from mechanical measurements. As an empirical fact this equation represents the relation between velocity and load quite as well as any other that has been proposed. Its application at different muscle lengths was examined critically by Abbott & Wilkie (1953).

Now these two equations can be written, respectively,

$$P+\alpha = \beta(P_0-P)v,$$

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

subtracting

$$\alpha - a = (\beta - b)(P_0 - P)/v.$$

Thus if α , a , β and b are all constant, $(P_0 - P)/v$ must also be constant; which is certainly not true. The difficulty is resolved if $\alpha = a$ and $\beta = b$.

Thus it came to be believed that the constant a of the characteristic equation was the same thing as the constant α of the heat of shortening. This has sometimes been questioned, e.g. by Sandow (1961, p. 431); but the original observations were never repeated and the conclusion persisted. It must now be abandoned in its simple form; but see below

It is important to examine how the discordance arose. In the original investigation it was stated (Hill 1938, table 3) that for the determination of a (i.e. α) 'the load lifted was usually small', and the mean value of α/P_0 in 11 experiments was given as 0.257 (variation from 0.21 to 0.31). In the present experiments with

a 'small' load, say $P/P_0 = 0.2$, α/P_0 would average (from the mean relation) 0.196. It seems likely, therefore, that the cause of the discrepancy was simply an error in the 1938 experiments, giving values of the heat of shortening about 30% too high (1.3 times 0.196 is 0.255). The usual value of a/P_0 being about 0.25, a 30% persistent error in α could make α and a appear to be the same.

The present methods are much superior to those of 1938, and knowing the difficulties experienced even now in obtaining accurate results I am not astonished if a persistent error of 30% occurred in the original investigation. An illustration of the difference between the methods of 1938 and of today is the fact that in the very first experiment of the present investigation the variation of α/P_0 with load was obvious; while in 1938, after many experiments (table 4), doubt was still expressed about its reality.

The original statement of the characteristic equation arose from the attractive hypothesis that the rate of extra energy liberation as work and heat together, namely $(P+a)v$, was proportional to (P_0-P) , i.e. the excess of the maximum isometric tension over the actual load lifted. The fact that α depends on P does not in itself invalidate this hypothesis; it is rather that the quantities appear to be wrong. Taking the mean relation $\alpha = 0.16P_0 + 0.18P$ the hypothesis would lead to the equation

$$(P+\alpha)v = (1.18P+0.16P_0)v = b'(P_0-P),$$

which can be written $(P+0.135P_0)v = (b'/1.18)(P_0-P)$.

This corresponds to $(P+a)v = b(P_0-P)$, if $a = 0.135P_0$ and $b = b'/1.18$. But $a/P_0 = 0.135$ is outside the range of observed values, so the equation would not fit any actual relation between P and v . If the mean relation had been

$$\alpha = 0.30P_0 + 0.18P,$$

with 0.30 instead of 0.16, the second equation would have been

$$(P+0.254P_0)v = (b'/1.18)(P_0-P);$$

so a would have been $0.254P_0$, which lies in the middle of the range observed. It is very difficult, however, to believe that the mean value of the first constant, namely 0.16, could be so much in error; in none of the 7 experiments from which the mean was derived was the first constant as great as 0.30. In its simple form, therefore, the hypothesis must be abandoned.

But the main idea of the original hypothesis need not be discarded if a modification of it is accepted. Assume that the rate of extra energy liberation $(P+\alpha)v$ depends on two variables, (P_0-P) and v , not on (P_0-P) alone; in other words, that $(P+\alpha)v$ is increased during shortening by a greater difference between P_0 and P , but diminished by a greater velocity v . Again taking the mean relation for α , this assumption leads to the equation

$$(1.18P+0.16P_0)v = b'(P_0-P) - \gamma P_0 v,$$

where γ is a constant to be determined (P_0 is introduced into the last term to keep the dimensions right, with γ a pure number). The equation can be written

$$\{P+(0.16+\gamma)P_0/1.18\}v = (b'/1.18)(P_0-P).$$

This is the same thing as the usual $(P+a)v = b(P_0 - P)$ if $a/P_0 = (0.16 + \gamma)/1.18$ and $b = b'/1.18$. If γ were taken as 0.135, a/P_0 would be 0.25; with $\gamma = 0.17$, a/P_0 would be 0.28; with $\gamma = 0.10$, a/P_0 would be 0.22. These values of a/P_0 cover most of the usual observed range in frog sartorii at 0 °C. But a is no longer the same thing as α , though it is related to it.

There is nothing inherently unlikely in the modification introduced. A coil of wire in a magnetic field takes less current when it rotates, because of the back e.m.f. it generates; though a more complicated analogue would be required to imitate the behaviour of muscle. It is realized that the two influences on the rate of extra energy liberation would work in opposite directions, a greater velocity requiring a smaller load, a greater load producing a lower velocity. Thus a balance between the two influences would be set up with any load or velocity.

Now it seems almost certain that some kind of relation must exist between α and a ; for α/P_0 and a/P_0 are always of the same order of size, whereas with nothing to connect them they might have been completely different. α and a are clearly not the same quantity, but the modified hypothesis does provide a reasonable relation between them. Without some connexion, their near equality could only be ascribed to 'chance'—which is merely an assertion of one's ignorance.

Throughout this paper the observed changes of α have been expressed in the simplest form as due to changes of the load against which the muscles shortened. They might have been related to the mechanical work done. In shortening a distance x the mean relation would then be,

$$(\text{heat of shortening}) = 0.16P_0x + 0.18 (\text{work}).$$

But this tells us no more than is contained in the original relation itself. The changes of α could also have been regarded as due to changes of the velocity of shortening, or of the time taken in shortening. This has been tested on the experimental results, but the relations found are not linear and look much more complicated than the relation between α and P .

It may be that the way of looking at the problem adopted in this paper, and indeed in all previous papers on the subject, was oversimplified, and that the heat of shortening and the maintenance heat are so mixed up that they cannot in principle be separated. This view was expressed by Aubert (1956, p. 254) in speculating on the constancy observed, during shortening, of the ratio (mechanical power developed)/(total power used). This is discussed in a later paper (Hill 1964*a*). Aubert wrote: 'il est presque impossible d'imaginer comment une telle constance pourrait être assuré si le mécanisme de raccourcissement ne dépendait pas étroitement des phénomènes de maintien et même d'activation'. But it remains certain that while a muscle is shortening against a load it does give out more energy both as work and as heat. This is obvious even in such simple experiments as that illustrated in figures 1 and 2 above. As regards work, it is evident that the work is extra to the heat. But in the case of the extra heat one is forced to ask, as was done earlier in this paper, 'extra to what?'. Does the maintenance heat itself change while shortening is going on? If so, what the present analysis has done is simply to describe *how* the maintenance heat changes. But that is really much the same

thing as to measure the change and describe it as heat of shortening. Only when the chemistry of muscular contraction has gone much further will it be possible to express the facts in more concrete terms.

But that invites a warning. The evidence for the heat of shortening (one can call it the alteration in the maintenance heat if one prefers) has come mainly from observed changes in the rate of heat production *during* shortening. The instruments available to Fenn (1923) allowed him to do no more than measure, as a single deflexion, the heat given out during the complete initial cycle of contraction and relaxation. His most significant experiments were those made with an inertia lever; this removed from the muscles all the mechanical energy produced, allowing them to return to their original length under only a small load, so no errors or complications arose from relaxing under a heavy load. In thirty-three experiments he found (p. 191) that the extra energy liberated was 1.3 times as great as the work performed at the optimum equivalent mass. In the seven experiments of his table 5, with various equivalent masses, the excess energy was always greater than the work (by 'excess heat', he tells me, he really meant excess energy expressed as heat). In view of present knowledge it is clear that, in spite of the inadequacies of the instruments (which were mostly what I lent him!), he had discovered not only the extra energy liberated as work but the extra heat produced by shortening. Another deficiency of his thermopiles was that they had no 'protecting' region, a device introduced only 14 years later. But since the heat deflexion was read only some seconds after the muscles had returned to their original position, that may not have had much effect.

The warning is this. There is still no certainty, when muscles relax under a heavy load, particularly in twitches, that no extra energy is liberated as the result of the sudden stretch (Fenn thought there was); and it is certain that the heat produced in such relaxation is liable to be non-uniformly distributed, so the heat readings are unreliable (as an extreme example, see Hill & Howarth 1957). When chemical changes are measured in a contracting and relaxing muscle it would be better to take all the mechanical energy out of it before it relaxes, by means of an ergometer of some kind (of which several exist). Then there would be a better chance of relating the chemical changes to the work and the shortening. And since the heat of shortening is much greater than the work with small loads (or high velocities), and much less than the work with large loads (or low velocities), it would be better to study the chemical changes in both ways, so as to avoid tangling up the two effects. Methods of measuring the chemical changes in a single contraction are not, as yet, so accurate as to make disentangling easy.

[*Added in proof*, 1 November 1963.] In a later paper (Hill 1964*b*) it will be shown that, when a muscle has completed its shortening and work, if it is still under tension it continues to liberate energy until the tension has disappeared. When the work and the tension are removed by an ergometer, this extra liberation of energy does not occur.

REFERENCES

- Abbott, B. C. 1951 *J. Physiol.* **112**, 438-445.
- Abbott, B. C., Aubert, X. & Hill, A. V. 1951 *Proc. Roy. Soc. B*, **139**, 86-104.
- Abbott, B. C. & Lowy, J. 1956 *J. Physiol.* **133**, 36P.
- Abbott, B. C. & Wilkie, D. R. 1953 *J. Physiol.* **120**, 214-223.
- Aubert, X. 1952 *J. Physiol. Paris*, **44**, 206-208.
- Aubert, X. 1956 *Le couplage énergétique de la contraction musculaire*. Brussels: Éditions Arscia.
- Fenn, W. O. 1923 *J. Physiol.* **58**, 175-203.
- Hartree, W. & Hill, A. V. 1928a *Proc. Roy. Soc. B*, **103**, 234-251.
- Hartree, W. & Hill, A. V. 1928b *Proc. Roy. Soc. B*, **104**, 1-27.
- Hill, A. V. 1937 *Proc. Roy. Soc. B*, **124**, 114-136.
- Hill, A. V. 1938 *Proc. Roy. Soc. B*, **126**, 136-195.
- Hill, A. V. 1939 *Proc. Roy. Soc. B*, **127**, 434-451.
- Hill, A. V. 1949 *Proc. Roy. Soc. B*, **136**, 220-228.
- Hill, A. V. 1953a *Proc. Roy. Soc. B*, **141**, 161-178.
- Hill, A. V. 1953b *Proc. Roy. Soc. B*, **141**, 503-510.
- Hill, A. V. 1964a *Proc. Roy. Soc. B*, **159**, 319-324.
- Hill, A. V. 1964b *Proc. Roy. Soc. B*. (In the Press.)
- Hill, A. V. & Howarth, J. V. 1957 *J. Physiol.* **139**, 466-473.
- Hill, A. V. & Woledge, R. C. 1962 *J. Physiol.* **162**, 311-333.
- Levin, A. & Wyman, J. 1927 *Proc. Roy. Soc. B*, **101**, 218-243.
- Sandow, A. 1961 Article in *Biophysics of Physiological and Pharmacological Actions*, edited by A. M. Shanes. Washington, D.C.: American Association for the Advancement of Science.
- Woledge, R. C. 1961 *J. Physiol.* **155**, 187-208.
- Woledge, R. C. 1963 *J. Physiol.* **166**, 211-224.
- Wyman, J. 1926 *J. Physiol.* **61**, 337-352.