

Energetics of Shortening Muscles in Twitches and Tetanic Contractions

I. *A Reinvestigation of Hill's Concept of the Shortening Heat*

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ABSTRACT Shortening heat was defined by Hill as the "difference between heat produced when shortening occurs and that produced in a similar contraction without shortening." For the tetanus the "similar contraction" was an isometric one at or near l_0 . By contrast, in a twitch the "similar contraction" was one in which only activation heat was produced. The applicability of Hill's concept of the shortening heat has been reexamined in both the twitch and tetanus of *Rana pipiens* semitendinosus muscles. Results of this investigation confirm the existence of an extra heat production accompanying shortening in the twitch and tetanus. In both cases, this shortening heat was proportional to distance shortened and relative afterload. However, at a given afterload the amount of shortening heat produced per distance shortened was greater in the twitch than the tetanus. This difference suggests that the base lines or "similar contractions" employed for the twitch and tetanus are not equivalent. The discrepancy is not remedied by utilizing in the tetanus the activation heat as the myothermic baseline and suggests that some heat producing factor(s) has been omitted in Hill's formulation of the shortening heat. Finally, the existence of Hill's feedback heat, an energy liberation associated with the presence of tension during mechanical relaxation, was not confirmed. This result strongly indicates that relaxation is energetically passive.

INTRODUCTION

A major goal of myothermic investigation has been the definition of the energy-consuming processes in muscular contraction and the determination of how these vary under different conditions of contraction and relaxation. In the first modern investigation of this problem, Fenn (1923, 1924) discovered that the energy liberation, E , in isotonic twitches can be described by

$$E = I + kW, \quad (1)$$

in which I is the isometric heat production at the standard length l_0 or another defined initial length, W is the external work performed when the muscle shortens, and k is a dimensionless constant approximately equal to unity (Carlson et al., 1963). By contrast, in studies of tetanic contractions, Hill (1938, 1964 *a*) found that the energy production, E_t , during the contraction phase over a time t is given by

$$E_t = M + \alpha x + W, \quad (2)$$

in which M is the maintenance heat at or near l_0 , x is the distance shortened, and α is a proportionality coefficient. The product αx was called the shortening heat (SH) and was defined as (Hill, 1964 *a*) "... the difference between the heat produced when shortening occurs and that produced in a *similar* contraction without shortening." In both Eqs. 1 and 2 this similar contraction was an isometric one at or near l_0 . In either case the isometric heat was regarded as a form of overhead, an energy usage needed to bring the muscle to a state of readiness to shorten. The occurrence of shortening leads to an energy usage in addition to this base line (the heat production by the isometric contraction), but whereas in Eq. 1 the additional energy equals the work done, in Eq. 2 it also includes the SH. Aubert and Lebacqz (1971) have confirmed Eq. 2 with the explicit demonstration that it applies to the complete tetanic contraction-relaxation cycle as well.

In Hill's investigation of isotonic twitches (Hill, 1949), the base line above which the shortening heat was liberated was not the isometric heat at l_0 but the activation heat, A , which was equal to about one-third of the isometric heat. Hill claimed that at any time during the contraction phase of the twitch the energy production could be accounted for by

$$E = A + \alpha x + W, \quad (3)$$

in which α had approximately the same value as found in tetanic contractions. In examining Eqs. 2 and 3, it should be noted that Hill considered M and A to be analogous, defining M as the "summated effect of the 'activation heat'." Studies by Homsher et al. (1972) and Smith (1972), however, have shown that only about 30% of the maintenance heat production is activation heat. Therefore, the base lines against which SH was measured in the twitch and tetanus were different.

Prompted by the failure of Carlson et al. (1963) to find either shortening heat or shortening chemistry in a series of twitches, Hill (1964 *c*) investigated the heat production in isovelocity twitches and found that the Eq. 3 had to be altered to include a fourth term, the feedback heat h , thus:

$$E = A + \alpha x + W + h. \quad (4)$$

Feedback heat production was associated with the presence of tension during relaxation. As the load against which the muscle shortens is reduced, αx increases while h decreases. According to Hill (1964 *c*), Fenn's Eq. 1 and Hill's Eq. 4 are reconciled by the apparent reciprocal relationship between αx and h .

Our goal was to reexamine Hill's definition of the SH and to determine its applicability to both the twitch and tetanus because the base line against which Hill determined the SH in a tetanus (*see* Eq. 2) is different than the base line used in a twitch (Eqs. 3 and 4), and because attempts to demonstrate the presence of a metabolic counterpart of the SH have met with failure (Mommaerts et al., 1962; Carlson et al., 1963; Kushmerick et al., 1969).

Results of this investigation confirm the existence of an extra heat production accompanying shortening in both the twitch and tetanus. However, the magnitude of Hill's shortening heat coefficient is very different in the twitch and tetanus. While the existence of Hill's feedback heat was not confirmed, evidence suggesting a heat production during the development of tension in a twitch was obtained.

METHODS

General

All experiments were performed on dorsal heads of pairs of semitendinosus muscles of *Rana pipiens*. The maintenance of frogs, dissection procedure, mounting of muscles upon the thermopiles, thermoregulation of the muscle-thermopile system, composition and aeration of the Ringer solution, stimulation procedure, and determination of the l_0 and the drained and blotted weights of the muscles, were the same as previously described (Homsher et al., 1972). The l_0 ranged between 18 and 23 mm, whereas the muscle weight (blotted) ranged from 47.0 to 114.8 mg per pair. Twitch tension per cross-sectional area ($P_0 \cdot l_0/M$) averaged $2.09 \text{ kg/cm}^2 \pm 0.05$ (SE of mean, $n = 29$), and the twitch: tetanus ratio averaged 0.86 ± 0.02 (SE of mean, $n = 16$).

Heat Measurements

Thermopiles (E1 and E2) used in this investigation were the conventional type constructed by the Ricchiuti technique (Ricchiuti and Mommaerts, 1965). Their dimensions, sensitivity, and equivalent half-thickness are given in Table I of the paper by Homsher et al. (1972). A third thermopile, E4, was of the same design and had the following characteristics: number of active junctions, 120; thermopile resistance, 1000 Ω ; length of protective region, 5.6 mm; length of active region, 12.8 mm; sensitivity, 4.11 mV/ $^{\circ}\text{C}$; equivalent half-thickness, 16.6 μm . Amplification and display of the thermopile output and correction of temperature recordings for heat loss were the same as previously described (Homsher et al., 1972). Absolute energy liberation (in gram-centimeters) by contracting muscles was calculated as described by Hill and Woledge (1962), using the values of the drained and blotted weight (assuming that the dry weight was 18% of the blotted weight), and the sensitivity of the thermopile in millivolts/degree celsius. When the time course of the heat production was desired,

the lag in the recorded heat trace was corrected for by the method of factors (Hill, 1965, p. 314). To allow for Ringer solution and any connective tissue interposed between muscle fibers and the thermopile, an equivalent half-thickness of 22.4 μm was assumed in the analysis.

Conventional myothermometry is open to the criticism of sampling errors and uncertain calibration. To counter these objections, Wilkie (1968) developed a calibrated integrating thermopile in which two active junctions measured the temperature of a silver plate upon which the muscles are placed. Because the experiments reported below require accurate measurement of absolute amounts of energy, we have built two calibrated integrating thermopiles, W1 and W2, as follows: conventional thermopiles were first constructed in which all the junctions were active and contained within a region 18 or 22.5 mm in length. Slabs of silver, 21- or 24.5-mm long, 4-mm wide, and 125- μm thick were insulated with a layer of 7.5 μm thick Kapton (E. I. DuPont de Nemours & Co., Wilmington, Del.) and attached with epoxy to both faces of the thermopile. A 12.5- μm diameter Nichrome wire, insulated with Isonel (California Fine Wire Co., Culver City, Calif.), was then bonded to the silver surface on either side of the thermopile to serve as a heating element by which the system could be calibrated. This type of thermopile has performance characteristics similar to those described by Wilkie (1968). The results of experiments using W1 and W2 agreed with those performed using E1 and E2.

Mechanical Measurements

Force measurements were made using Schilling capacitance transducers (Schilling, 1960), having a resonant frequency of 3 kHz and a compliance of 0.2 $\mu\text{m/g-wt}$. The isotonic transducer was likewise a capacitance transducer (Schilling, 1960), with a lever ratio of 22.7 to 1 and an equivalent mass of 500 mg. In instances in which the muscle was to be suddenly released to some predetermined force, the lever arm was held at a fixed position by a solenoid-triggered stop which could be withdrawn at any desired time. When the muscle was to contract at a set velocity, an ergometer (constructed from a modified speaker magnet and voice coil; Brady, 1966) was used. The voice coil was attached to the muscles through a thin aluminum cone and stainless-steel shaft. The end of the shaft was fitted with a small capacitance transducer so that continuous tension measurement could be made. The ergometer was driven by a DC power amplifier with position feedback from the voice coil shaft. The monitored position signal provided a record of the displacement of the muscle. The overall frequency response of the system was flat from 0 to 70 Hz and was 3 dB down at 200 Hz. The wave-form generator and power amplifier driving the ergometer were capable of producing positive or negative displacements with velocities ranging from 0 to 100 cm/s, reaching the preset velocity within 1.5 ms. Displacements were predetermined within the range of 0–2 cm. The beginning of the displacement was accurately timed within the range of 0–10 s with respect to the stimulus. Work performed when the muscle shortened against the ergometer was determined by measuring the area under the tension trace during the release with a planimeter.

The ergometer shaft was also used as a movable afterload stop in isotonic twitch experiments in which the afterload was to be prevented from stretching the muscle

during relaxation. In this situation the ergometer shaft was positioned above the isotonic lever to form an afterload stop. The muscle was then stimulated and allowed to contract and relax against its afterload. The distance shortened and the time used to shorten that distance were measured. The ergometer was then programmed so that, at the peak of shortening in the subsequent isotonic twitch, the ergometer shaft-afterload stop would rapidly move to a position to prevent the afterload from falling. In this manner myothermal recordings were obtained which were free of the dissipation of the potential energy of the lifted load.

RESULTS

Shortening Heat in a Tetanus

Shortening heat was classically determined in tetanic contractions (Hill, 1938 1964 *a*), and such measurements are described here for the *R. pipiens* semitendinosus muscle, in order to obtain values directly applicable to this muscle. These measurements were performed in a manner essentially identical to those of Hill (1964 *a*): tetanically stimulated muscles, released 700–800 ms after the beginning of a tetanus, were allowed to shorten a fixed distance, 3 mm, against a constant load or at a constant velocity. The initial (before shortening) and final (after shortening) muscle lengths were adjusted so that the maximum isometric tetanic tension and maintenance heat rates were nearly identical. In practice the muscles shortened from about $l_0 + 1$ mm to about $l_0 - 2$ mm. Stimulation of the released muscles continued until tension redevelopment after shortening was approximately complete. The base line maintenance heat is that observed at the final muscle length.

A typical series of determinations of the shortening heat are shown in Fig. 1. From the isometric maintenance heat production as the base line, shortening at a constant velocity against an ergometer leads to an increased rate of heat production. With the cessation of shortening, the heat rate returns to that of the isometric condition. In four pairs of muscles contracting against an ergometer, it was found that after the cessation of shortening the redeveloped tetanic tension was $96.4\% \pm 0.7$ (SE of mean, $n = 18$) of that seen in the muscles tetanized at the short muscle length. In Fig. 2 the difference in heat production between the shortening and isometric contractions of Fig. 1 is plotted as a function of time after the beginning of shortening. The difference has been corrected for lag in heat conduction from muscle to thermopile. From Fig. 2 it is clear that the rate of SH production is proportional to the velocity of shortening and that the amount of SH liberated per unit distance of shortening increases with the force exerted by the muscle. A regression analysis of the normalized shortening heat coefficient (α/P_0) calculated from this experiment on the average relative load during shortening (\bar{P}/P_0) was made and showed that $\alpha/P_0 = 0.16 + 0.26 \bar{P}/P_0$ ($r = 0.98$, $n = 4$). In all, seven pairs of muscles were studied and the average normalized shortening

heat coefficient (see Table I) was found to be in excellent agreement with Hill's (1964 *a*) results for sartorius muscles of *Rana temporaria*.

Force and displacement records obtained in these experiments were used to

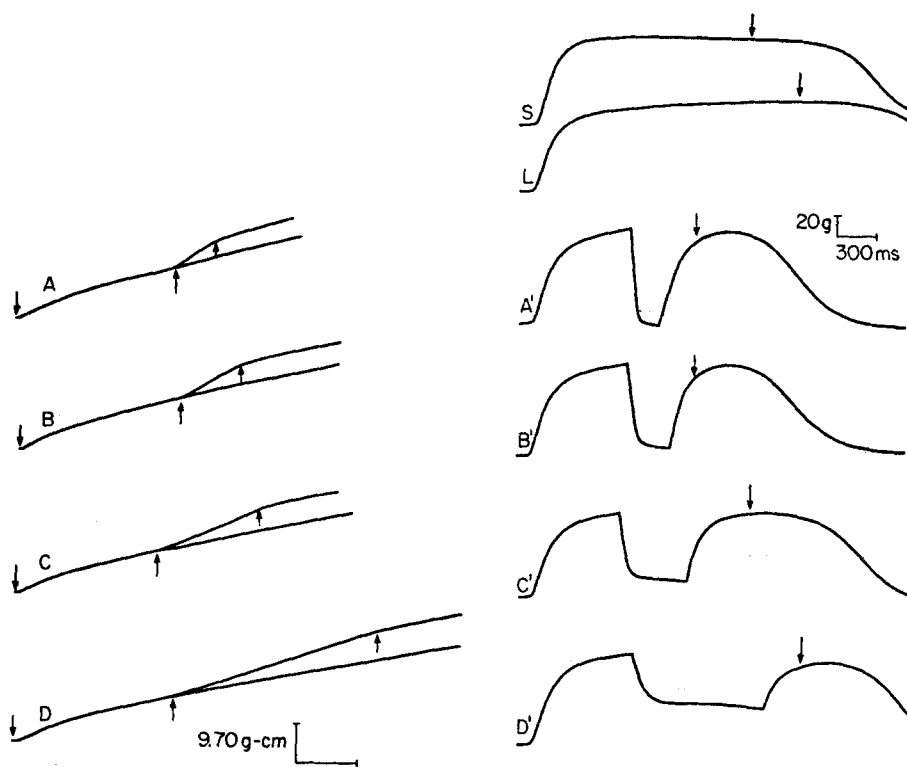


FIGURE 1. Shortening heat production in tetanic contractions. The records to the left, A, B, C, and D are tracings of heat records obtained from a muscle pair shortening a distance of 0.3 cm against an ergometer at velocities (centimeters/second) of 1.5, 1.0, 0.6, and 0.3, respectively. To the right are tracings of the corresponding tension records (A', B', C', and D'). Tension records L and S are isometric tetani at the muscles' beginning (L) length and their final (S) length. Upward pointing arrows indicate beginning or end of shortening; downward pointing arrows, the beginning or end of tetanic stimulation. When shortening begins two heat records appear; the upper trace is that of the shortening contraction, the lower trace, the isometric tetanus at the short muscle length. The external work (gram-centimeters) performed in records A', B', C', and D' was 4.54, 5.25, 8.75 and 15.85, respectively. Calibration of the records is given. Time calibration, shown below heat records, is 300 ms. In this experiment P_o was 98 g, M , 82.0 mg and l_o , 2.2 cm. Thermopile E2 was used.

construct force-velocity curves from which values of Hill's coefficients a and b were obtained and with other pertinent averages relating to these tetanic experiments, these values are given in Table I. They are in general agreement with Hill's (1938) results with the possible exception of b which is less than the

usual value of 0.33 l_0/s . The reason for the difference may be that the actual fiber lengths in the semitendinosus muscle are less than the measured muscle length (Délèze, 1961).

Shortening Heat in a Twitch

According to Hill (1964 *c*) the heat production in an isotonic twitch is given by Eq. 4. During the time-course of an afterloaded isotonic twitch, the heat,

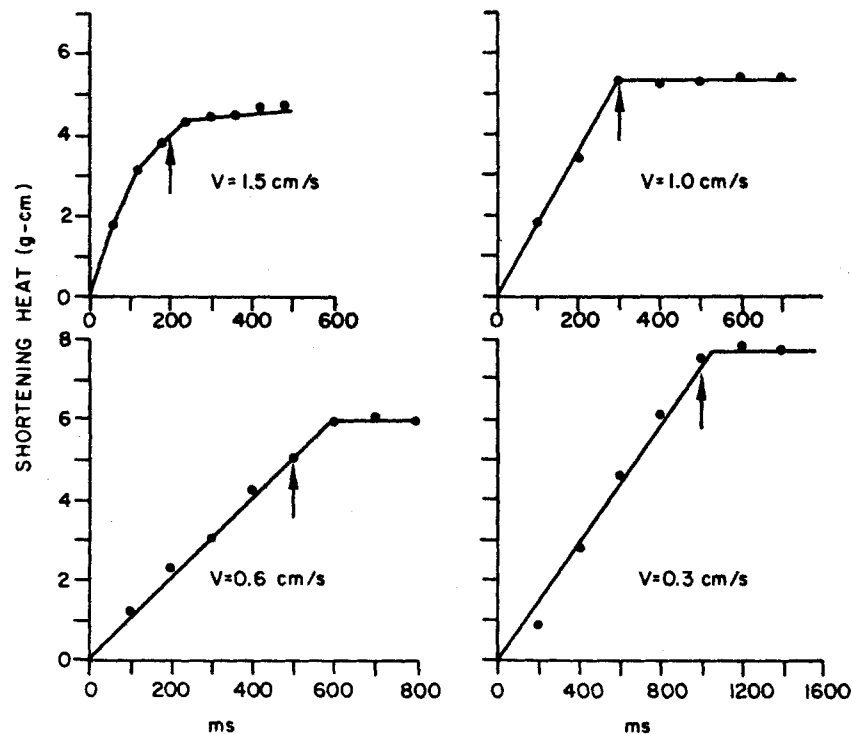


FIGURE 2. Time-course analysis of heat records in Fig. 1. The difference between heat produced by a shortening muscle and isometric control was corrected for delay in heat transfer from muscle to thermopile and was plotted as a function of time after the beginning of shortening. Upward pointing arrows indicate cessation of shortening. The value of the shortening velocity, v , is given. Average relative tension \bar{P}/P_0 for shortening velocities (centimeters/second) of 1.5, 1.0, 0.6, and 0.3 was 0.16, 0.19, 0.33, and 0.56, respectively.

E_s , liberated during the shortening phase should be simply the sum of the activation heat and the SH,

$$E_s = A + \alpha x, \quad (5)$$

since neither the work done on the load nor the feedback heat will begin to appear thermally until later times, after shortening has ceased (Hill, 1964 *c*).

TABLE I
MECHANICAL AND THERMAL PARAMETERS FOR *R. PIPIENS* SEMITENDINOSUS
MUSCLES AT 0°C

Tetanic contractions ($n = 7$)	
a/P_o	$0.26 \pm 0.03^*$
$b/l_o, s^{-1}$	0.25 ± 0.01
l_o, cm	2.06 ± 0.05
M, mg	82.8 ± 7.6
P_o, g	81.9 ± 6.0
$P_o l_o / M, kg/cm^2$	2.08 ± 0.14
α/P_o	$0.18 (\pm 0.02) + 0.15 (\pm 0.02)P/P_o$
Twitch contractions ($n = 4$)	
α_T/P_{o_t}	$0.20 (\pm 0.01) + 0.68 (\pm 0.05)P/P_{o_t}$

* Values given as mean \pm SE of mean.

Therefore, to measure the SH in a twitch, the time-course of the activation heat production is subtracted from the time-course of the heat liberation during shortening. The activation heat is determined from twitches in which the muscles have been stretched to a length at which thick and thin filament overlap is vanishingly small. It should be noted that the technique employed here for the activation heat measurement was not available to Hill in his studies of the activation heat and shortening heat in a twitch (Hill, 1949, 1964 *c*). Fig. 3 shows traces of displacement (panel A), isometric tension (panel B), and heat production (panel C) from an experiment in which muscles at l_o were afterloaded with 40 g (trace 4), 25 g (trace 3), 10 g (trace 2), or 2 g (trace 1), and caused to give single twitches, the afterload not being permitted to return the muscle to its original length. Isometric heat liberation (trace 5) and activation heat production (trace 6) are also included in the figure. The most obvious feature of the thermal traces is, as Hill (1949) has previously observed, that the lighter the afterload, the more rapid the heat evolution.

To determine the time course of the SH production, after correcting for thermal lag, the heat produced beyond the activation heat is plotted as a function of the distance shortened under the various afterloads in Fig. 4. The extra heat (Hill's shortening heat in a twitch) is liberated in proportion to the distance shortened. Further, the increase in the slope of the regression line with an increase in afterload indicates that the shortening heat coefficient (α_T) increases strongly with afterload. Regression analysis of the twitch-shortening heat coefficient (normalized for maximum isometric force P_{o_t} at l_o) against relative afterload, P/P_{o_t} , from the results from Fig. 4, show that $\alpha_T/P_{o_t} = 0.23 + 0.84 P/P_{o_t}$ ($r = 0.99$). Averaging the data from four pairs of muscles, it was found that $\alpha_T/P_{o_t} = 0.20 (\pm 0.01) + 0.68 (\pm 0.05) P/P_{o_t}$. This result indicates that more SH is liberated when the muscle shortens in the twitch than in the tetanus. Specifically, the tension-dependent portion of the normalized shortening heat coefficient is more than four times greater than that

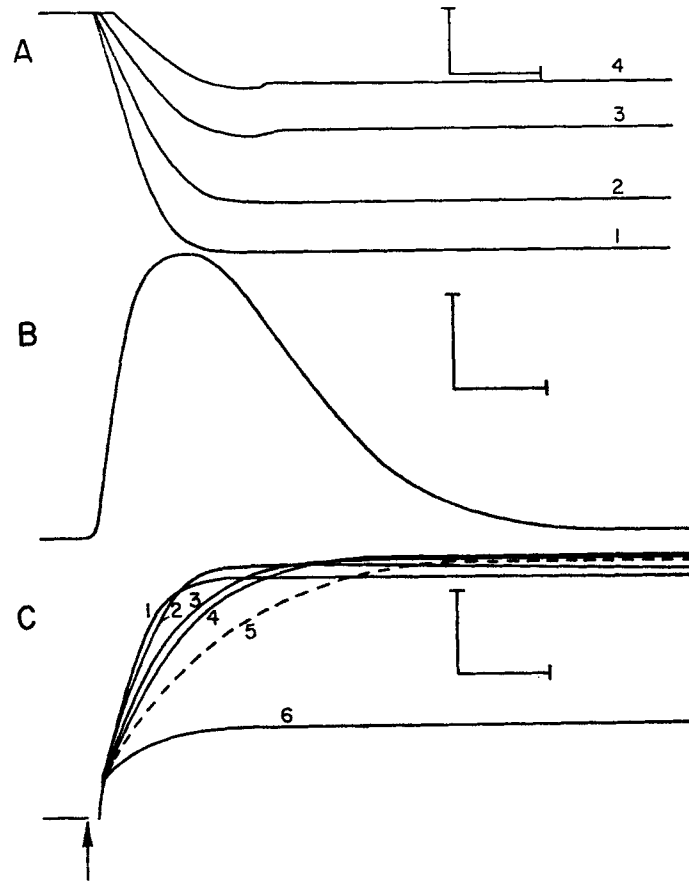


FIGURE 3. Shortening, isometric tension, and myothermic traces of isotonic twitches at 0°C. Panel A, displacement records, panel B, isometric tension at l_0 , panel C, myothermic traces. The horizontal bar in each panel represents 400 ms, while the vertical bar corresponds to 1 mm in panel A, 25 g (force) in panel B, and 4 g-cm in panel C. Experiments were performed on thermopile E4. Here M was 72.0 mg, l_0 , 2.0 cm, and P_{oi} , 78 g. Traces 1, 2, 3, 4, 5, 6, correspond to afterloaded isotonic twitches against 2 g, 10 g, 25 g, 40 g, the isometric twitches at l_0 , and activation heat production, respectively. Activation heat was measured at a muscle length of $l_0 + 9$ mm. The isometric tension at this length was 2 g. See text for further details.

seen in the tetanic studies (Table I). This result further illustrates the fact that the base line against which Hill's shortening heat is measured in the twitch and the tetanus (as indicated by Eqs. 2 and 4) is different.

Examination of the thermal traces in Fig. 3 reveals a very pertinent fact. When the afterload is not allowed to dissipate its potential energy, the heat production at various afterloads (in this case from 0.028 to 0.56 P/P_{oi}) is approximately equal to the isometric heat. This result corresponds to Fenn's

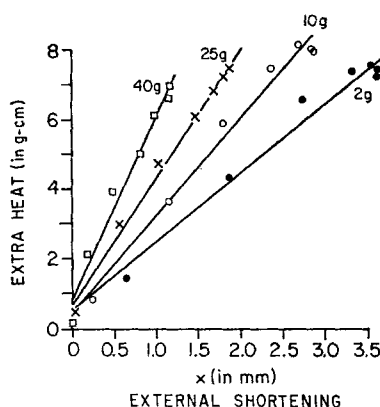


FIGURE 4. The heat produced beyond the activation heat as a function of the distance shortened. The heat records of Fig. 3 were corrected for the lag in conduction of heat from the muscle to the thermopile. The difference between the heat produced when shortening against the afterloads of 40 g (\square), 25 g (\times), 10 g (\circ), and 2 g (\bullet) and the activation heat (trace 6) is plotted (ordinate) against the distance shortened (abscissa). The lines through the data points are the results of regression analysis of the extra heat on the external shortening. The correlation coefficient for the various afterloads is 0.98, 0.99, 0.99, 0.98 at 2, 10, 25 and 40 g, respectively. See text for further details.

observations (as given by Eq. 1), and represents the Fenn effect in its classical sense.

Feedback Heat

A second fact to be drawn from Fig. 3 is that for all afterloads, the active heat production is nearly complete by the cessation of shortening; e.g., under the 40 g afterload in Fig. 3, shortening just ends at 700 ms at which time 10.90 g-cm of heat has been liberated of an eventual total of 12.4 g-cm. At 700 ms the muscle is exerting a force of 40 g so that a certain amount of thermoelastic heat and stored series elastic energy remain to be dissipated. Assuming a thermoelastic heat coefficient, R , of 0.01, and since P is 40 g and l_o is 2.0 cm, the thermoelastic heat, $R\Delta Pl$, to be liberated is 0.80 g-cm. Since the muscle weighed 0.072 g, Pl_o/M at the cessation of shortening is 1.10 kg/cm². From the relationship between elastic energy and Pl_o/M (Fig. 6.4, Hill, 1970), 0.50 g-cm of internal work remains to be dissipated. Thus a total of 1.30 g-cm of heat are produced from internal work and thermoelastic heat, leaving only 0.2 g-cm of active heat to be generated by the muscle during relaxation. Hill's concept of the feedback heat requires that an additional 1.3 g-cm of heat be generated from 700 ms onward. This observation is explicable only if there is no feedback heat generated during relaxation.

To determine explicitly whether there is a feedback heat in *R. pipiens* semitendinosus muscles, we have duplicated Hill's original experiments (Hill, 1964 *b*) as shown in Fig. 5. In these experiments, the isometric heat production

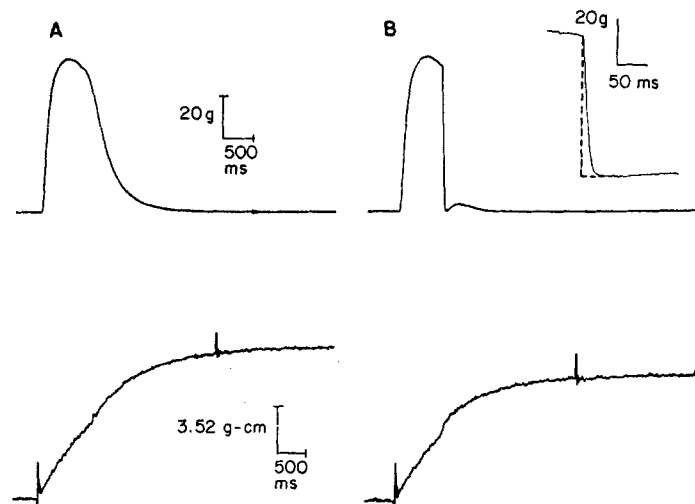


FIGURE 5. The effect of the presence of tension during relaxation on total initial heat production in an isometric twitch. Upper records in panels A and B are tension recordings and the lower are heat recordings. Records were made on a calibrated integrating thermopile (W1); calibration for tension, heat, and time are given. Panel A is an isometric twitch, panel B an isometric twitch which was released, at 750 ms after the stimulus, against an ergometer at a velocity of 3.0 cm/s over a distance of 1.5 mm. The inset of panel B is the tension recording during the quick release (on an expanded time base) from which the work done on the ergometer by the series elastic element was calculated. The area enclosed by the tension recording and the dotted lines represents an internal work of 1.6 g-cm. For this muscle pair M was 72.0 mg and l_0 , 2.0 cm.

H_i (panel A), is compared to that which was observed when the muscle was released over a distance of 1.5 mm against an ergometer at a velocity of 3.0 cm/s shortly after the peak of tension (H_r , panel B). This maneuver reduces the tension to zero at a time when relaxation has just begun. During the relaxation phase of a normal isometric cycle, there is a heat liberation due to at least two causes: (a) the disappearance of tension, hence the appearance of heat as the thermoelastic effect vanishes, and (b) the dissipation of internal work stored in the series elastic element. In the cycle with release, the first term appears suddenly and can be recognized in the heat record, whereas the second term does not appear as it is done upon the ergometer. Its amount, W_r , is estimated by measuring the area under the tension recording during the release; and in the experiment in Fig. 5, W_r amounted to 1.6 g-cm. Thus, the feedback heat beyond the time of release is found as $h = (H_i - [H_r + W_r])$. From Fig. 5, H_i is 11.5 g-cm and H_r is 9.8 g-cm. Hence h is 0.1 g-cm which is not significantly different from zero. In a total of nine separate pairs of muscles (four of which were mounted on integrating thermopiles) released at times ranging from 500 ms to 1,300 ms after the stimulus, over distances from 1.5 to 2.0 mm, and at velocities of 2.5 to 3.0

cm/s, the average ratio of $(H_r + W_r)/H_i$ was 1.01 ± 0.01 (SE of mean); and the ratio of H_r/H_i averaged 0.88 ± 1.01 (SE of mean). These experiments provide no evidence for a feedback heat and are, therefore, in agreement with earlier results of Hill (1953) on frog muscles, though not with later ones obtained from toad muscles (Hill, 1964 *b*). This result indicates that there is very little, if any, active heat generated during relaxation.

DISCUSSION

The results of these experiments confirm the fundamental observations by Hill (1938, 1964 *a*) that during shortening of a contracting muscle the rate of heat production increases. Our results also, however, clearly expose a discrepancy which has been present in the literature and which has not been explicitly noted, though it could have been recognized in the resulting inconsistencies. Thus, we found a certain set of values for the shortening heat coefficient α and its load dependence when obtained from tetanic contractions using the maintenance heat as a base line as given by Eq. 2 (Hill, 1938); and another set of values was obtained from twitches when using the activation heat as a reference as in Eqs. 3 or 4 (Hill, 1964 *a*). The discrepancy between α/P_o and α_T/P_{ot} might be due to three factors. (*a*) In the afterloaded isotonic twitch, before external shortening, the muscle develops tension isometrically and, as a consequence of the accompanying internal shortening, liberates internal shortening heat. Such a heat liberation would cause the total heat production above the activation heat to be greater than that associated with just external shortening. However, in the type of experiment plotted in Fig. 4, α_T was determined from the *slope* of the regression equation of extra heat on external shortening and should be independent of internal shortening. An internal shortening heat production prior to external shortening would manifest itself as a positive intercept on the extra heat axis at zero external shortening. (*b*) The SH production in the twitch would be overestimated if the technique for the measurement of the activation heat yielded a value *less* than actually occurs at or near l_o . This possibility is rendered unlikely by Smith's (1972) observation that the twitch:tetanus ratio does not decline with an increase in muscle length and by the observation of Homsher et al. (1972) that the mechanical threshold is little affected by muscle length beyond l_o . Finally the magnitude of the activation heat seen in these experiments is similar to that estimated by Hill in his work on twitches (Hill, 1949). (*c*) Whereas the base line for shortening heat measurements in the twitch is the activation heat, in the tetanus it is the maintenance heat rate at l_o which is about three times greater than the activation heat rate (Smith, 1972; Homsher et al., 1972). However, using measurements of the SH production in the tetanus, the observed heat production can be corrected for the difference in base line. According to Hill's definition of tetanic SH, the observed heat production (h_{obs})

from the beginning of shortening is equal to the sum of the shortening heat (αx) plus the maintenance heat, or

$$h_{obs} = \alpha x + \dot{M}\Delta t, \quad (6)$$

where \dot{M} is the stable maintenance heat rate at l_o , and Δt is the duration of shortening. Taking the tetanic activation heat rate ($0.3 \dot{M}$, [Homsher et al., 1972]) as the base line against which SH should be measured in the tetanus (as in Eq. 4), the heat production upon tetanic shortening can be written

$$h_{obs} = \alpha_A x + 0.3 \dot{M}\Delta t, \quad (7)$$

where α_A is the SH referenced to the activation heat production. Equating Eqs. 6 and 7, substitution of x/v for Δt (v is the shortening velocity), division of both sides of the equation by x and P_o leads to

$$\alpha_A/P_o = \alpha/P_o + \frac{0.7 \dot{M}}{P_o v}. \quad (8)$$

Setting $\dot{M} = 0.035 P_o l_o/s$ (Homsher, unpublished data), $v = (P_o - P)b/(P + a)$ (from the force-velocity curve), $b = l_o/4$, $a = P_o/4$, and $\alpha/P_o = 0.18 + 0.15 P/P_o$ (from Table I) Eq. 8 becomes

$$\alpha_A/P_o = 0.18 + 0.15 P/P_o + \frac{0.024 + 0.098 P/P_o}{1 - P/P_o}. \quad (9)$$

Comparison of α_A/P_o from Eq. 9 (for tetani) to α_T/P_{ot} (for twitches, Table I) reveals several interesting features. First, when $P/P_o = 0$, α_A/P_o and α_T/P_{ot} have the same value. However, the relationship between α_A/P_o and P/P_o is nonlinear while that between α_T/P_o and P/P_{ot} is linear. At $P/P_o \leq 0.5$, the tension-dependent portion of α_A/P_o is about one-half of that of α_T/P_{ot} , whereas at $P/P_o > 0.8$, α_A/P_o greatly exceeds α_T/P_{ot} . These calculations suggest that an additional heat-producing factor related to tension development and maintenance has been omitted in Hill's definition of the SH. It will be shown in the following paper that by using a redefinition of the shortening heat, consistent results for both the twitch and the tetanus can be obtained.

Our failure to detect a feedback heat is difficult to reconcile with Hill's (1964 *b*) results. There may perhaps be a species difference and this possibility should be examined.

This work was supported in part by a U.S. Public Health Service Program Project HL-11351 and by a Los Angeles County Heart Association grant no. 479.

Dr. J. A. Rall is a Postdoctoral Fellow of the Muscular Dystrophy Associations of America, Inc.

Received for publication 7 February 1973.

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