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THE HEAT PRODUCTION ASSOCIATED WITH THE MAINTENANCE OF A PROLONGED CONTRACTION AND THE EXTRA HEAT PRODUCED DURING LARGE SHORTENING

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In a recent paper (Hill, 1949*a*), it was shown that the heat produced in a single twitch is made up of two parts: (*a*) the heat of shortening which is simultaneous with and proportional to the shortening, and (*b*) the heat of activation. The latter starts at its maximum speed shortly after a shock, falling in rate from then on and finishing by the time that relaxation begins. In another paper (Hill, 1949*c*) the use of a quick stretch applied shortly after a shock showed that the full strength of a contraction (equal to that in a maximal tetanus) is developed very rapidly after the end of the latent period, remaining on a plateau for a time, then gradually disappearing in relaxation.

These facts suggested that each of the successive shocks required to maintain a prolonged contraction merely restored the full strength of the contraction from the level to which it had relaxed in the interval between shocks, and that the heat produced in a maintained contraction was no more than the summated effect of the heats of activation of the successive responses. If this was so, we should expect the maintenance heat, like the activation heat, to be little affected by muscle length. The first object of the present investigation was to test this conclusion.

If the maintenance heat is the summated accompaniment of the succession of re-activations by which the onset of relaxation is deferred, it should be greater or less according as relaxation is faster or slower. In two respects this is known already to be the case: (*a*) a rise of temperature increases the rate of relaxation and of maintenance heat production (Hartree & Hill, 1921), and (*b*) previous activity (Bronk, 1930) and the presence of CO_2 (Bozler, 1930) decrease both. The second object of the present experiments was to find out, in a single maintained contraction, whether the two effects run parallel.

In an isometric contraction considerable shortening of the contractile material, with consequent stretching of the series elastic material, occurs in the earlier stages. During this process a significant part of the observed heat is heat of shortening, which cannot be allowed for exactly because the amount of internal shortening is not known. After a time, depending on the temperature (about 1·5 sec. for a frog sartorius at 0° C.), the internal shortening is complete, and then so long as the stimulus continues, all the heat is associated with maintaining the contraction. Soon after the stimulus ends the muscle relaxes, and all the mechanical energy stored in the stretched elastic elements appears as heat. The total heat, therefore, is made up of maintenance heat, heat of shortening, and work, of which the second and third cannot be accurately known. The complication is avoided by measuring the rate of heat production directly, after the heat of shortening is over and before relaxation begins. This was not possible with the older myothermic equipment, at any rate before 1938; it was much too slow, and a very laborious numerical analysis would have been required. The present instruments, however (see Hill, 1949*b*), are so rapid that the only allowance necessary is for heat lost by conduction, and this is easily made. The rate of heat production, therefore, can be determined throughout a prolonged contraction from a single record, with much more accuracy and less effect on the muscle than by a long series of stimuli of various durations. Similarly, if a muscle is released and allowed to shorten during a maintained contraction the shortening heat can be determined throughout the shortening. In the third group of experiments described below, this was carried out over a wide range of shortening.

METHOD

Heat measurements were made at 0° C. on frog (*Rana temporaria*) and toad (*Bufo bufo*) sartorii. The equipment consisted of thermopile, galvanometer, photocell amplifier and cathode-ray tube display similar to that described by Hill (1949*b*). A linear time-base was used and the time-base speed was adjusted so as to give several sweeps during each tetanus. The trace was brightened up at the instant of the first stimulus and photographed with time markers every $\frac{1}{50}$th and $\frac{1}{10}$th sec.

A pair of muscles was mounted on the thermopile (P IV described by Hill, 1938) and soaked overnight in oxygenated Ringer at 0° C. The thermopile container was placed inside a Dewar flask filled with well-stirred ice and water, and it was connected at the bottom to a reservoir of Ringer solution. The levels were arranged so that with both systems open to the atmosphere, the solution in the thermopile chamber fell below the bottom of the muscle; when an oxygen supply was attached to the reservoir inlet the solution was pushed completely out of the reservoir, thus filling the thermopile chamber above the top of the muscle. The Ringer's solution was thus kept accurately at 0° C. and the muscle could be soaked when required without temperature disturbance. During experiments on the variation of the heat rate during maintained isometric contractions, soaking was allowed for 20 min. after each tetanus.

It has been shown by Hill (1913), and verified by Feng (1931), that in an isometric contraction the heat produced per unit of tension developed and maintained is independent of the frequency of stimulation, provided fusion is obtained. Condenser discharges were employed, alternating in direction with a time for the complete cycle varying between 0·2 and 1·1 sec.; the frequency chosen was high enough to produce fusion. Tetanus durations of 6 sec. at the higher stimulus frequencies and 20 sec. at the lower values were used. The muscles were attached by a light chain to an isotonic lever giving a tension of about 1 g. weight. Shortening was allowed until a certain muscle length was reached, after which the contraction became isometric. A series of records consisted of a set of contractions at decreasing lengths, followed by a corresponding set at increasing lengths. The average of the two heat rates at any given muscle length was calculated: this procedure helped to compensate for any steady slow change in the muscle.

Correction had to be applied for heat loss. The loss factor was determined for each muscle length from the cooling curve after the muscle had been heated during a short period by a current of 300 kcyc./sec. The thermopile and galvanometer were so rapid that no further analysis was necessary, delays in their response having the effect only of moving the curve of heat production a short distance parallel to itself. The heat rate observed was the true rate a few hundredths of a second earlier.

In the second group of experiments, records of the fall of tension after the end of a tetanus at 0° C. were made with an isometric lever on a smoked drum. In order to study the change in relaxation rate as a tetanus progressed, stimulation was stopped for short intervals throughout a single prolonged tetanus. The stimulus frequency was 2 per sec. and the shocks were registered on the drum by a signal magnet. Five times during a 45 sec. tetanus the stimuli were switched off just long enough for the relaxation of tension to be visible, and then re-established. The time taken for the tension to fall by 5% was measured.

In the third set of experiments a pair of muscles was stimulated isometrically at a length about 1 mm. longer than when in the body, until all internal shortening was ended. The operation of a quick-release mechanism then permitted shortening for a known distance. The only load was that from a light chain moving in a very viscous medium (silicone) used to damp out oscillations resulting from the quick release when the undamped elastic component of the muscle is suddenly relieved of tension. Movement was translated into electrical signal by a shadow of the lever moving across a photocell, and simultaneous records of heat and movement were obtained. Isometric heat traces were recorded at the terminal lengths, and the average subtracted from the trace in which quick release occurred. Heat loss correction needed only to be applied to this difference. The extra heat up to any time was then plotted against the amount of shortening up to that time.

Within this series of unloaded shortenings, several experiments were carried out using the pharynx retractor muscle of the common snail (*Helix aspersa*). The experimental procedure was the same as for frog and toad, but only one side of the thermopile was covered. The muscle was soaked in a bathing solution described by Pantin (1946), and temperatures of 7° and 16° C. were employed. The fibres in this muscle run half the length of the muscle (Ramsay, 1940) so the use of condenser shocks alternating in direction (applied through electrodes at each end of the thermopile) ensured stimulation of all the muscle.

RESULTS

Maintenance heat rate

The heat rate in an isometric contraction has a high initial value, which falls to a steady level as the tetanus is prolonged (Hartree & Hill, 1920). The time after which this occurs depends on the muscle, its temperature and the frequency of stimulation. For a frog muscle at 0° C., the effect of stimulus frequency is illustrated in Fig. 1, which shows that a lower frequency extends the time scale. The initial burst of heat includes that due to internal shortening, but for a frog muscle at 0° C. this is finished by 1·5 sec., leaving only the maintenance heat, the rate of which continues to decrease. As the tetanus proceeds the muscle becomes more economical and reaches a constant level of heat production after about 9 sec. with 1·8 shocks/sec., after 4 sec. with 8 shocks/sec.

In order to compare maintenance heat rates at different lengths, the slopes of the heat-production curves were measured at times after the beginning of excitation such that the heat rate had become steady. The results are plotted in Figs. 2 and 3 for toad and frog respectively. Length is expressed in percentage of the maximum muscle length in the body (resting length) and heat in percentage of the heat rate at this resting length. The heat is that in the whole muscle, not the variable part on the thermopile. All points of all the experitents are plotted.

A variation of heat rate with length occurred in both frog and toad muscle at 0° C. The general result agreed with that of Fenn & Latchford (1933), who used frog muscle at room temperature and determined the heat rate from the difference in total heat of two tetani of different durations. The variation with length, however, was appreciably less than that found by Fenn & Latchford and considerably less than that of the results recalculated by Ramsey (1943). The difference in method probably explains the somewhat different results.

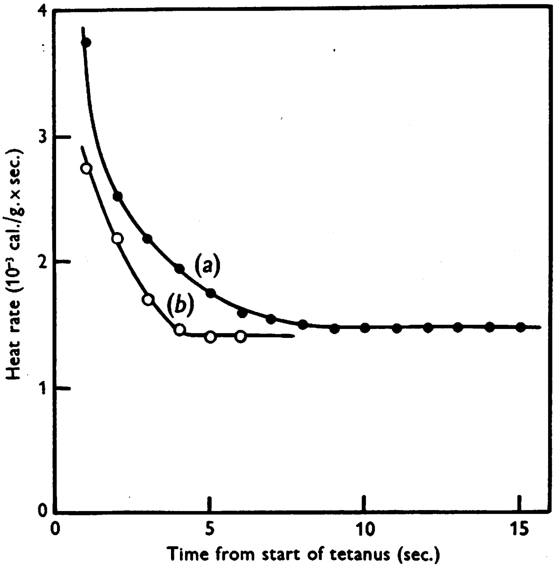

Fig. 1. **Maintenance heat rate during prolonged isometric contraction. Frog sartorii 0° C. Length 30 mm., weight 285 mg. Curve (*a*) stimulus frequency 0·9 double shocks per sec. Curve (*b*) 4·0 double shocks per sec.**

The maintenance heat rate for frog muscle at 80% of resting length was about 10% less than the value at the resting length; for toad muscle the heat rate was down by 10% at about 65% of the resting length. At lengths above the resting value the maintenance heat rate again decreased. This was expected, because as extension increases the muscle relaxes more slowly (Hartree & Hill, 1921) and so less reactivation is required at each stimulus. The same explanation, however, cannot be given of the smaller maintenance heat rate at shorter lengths, for there is no sign of a slower relaxation at such lengths. The activation heat after a shock is about the same at different lengths (Hill, 1949*a*, 1950), but a variation of the extent shown in Figs. 2 and 3 could not be detected with certainty. It is possible, therefore, that the observed variation (with length) of maintenance heat rate is due, at least in part, to a similar variation of the activation heat.

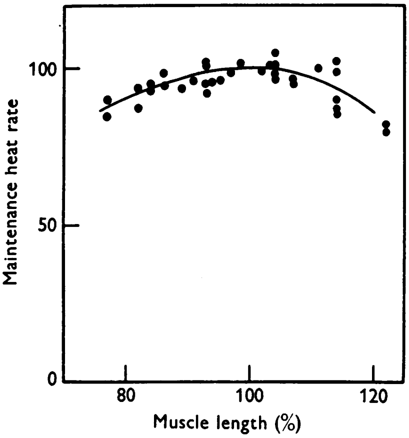

Fig. 2.

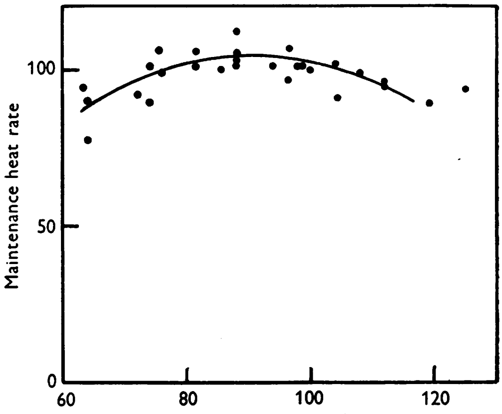

Fig. 3.

Fig. 2. Variation of maintenance heat rate with length, expressed as percentage of heat rate at the resting length in the body. Frog muscle, 0° C.

Fig. 3. Variation of maintenance heat rate with length, expressed as percentage of heat rate at the resting length in the body. Toad muscle, 0° C.

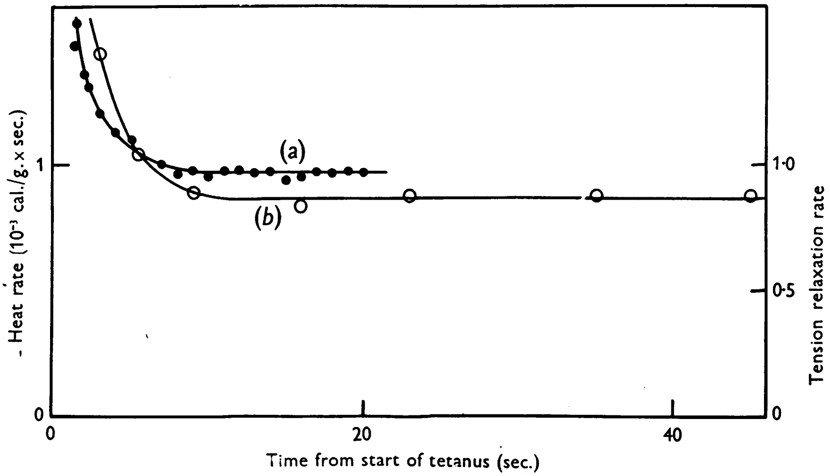

Fig. 4. Curve (*a*) maintenance heat rate during a prolonged tetanus. Curve (*b*) rate of tension relaxation (reciprocal of time to tension fall of 5 %) measured during gaps in stimulation during a prolonged tetanus. Toad muscle, 0° C. Length 25 mm., weight 106 mg.

Rate of relaxation

The relaxation rate was measured as the reciprocal of the time taken for the tension to drop by 5 % after the last stimulus of an isometric contraction.

This rate, in a frog muscle at 0° C. stimulated twice a second, decreased for about 9 sec. and then became steady at a value which remained unaltered after as much as 45 sec. of stimulation (curve *b*, Fig. 4).

The maintenance heat rate during a prolonged tetanus of the same muscle is given in curve *a*, Fig. 4. The similarity of curves *a* and *b* is obvious. As the tetanus continued the contraction became more economical (Bronk, 1930), i.e. the amount of reactivation necessary to maintain the contraction decreased: but after a certain duration of stimulus it remained constant.

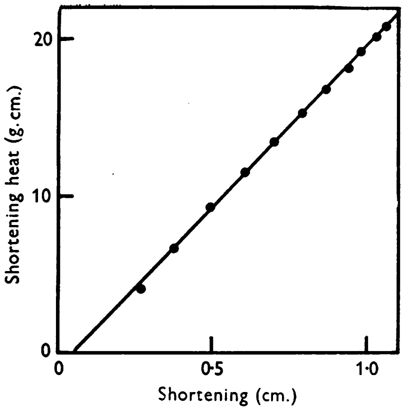

Fig. 5. Heat of shortening. Frog sartorius 0° C. Length in body 32 mm., weight 205 mg. Slope $a = 20{\cdot}5$ g. weight. $a/A = 335$ g./cm^2.

Heat of shortening

With a frog sartorius the relation of heat of shortening to shortening is linear up to more than 30% shortening, and with a toad sartorius up to more than 50%. Fig. 5 shows the results of an experiment in which a frog muscle initially of length 32 mm. shortened freely for 10 mm. The slope of this line is 20·3 g. weight and represents '*a*' in Hill's paper (1938). The fact that the line does not go through the origin is to be attributed to the sudden elastic shortening which occurs immediately after release. In order to compare the shortening heat from different muscles the value a/A was calculated, where A is the cross-section of the muscle at the resting length in the body. For this muscle a/A was 335 g. weight/cm.^{2}. Table 1 shows the results of a series of experiments.

With a snail muscle of weight 15 mg. and initial length 28·5 mm., linearity of heat with shortening occurred with more than 12 mm. shortening.

The implications of the fact that the heat liberated for a given amount of shortening is independent of the muscle length at which shortening occurs has been discussed elsewhere (Hill, 1949*c*).

TABLE 1. Heat of shortening

(In the second column a is the constant of the observed heat of shortening ax, and A is the cross-section of the muscle at rest in the body.)

Date	a/A (g./cm.^{2})	Shortening (mm.)	Resting length (mm.)	Initial length (mm.)
		Frog, 0° C.		
1 April 1949	490, 554	10	28	28
2 April 1949	437	10	28	31
25 May 1949	335	10	32	—
26 May 1949	335	10	32	33
3 June 1949	468, 474	11·5	31	32
10 June 1949	544, 555	10	30	31
Mean	455	—	—	—
		Toad, 0° C.		
21 March 1949	272	12	23	25
23 April 1949	242	11	28·5	31
26 April 1949	430, 435, 530	11	26	27
8 June 1949	380	10·5	27	28
9 June 1949	385	10·5	27	28
Mean	383	—	—	—
		Snail		
23 June 1949, 16° C.	445	9	—	30
25 June 1949, 16° C.	370	13	—	28·5
6 July 1949, 7·5° C.	380, 377	10	—	26·5
Mean	393	—	—	—

SUMMARY

1. During a prolonged stimulus the rate of heat production falls from a high initial value towards a steady level reached after an interval depending on stimulus frequency. The rate of relaxation, measured during a gap in the stimulus, falls in the same way.

2. The steady value of maintenance heat rate at 0° C. varies with muscle length but only to a small extent: the decrease at lengths shorter than the resting length is less than that found by Fenn & Latchford (1933), by another and possibly less reliable method at room temperature. The effect of length on maintenance heat rate is less for toad than for frog muscle.

3. Heat of shortening is proportional to shortening over a wide range; for 50% shortening with toad, for 30% shortening with frog and for 50% shortening with snail muscle.

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