Work and heat in a muscle twitch

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In a single twitch, when a muscle shortens against a load, doing work, the heat produced is independent of the work done, provided the amount of shortening is kept constant. The total energy liberated may be expressed as \( A + W + ax \), where \( A \) is the heat of activation, \( W \) is the work and \( ax \) is the heat of shortening. This relation is true not merely for the whole contraction but for any part of it.

The rate at which energy is liberated by a muscle during a twitch, in excess of the activation heat, is a decreasing linear function of the load \( P \): 

\[ \frac{dW}{dt} + a \frac{dx}{dt} = b(P_0 - P) \]

This relation is the basis of the characteristic equation connecting the speed of shortening to the load.

These relations are the same as were previously found for tetanic contractions, with similar constants.

The active state appears to be set up suddenly very soon after a shock.

The physical basis of these conclusions is discussed.

It was shown (Hill 1938) that when a muscle shortens in a tetanically maintained contraction it liberates extra energy in two forms, (i) as 'shortening heat', in amount proportional to the shortening, and (ii) as external mechanical work. The shortening heat per cm. of shortening was independent of the load, and therefore of the work done and the speed of shortening.

In the first paper of the present series it was shown that, apart from mechanical energy turned into heat in relaxation, the heat produced in a single twitch occurs in two forms, (1) heat of activation, which (as a first approximation at least) is independent of length, load, shortening or work, and (2) heat of shortening, proportional to the amount of shortening but, per unit of shortening, independent of its speed and therefore independent of load. In addition to these heats, energy is liberated in the form of mechanical work, depending on the load and the shortening. The first purpose of this paper is to show that, provided the amount of shortening is kept constant, the work can be varied over a wide range without any effect on the heat: or, more generally, that the total energy \( E \) set free in a muscle twitch can be expressed in the form:

\[ E = A + W + ax, \]

where \( A \) is the heat of activation, \( W \) is the work done, \( x \) is the amount of shortening and \( a \) is a constant of the order of 350 g.cm. per cm. shortening, reckoned per sq. cm. of muscle cross-section.

In order to vary the work without changing the amount of shortening, the ergometer described in the preceding paper was used. With initial length constant, the load could be varied from the least weight required to hold the lever \( A \) down to the screw \( H \), up to the greatest which the muscle would lift 'over'. Provided that the weight was lifted 'over' the muscle was then left free to shorten as much as it could. With frogs' muscles the total amount of shortening was practically
he same whatever the load on the ergometer. With toads' muscles the total shortening was rather less with the greater loads: the reason for this was that more time was taken in lifting the greater loads, so less time remained for subsequent shortening. Toads' (*Bufo bufo*) muscles shorten considerably more in a twitch than frogs', so the effect of the greater load was more apparent.

Since the ergometer lever was always tipped over, no load remained on the muscle after shortening and the heat, recorded photographically, contained no degraded mechanical work. A small correction was applied to the heat record to allow for heat loss but no other analysis was necessary. In order to make the results independent of possible progressive change in the muscle, observations were recorded at regular intervals and repeated in the reverse order, or otherwise distributed so as to eliminate change. In many cases the whole series was repeated with the muscle reversed on the thermopile, and mean values taken to avoid the effects of possible inequality between the inside and outside of the muscle. Details of two experiments on frogs' sartorii follow.

**Experiment 1.** Muscle 34 mm. long, 113 mg., 0°C. Single shocks (supermaximal) every 3 min. Ergometer provided initial load 0·86 g., afterloads 0, 8 and 10 g. Additional isotonic load 0·43 g., lifted 10 mm. Ergometer load lifted 4·05 mm., then 'over'. Muscle failed to lift 11·86 g. 'over', large relaxation heat recorded.

<table>
<thead>
<tr>
<th>load on ergometer (g.)</th>
<th>0·86</th>
<th>8·86</th>
<th>10·86</th>
</tr>
</thead>
<tbody>
<tr>
<td>heat (g.cm.)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10·1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10·1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10·0</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>10·5</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>10·5</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>10·3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10·4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean heat</td>
<td>10·25</td>
<td>10·35</td>
<td>(10·7)</td>
</tr>
<tr>
<td>work (g.cm.)</td>
<td>0·8</td>
<td>4·0</td>
<td>4·8</td>
</tr>
<tr>
<td>efficiency (%)</td>
<td>7</td>
<td>28</td>
<td>31</td>
</tr>
</tbody>
</table>

**Experiment 2.** Muscle pair, 174 mg. Twitches in succession, load varied. 0°C.

<table>
<thead>
<tr>
<th>work (g.cm.)</th>
<th>0·7</th>
<th>4·4</th>
<th>6·5</th>
<th>7·2</th>
<th>0·7</th>
<th>2·4</th>
<th>4·8</th>
</tr>
</thead>
<tbody>
<tr>
<td>heat (g.cm.)</td>
<td>18·3</td>
<td>17·8</td>
<td>17·9</td>
<td>18·4</td>
<td>18·8</td>
<td>19·0</td>
<td>18·6</td>
</tr>
<tr>
<td>work (g.cm.)</td>
<td>7·2</td>
<td>2·4</td>
<td>0·7</td>
<td>0·7</td>
<td>6·8</td>
<td>3·5</td>
<td>0·7</td>
</tr>
<tr>
<td>heat (g.cm.)</td>
<td>19·2</td>
<td>19·9</td>
<td>19·9</td>
<td>20·6</td>
<td>21·7</td>
<td>19·9</td>
<td>20·6</td>
</tr>
</tbody>
</table>

In experiment 1 the work changed from 0·8 to 4·0 g.cm. without any significant change in the heat. The heats in experiment 2, if plotted successively, show a slight progressive increase in the response of the muscle, but no correlation at all between heat and work. Eight other experiments at 0°C on frog's muscle are
summarized in the following table. Each recorded number is the mean in a series and reverse with varying load, sometimes several times repeated, so as to avoid the effect of any progressive change in the muscle. In each experiment the heats are expressed as percentages of the heat with the smallest load. In order to make the results of different experiments comparable, the work is given as a percentage of the heat. The average value of the heat was 125 g.cm. (about $3 \times 10^{-3}$ cal.) per g. of muscle.

<table>
<thead>
<tr>
<th>work/heat (%)</th>
<th>6</th>
<th>12</th>
<th>16</th>
<th>19</th>
<th>22</th>
<th>25</th>
<th>27</th>
<th>30</th>
<th>32</th>
<th>35</th>
<th>45</th>
<th>45</th>
<th>47</th>
<th>mean heat (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>99</td>
<td>99</td>
<td>100</td>
<td>99</td>
<td>93</td>
<td>98</td>
<td>103</td>
<td>100</td>
<td>95</td>
<td>102</td>
<td>101</td>
<td>94</td>
<td>100</td>
<td>92</td>
</tr>
</tbody>
</table>

We see how the work can be varied from almost nothing to nearly half the heat, without any effect on the heat.

With toads’ muscles the results were slightly complicated by the occurrence of rather less shortening after lifting greater loads. The following experiment is typical.

**Experiment 3.** Toad’s sartorius, 75 mg., 32 mm. long, 0°C. ‘Over’ 3-9 mm. corresponded to 7 mm. shortening. Each result is the mean of four, in a series and reverse, repeated with the muscle turned round on the thermopile.

| load lifted (g.) | 1·74 | 5·74 | 10·74 | 15·74 |
| heat (g.cm.)     | 10·15| 10·1 | 9·7   | 9·35  |
| work (g.cm.)     | 0·7  | 2·2  | 4·2   | 6·1   |
| efficiency (%)    | 6    | 18   | 30    | 39    |
| max. shortening (mm.) | 14·1 | 13·6 | 12·9  | 11·5  |

If the differences of heat were due to differences of shortening they would correspond to a heat of shortening of 3·5 g.cm. per cm., or 160 per sq. cm. of muscle cross-section. This is smaller than the mean value found in the previous paper, over the main range of shortening, but a smaller value at the extreme limit of shortening was indicated by the results there given.

Other similar experiments showed the same result. With greater loads the heat was generally slightly less, but so was the total shortening, the difference requiring a reasonable allowance for the heat of shortening.

We may conclude therefore that when the work is varied by changing the load there is no corresponding variation of the heat, except in so far as the shortening also is changed. The equation:

$$E = A + W + ax$$

gives us three separate terms for the total energy; the heat of activation, the work and the heat of shortening. In general the amount of shortening will depend on the conditions of loading, so to that degree the second and third terms are not strictly independent. In an isotonic contraction under load $P$ the equation reduces to the simple form:

$$E = A + (P + a) x.$$

These equations should hold, not only for the whole contraction but for any part of it; in the last one, for example, $E$, $A$ and $x$ can all be regarded as functions of $t$, the time after the shock.
The results of this paper confirm, on the single twitch, the conclusions reached in the earlier investigation (Hill 1938) of the tetanic contraction. They differ substantially, however, from those of previous papers. Hartree & Hill (1928b), for example, concluded that in a twitch the total energy set free is the same whether work is done or not. The chief reason for the disagreement is that they took the isometric twitch as the standard example of a contraction in which no work is done, and compared the total energy in a contraction in which external work was performed with the heat under isometric conditions. We know now (see the preceding paper) that the isometric contraction is a very complex affair, in which a considerable amount of work is actually done and transformed into heat both during and after contraction. Hartree & Hill were unaware of the shortening heat and their results on muscles allowed to shorten may have been affected by the errors* which dogged the footsteps of all myothermic investigation before the ‘protected’ thermopile was introduced. Their results on tetanic contractions are similarly suspect. In fact, no conclusions for which isometric contractions were taken as standard, for comparison with contractions in which work was performed, can now be accepted as valid: while any earlier results of experiments in which shortening occurred ought now, before acceptance, to be checked with ‘protected’ thermopiles.

In an earlier paper (1928a), on the maximum work and mechanical efficiency, Hartree & Hill did not assume the isometric contraction as the base-line of zero work: their results are in principle valid, but the lowness of the maximum efficiency they obtained (26 %) is suspicious in view of the much higher values (up to 40 %) found later by Hill (1939b) and in the present work. Possibly the classical error due to differences of temperature along a muscle shortening on to an ‘unprotected’ thermopile may have made their heat readings too high. Wyman’s (1926) results on the relation of work and heat in tortoise muscle should now be repeated in view of present knowledge and with the much better instruments now available.

Most of the earlier myothermic observations did no more than record the maximum deflexion, giving the total heat. As we now know, the heat production is a very complex business and present methods, allowing a more or less undistorted

* These errors were due to differences of temperature along the length of the muscle. Even at rest, and particularly during recovery from previous activity, a muscle produces enough heat to keep its temperature measurably above that of its surroundings. The excess temperature is inversely proportional to the thermal conductivity of the environment, so that the part of the muscle lying on the thermopile is bound to have a lower temperature than the part beyond it surrounded only by poorly conducting gas. If therefore a muscle is allowed to shorten, parts of it previously off the thermopile come on to it and the rise of temperature recorded is due not only to heat production but to a warmer region of the muscle making contact with the thermo-junctions. This is avoided by ‘protecting’ the active region of the thermopile by a similar ‘dummy’ region beyond it, long enough to ensure that any part of the muscle coming on to the active thermo-junctions has been losing heat previously at precisely the same rate as the part already on them. The protected thermopile has been described in earlier papers (Hill 1937, 1938, 1939a). Its heavy metal frame, together with good thermostat control, ensures that no significant differences of temperature exist along the thermopile itself.
picture of its whole course to be recorded photographically, give much greater
certainty for understanding its nature. In the past a laborious numerical analysis
was required before the time-course of the heat was revealed, and this could
scarcely be applied as a routine in every kind of measurement.* Consequently,
much was missed which is now evident. Some of the results of older experiments
in which shortening occurred (including those of Fenn (1923, 1924); Azuma (1924);
Hartree (1925, 1928); Hill (1930); Feng (1932)) can now be interpreted in the light
of present knowledge. Others ought to be repeated with present technique.

In the experiments (Hill 1938) on tetanic contractions it was found that the
rate of extra energy liberation, over and above the 'maintenance heat', is a linear
function of the load:

\[(P + a) \frac{dx}{dt} = b(P_0 - P),\]

where \(P_0\) is the isometric tension. This led to the characteristic equation:

\[(P + a) (v + b) = (P_0 + a) b,\]

relating the speed of shortening to the load. The constant \(a\) was the same whether
derived from thermal measurements or from purely mechanical ones. The accuracy
of the characteristic equation was examined in greater detail by Katz (1939) and
has recently been confirmed by Wilkie (1949) for the contraction of human arm
muscles.

The accuracy of the equation \((P + a) \frac{dx}{dt} = b(P_0 - P)\) has been tested against
the results of the present experiments and confirmed. The true value of \(P_0\) cannot
be determined directly for a single twitch: relaxation sets in before the contractile
elements of the muscle have had time to complete their shortening against the
increasing tension of the series elastic elements (see Hill 1938, figure 15). If,
however, we plot the observed values of \((P + a) \frac{dx}{dt}\) against \(P\) in a series of isotonic
contractions under different loads we obtain a straight line, the extrapolation of
which back to the axis should give the true value of \(P_0\). The fact that a linear relation
is obtained confirms the equation. The procedure is illustrated by the following
experiment.

**Experiment 4.** Pair of toad’s semi-membranosi, 159 mg., 2·7 cm. long, 0°C.
Single shocks. Initial load 6·0 g., afterloads 0·0, 15·6, 37·2 and 63·2 g. Heat and
shortening simultaneously recorded, and heat of shortening, 32 g.cm. per cm.,
calculated as described in a preceding paper. The curves of shortening are given
in figure 1. They are linear over a considerable extent, the velocities being as follows:

<table>
<thead>
<tr>
<th>Load (P) (g.)</th>
<th>6</th>
<th>21·6</th>
<th>43·2</th>
<th>69·2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Velocity (\frac{dx}{dt}) (cm/sec.)</td>
<td>1·8</td>
<td>1·02</td>
<td>0·50</td>
<td>0·17</td>
</tr>
<tr>
<td>(P + a)</td>
<td>38</td>
<td>53·6</td>
<td>75</td>
<td>101</td>
</tr>
<tr>
<td>((P + a) \frac{dx}{dt})</td>
<td>68</td>
<td>54·5</td>
<td>37·5</td>
<td>17</td>
</tr>
</tbody>
</table>

Adding \(a\) to \(P\) the values of \((P + a) \frac{dx}{dt}\) are calculated in the last row. These are
plotted in figure 2 (upper line). The linear relation shown has a slope \(b = 0·82\) and
extrapolated to the horizontal axis gives \(P_0 = 90\).

* W. Hartree once estimated that in his analyses of muscle heat he had written down
between \(10^7\) and \(10^8\) figures.
Similar calculations were applied to two other experiments. The lower line in figure 2 gives the relation for a pair of rather smaller toad muscles (116 mg., 5.5 mm.), the results being \( a = 15.5, P_0 = 60, b = 0.54 \). Another pair of toad muscles (69 mg., 24 mm.) gave \( a = 7.9, P_0 = 23, b = 0.66 \). The mean value of \( b \), reckoned not in cm./sec. (as above) but in terms of muscle length per sec., was \( 26 \), while the mean value of \( a/P_0 \) was \( 0.32 \). The mean values given (Hill 1938) \( y \) tetanic contractions of frog muscles at \( 0^\circ \mathrm{C} \) were, \( b = 0.33, a/P_0 = 0.26 \). The

![Figure 1](http://rspb.royalsocietypublishing.org/Downloaded from http://rspb.royalsocietypublishing.org/)

**Figure 1.** Isotonic contractions at \( 0^\circ \mathrm{C} \), recorded photoelectrically, of pair of semi-membranosus muscles of toad. 6 g. initial load, total loads as shown. For details see text.

![Figure 2](http://rspb.royalsocietypublishing.org/)

**Figure 2.** \((P+a)\frac{dx}{dt}\) plotted against \( P \). \( P \), load (g.); \( x \), shortening (cm.); \( ax \) heat of shortening (g.cm.); \( t \) time. Upper line for the experiment of figure 1. See text.

The number of the present experiments is too small for accurate mean values, but it is clear that \( b \) and \( a/P_0 \) are of the same order of size, the slower toad muscles having a rather smaller value of \( b \).

It had been expected that \( b \) (expressed as a fraction of muscle length per sec.) would be about one-half as great in toad muscles as in frog muscles, in proportion to their relative speeds. It is clearly more than one-half. The reason may be as follows. Toad muscles can shorten considerably more than frog muscles, and \( b \)
ought really to be expressed as a fraction of total possible shortening rather than of total length, per sec. Reckoned in this way \( b \) is probably about half as great as for frog muscle.

The physical basis of the fact that the rate of total energy liberation, \((P + a) \frac{dx}{dt}\), in excess of the heat of activation, is a linear function of the load, was discussed in the 1938 paper (p. 164). No new evidence of the nature of this simple but mysterious relation has appeared since: nor indeed has any new light been shed on the physical nature of the heat of shortening. It is very satisfactory, at any rate, that the present results with the single twitch agree so exactly with the earlier ones on the tetanically maintained contraction. The question naturally arises whether, or to what extent, the three quantities \( A, W \) and \( ax \) which make up the total energy in a twitch are independent of one another, and whether they are derived from the same, or different, physical or chemical changes. That \( A \) is independent of the other two seems most probable: but the work \( W \) and the heat of shortening \( ax \) are connected with one another and the load by the relation we have been discussing, which can be integrated in the form \( W + ax = \int (P_0 - P) \, dt \), so they cannot be regarded as really independent. In fact, the load determines the rate and the total amount of shortening, and the work is determined by the load and the shortening. It is scarcely pertinent, therefore, to inquire whether work and heat of shortening are derived from independent physical or chemical changes.

If \( a \) could be regarded as a constant internal resistance to shortening the matter would be simpler, for then the shortening heat \( ax \) would be equivalent to the work done in overcoming this resistance and the whole of the energy set free in excess of the activation heat could be treated as work. An objection to this is that there should then be a difference \( 2a \) between the loads (i) at which a muscle just shortens, and (ii) at which it just lengthens, and Katz's (1939) results show that the difference, if it exists, is much less than \( 2a \). This objection is avoided if a muscle fibre is regarded not as a single contractile element with a parallel constant resistance, but as a large number of such elements in series. At the full isometric tension the stronger of these might be on the point of shortening and stretching the weaker: a small decrease of tension would allow the former to shorten, a small increase of tension would stretch the latter, and the difference of tension between shortening and lengthening would be small. We cannot attribute the heat of shortening to a viscous resistance, for it is independent of the velocity of shortening. Whether \( ax \) changes sign when \( x \) changes sign (lengthening instead of shortening) is not certain: frogs' muscles do not stand stretching well enough to give decisive results (Hill 1938, p. 179). Possibly the jaw-muscles of dog-fish which stand stretching well (Levin & Wyman 1927, p. 224) would allow a decision to be reached. It may still be possible, when we come down to its molecular basis, to regard \( a \) as a constant internal resistance to shortening, so that \((P + a) \frac{dx}{dt}\) would be the total rate at which work was being done. We should then have to think of a system in which the rate of doing work is a decreasing linear function of the load. No simple mechanical or electrical arrangement has this property and without some clearer idea of the general nature of the muscular machine it seems
It has been a frequent astonishment in this work to find how accurately and consistently certain simple relations occurred, in some cases over a wide range. Toad muscles, for example, shorten by very considerable amounts, and one had expected that the heat of shortening per cm. would change as the muscle shortened. It might for example, have increased in proportion as the muscle got thicker, in which case the element of shortening heat would not be proportional to $-81$, where $l$ is length, but to $-8l/l$. To test this, $\Delta H$ between two heats was plotted, not against $-\Delta l$ as in the first paper of this series, to give the heat of shortening, but against $-\Delta \log l$. No regularity, however, was found. The heat of shortening appears to be proportional to the shortening itself over a wide range. Again, with a shock applied at the middle of a muscle with anodes near its ends, the form of the isotonic twitch, recorded without significant friction, is linear over a large part of its course as shown in figure 1: had it not been for this fortunate simplicity the argument relating speed of shortening to load would have been very complicated and no simple relation could have been established. The relatively small variation of the heat of shortening from muscle to muscle gave confidence that one was dealing with a real thing. The complete absence of relaxation heat when the muscle was under zero tension, and the fact that the amount of work done had no effect on the heat provided that shortening was constant, were other examples of simple regularities. They encourage one to believe that when the mechanism of muscular contraction is discovered it will be found to be of a rather simple nature.

One final regularity should be noticed, viz. the way in which all the relations here established appear consistently in the twitch from the earliest moment at which they can be examined. There is no sign of a gradual building up of a state of activity. No doubt that building up does take time, but the time taken seems to be very short. When a slower development of activity appears to occur it is found to depend on such things as propagation of contraction away from the stimulating electrodes, or on internal shortening by contractile elements against the rising tension of elastic elements. Gasser & Hill (1924) concluded from experiments on quick stretches that ‘the fundamental mechanical response’ attains its maximum intensity quite early in the contraction. Brown’s experiments (1934, 1936) support the view that the greatest activity in a twitch occurs very soon after stimulation. The ‘activation heat’, which is probably a sign of the process by which the muscle is set ready to shorten or develop a force, begins very soon after a stimulus, with its maximum rate at the start; details will be given in a later paper. As soon as the whole muscle is excited it shortens at the full rate corresponding to the load. We may, in fact, regard the active state as being established suddenly soon after the shock. It is maintained during a tetanus; in a twitch it disappears, apparently without any accompanying heat, in the process known as relaxation.
Myothermic methods

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[Plate 8]

The recent development of galvanometers has led to substantial improvements in the technique of recording and analyzing the heat production of muscle, particularly in facilitating the correlation in time and magnitude between thermal and mechanical events. The heat changes can be resolved in time to within a few milliseconds; the changes of length or tension, recorded simultaneously, are practically unaffected by friction or inertia. The physical properties of the instruments, and numerical methods of analysis, are discussed.

Introduction

The rise of temperature in a muscle twitch is small, being of the order of $3 \times 10^{-3}$ °C. To obtain sufficient accuracy it is necessary to record this to a few parts per thousand, say to $10^{-5}$ °C. But the heat production of muscle is a complicated process, and only a limited amount is learnt by simply measuring its total quantity; for most purposes it is necessary to record its course as a function of time. A single twitch, however, is a very rapid affair. Even at 0° C the heat in the twitch of a frog's skeletal muscle begins to appear about 10 msec. after the stimulus, and is complete.