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THE RELATION BETWEEN FORCE AND SPEED IN MUSCULAR CONTRACTION

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In a recent paper Hill [1938b] has shown that the rate at which energy is liberated by a tetanized muscle increases linearly as the external force is reduced below the isometric tension. If a muscle shortens against a force $P$, which is smaller than the isometric tension $P_0$, work is done by the muscle, and in addition heat is liberated, in excess of the isometric, at a rate proportional to the speed of shortening $v$. The rate of total energy production exceeds the isometric heat rate by an amount proportional to the reduction of external tension $P_0 - P$. These findings were expressed by the equation

$$v (P + a) = b (P_0 - P), \quad \ldots (1)$$

where $a$ [g.] and $b$ [cm./sec.] are constants ($a$ g.cm. being the "extra heat" for 1 cm. shortening, $b$ g.cm./sec. the increase of the rate of energy production for 1 g. tension loss).

This formula relates two variables, the speed of shortening $v$ and the external force $P$, which can be determined without any heat measurements. According to this formula, which can also be written as

$$(v + b) (P + a) = (P_0 + a) \ b = \text{const.},$$

the relation between force and speed is a rectangular hyperbola, with asymptotes at $P = -a$, and $v = -b$. As has been verified by Hill [1938b], the value of $a$ derived from a mechanical $P$-$v$ relation is equal to the extra heat per cm. shortening (frog's sartorius, $0^\circ$ C.). It was of particular interest to find whether this relation remains valid if the applied force becomes greater than the isometric tension. Obviously, for $P > P_0$, $v$ becomes negative: the muscle lengthens as was found already by Fick.
[1882]. Quantitative information on this point, however, was not yet available, and the heat measurements failed to give any conclusive result.

Hill has further shown that, by introduction of some simple additional assumptions, the $P-v$ relation can be used to calculate the development of isometric tension during a tetanus. There is good reason to believe [see Hill, 1938a, b] that during an isometric contraction, although the total length of the muscle remains practically unchanged, the active contractile elements shorten against elastic, passively extending tissue parts. If the latter have little or no damping and follow Hooke's law, the rate of development of isometric tension would be proportional, at any moment, to the speed of internal shortening of the active part and could be calculated.

In continuation of Hill's recent work the mechanical relations have been studied in some detail. The experiments on the $P-v$ relation and on the development of isometric tension can be dealt with rather shortly, since they are essentially a confirmation, or extension, of previous findings [Hill, 1938a, b]. Special attention, however, will be paid to the mechanical effect of forces greater than isometric since this differs from the theoretical expectations.

**Method**

The experiments were made mostly on sartorius muscles of English *Rana temporaria*, also of Hungarian *R. esculenta*, and on the retractor penis of the tortoise [see P. Hoffmann, 1913], at 0–20° C. The muscles were stimulated usually in oxygenated Ringer's solution. The arrangements for stimulation and for mechanical recording were the same as described by Hill [1938b]. In the later experiments, a lever system of slightly different properties was used:

Isotonic: Magnification, 4.04 times.
   Equivalent mass with zero load, 3.1 g.
   Ratio of lever arms, initial load: 10 : 1, after-load: 11.5 : 1.

Isometric: Sensitivity, 1 mm. deflexion for 3 g.
   Period, 40 msec.
   Extensibility of lever + chain, 1.2 mm./100 g.

To study the form of the isometric record, at 0° C., a lever of shorter period (22 msec.) was used.

With forces greater than isometric, the load was held up by a magnet, until the muscle had developed its isometric tension after an initial shortening of several mm. The muscle was never stretched beyond its resting length. If required, the development of tension at the short
FORCE AND SPEED IN MUSCULAR CONTRACTION

length was recorded by an isometric lever which became disengaged when the muscle lengthened under the applied force. A Lucas' rotating contact breaker was used to time the release of the magnet. By employing, in addition, an adjustable contact breaker rotating on the same shaft as the stimulating commutator (Pye), a more accurate timing, at a given interval between a pair of shocks, could be obtained. In some experiments the magnet was replaced by the Levin-Wyman apparatus which permitted a more gradual increase of the applied force. The load was connected with the apparatus by a slightly elastic chain which was released gradually, depending (i) upon the setting of the needle-valve, (ii) upon the speed of lengthening of the muscle under the increasing tension. A rapid initial "yielding" of the muscle (p. 57), therefore, automatically delayed the further rise of tension. The arrangement was needed only for a qualitative comparison of instantaneous and gradual loading.

RESULTS

(1) The relation between force and speed of isotonic shortening

The muscle was extended by a small initial load and allowed to shorten several millimetres against various after-loads. Usually, with not too large loads, shortening over most of the distance occurred at practically uniform speed which was measured from the slope of a kymograph record.

The fact that the speed of shortening was nearly constant over a distance of several millimetres seems a little surprising, since one would expect it to vary with the isometric tension. Actually, the changes of length remained within a range near the flat maximum of the \( P_0 \)-length relation. With large after-loads, distinct changes of the speed were observed, depending upon the variation of \( P_0 \) with actual length of muscle. Qualitatively, this agrees with equation (1), according to which \( v \) is proportional to \( (P_0 - P) \), i.e. a change of \( P_0 \) becomes more important the larger the load.

In some experiments all observations were repeated in symmetrical order, in other cases the isometric tension was determined at beginning and end of a single series. In a few cases, the speed of shortening was compared (i) at the beginning of stimulation, (ii) after the full isometric tension had developed (quick release). While little or no difference was found in the frog's sartorius [cf. Fenn & Marsh, 1935; Hill, 1938b], an appreciable difference was observed in tortoise muscle (see Table I).

The predicted relation can be tested, and the constants \( a \) and \( b \) determined in various ways, e.g. by simultaneous equations with different
TABLE I. Tortoise muscle, 17° C. Speed of isotonic, after-loaded shortening, with "initial" and "delayed" (5 sec.) release

<table>
<thead>
<tr>
<th>Force g.</th>
<th>Speed, cm./sec.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-6</td>
<td>3-44</td>
</tr>
<tr>
<td>6-0</td>
<td>2-53</td>
</tr>
<tr>
<td>36-4</td>
<td>0-88</td>
</tr>
<tr>
<td>71-0</td>
<td>0-3</td>
</tr>
</tbody>
</table>

"Initial" "Delayed"

Po = 116 g.

Fig. 1. Relation between force and speed of shortening. (a) Sartorius of English R. temp., 0° C. Single series. Curve calculated for $a = 20$ g. ($a/P_0 = 0-2$), $b = 1-08$ cm./sec. (0-31 length/sec.), $P_0 = 99-6$ g. Divergences between observed and calculated speeds <3%. (b) Retractor penis of tortoise, 19-8° C. Single series. Curve calculated for $a = 11-85$ g. ($a/P_0 = 0-1$), $b = 1-20$ mm./sec. (0-037 length/sec.), $P_0 = 121$ g. Divergences <5%.

TABLE II. Summary of constants $a$ and $b$

(1) Frog's sartorius (English R. temp.).

0° C.: mean of twelve experiments, $a/P_0 = 0-26$ (0-18-0-33):

$b = 0-34$ length/sec. (0-24-0-42 length/sec.).

10-9° C.: mean of three experiments, $a/P_0 = 0-38$ (0-32-0-43):

$b = 1-12$ length/sec. (1-1-1-15 length/sec.).

(2) Tortoise (retractor penis).

$b$: mean of six experiments in July/August:

$b = 0-032$ length/sec. at 16-2° C. (varying between 0-018 at 9-7° C. and 0-057 at 19-5° C.);

mean of two experiments in December, on faster muscles:

$b = 0-07$ at 14° C., 0-09 length/sec. at 17° C.

$a/P_0$: mean of eight experiments:

$a/P_0 = 0-11$ (0-07-0-16).
values of $P$ and $v$, by plotting $P$ against $(P_0 - P)/v$ (Shapiro, personal communication), or graphically as illustrated in Fig. 2. The results of two typical experiments (frog, 0° C.; tortoise, 20° C.) are shown in Fig. 1. A summary of the values of $a$ and $b$ is given in Table II. In most cases the observed data fitted the hyperbola well and, what is more important, gave a value of $a$ similar to that derived from the heat measurements [Hill, 1938b]. While $b$ greatly changes with temperature [Hill], and with

the particular kind of muscle used, the value of $a/P_0$ varies to a less extent. At the same temperature, the relative value of $b$ (per length of muscle) is about 14–40 times greater, $a/P_0$ 2.5 times greater in frog’s than in tortoise muscle.

It will be necessary to compare the data, for tortoise muscle, with direct measurements of the heat of shortening. The fact that the speed of shortening, with small after-loads, is greater if the shortening occurs some time after the beginning of stimulation (Table I) indicates that the full active state is not developed immediately; in this case, the observed initial velocities, with small loads, would be too low, and the derived

Fig. 2. Graphical determination of $a$ and $b$. $v$ is plotted against $P$ as in Fig. 1. The lines connecting the projections of the plotted points on (i) the horizontal axis and (ii) a vertical line through $P = P_0$, meet at the centre of the hyperbola. (1) Sartorius of English R. temp., 0° C. It can be seen from the figure that $v (P + a) = b (P_0 - P)$, i.e. equation (1) is obeyed. (2) Sartorius of Hungarian R. esc., 11.7° C. The curvature is slight, and the lines have been extrapolated only for illustration (see p. 50).
value of \( a \) too large. The speeds observed after a late release may be affected by other complications, as will be seen below (possibly partial "give" during isometric contraction, pp. 62, 63). Even if these errors are not serious, one must admit that, without direct confirmation by heat measurements, the constants derived from the mechanical data alone may have little meaning.

Furthermore, as is almost obvious from the equation (1) itself, it is sometimes impossible to derive the constants from the observed curve with any reasonable degree of accuracy. This is due to the fact that the observed curve forms only a section of the theoretical hyperbola (Fig. 2). The greater the values of \( a \) and \( b \) (which are the distances between the \( P \) and \( v \) axes and the asymptotes of the hyperbola), the smaller the observed section of the theoretical curve, hence the smaller the degree of exactitude with which this curve can be fitted to the results. In frog's muscle (especially in Hungarian \( R. \) esc.) at medium and high temperature, the curvature of the observed \( P-v \) relation was sometimes so slight (cf. Fig. 2) that an exact evaluation of the constants, from the mechanical results alone, became impracticable.

(2) The development of isometric tension [cf. Hill, 1938b]

A muscle consists not entirely of active contractile substance, but contains, in addition, inert tissue, cell membranes, connective fibres, tendon and other parts which do not contract but can be stretched passively. The elastic force of a stretched resting muscle is due partly, if not entirely, to these inert structures in parallel, and in series, with the contractile matter. In an isometric contraction, the active part actually shortens to some extent and stretches the inert structures in series with it. The speed of shortening becomes smaller the greater the elastic force of the stretched portions, in accordance with equation (1); the internal shortening stops when the elastic force becomes equal to \( P_0 \). If one assumes (i) that the active state is set up immediately at stimulation, (ii) that \( P_0 \) does not vary with the changes of length considered, (iii) that the force is proportional to the amount of lengthening of the passive elastic part (Hooke's law), and that this is free from any appreciable damping, then one can calculate the isometric tension curve as

\[
2.3 \times (1 + a/P_0) \times \log_{10} \frac{1}{1 - P/P_0} = t \times b/C, \quad ......(2)
\]

where \( t \) is the time interval reckoned from the start of tension rise, and \( C \) the total amount of elastic lengthening.

The general form of the calculated curve (Fig. 3) obviously resembles that of a typical isometric record, except for the slightly S-shaped start of the latter. The time-scale of the tension curve depends mainly upon the value of \( C/b \), the value of \( 1 + a/P_0 \) being approximately constant \((1.2 - 1.3)\).
The values of $a$, $b$ and $P_0$ being known, there are three ways of finding $C$: (i) directly, by determining the amount of quick release required to let the isometric tension drop to zero [Gasser & Hill, 1924; Hill, 1938a]; (ii) indirectly, by fitting calculated curves to the observed isometric tension records; (iii) by altering $C$ and measuring the resulting change in the rate of tension development. It is satisfactory that in the frog's sartorius, the three methods lead to consistent values of $C$.

Method (iii) was adopted in several experiments (examples in Fig. 3 and Table III). If the extensibility of the lever is increased by a known amount, it follows from equation (2) that the ratio of the times $t/t_1$
required for the development of \( P \) g. tension is equal to \( C/(C+C_1) \), \( C_1 \) being the known additional amount of elastic stretch. The method is very simple, since it merely requires attaching the muscle at two different distances from the torsion spring of the isometric lever. It depends, however, being an indirect method, upon the accuracy of the assumptions involved in equation (2).

Since \( P_0 \) changes slightly, if \( C \) increases, only a portion of the two tension curves can be used (Fig. 3, Table III). One obtains then an average value of \( C \) from a relatively low range of tensions. Since the extensibility of the elastic part probably decreases with increasing tension (p. 54), this method may lead to slightly too large a value of \( C \), hence to a theoretical curve which, in its later part, is relatively too slow. Furthermore, if the initial development of the active state introduces a small constant delay adding on to the times of tension development, this would again give slightly too large a value of \( C \).

### Table III. Development of isometric tension. Frog’s sartorius, 0° C.

Complete series and reverse

<table>
<thead>
<tr>
<th>A.</th>
<th>( P ) (g.)</th>
<th>( v_{\text{obs.}} ) (cm./sec.)</th>
<th>( v_{\text{calc.}} ) (cm./sec.)</th>
<th>( t_{\text{obs.}} ) (sec.)</th>
<th>( t_{\text{calc.}} ) (sec.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-6</td>
<td>15-65</td>
<td>4-03</td>
<td>2-31</td>
<td>1-17</td>
<td>0-565</td>
</tr>
<tr>
<td>3-2</td>
<td>59</td>
<td>4-0</td>
<td>2-39</td>
<td>1-15</td>
<td>0-54</td>
</tr>
</tbody>
</table>

B. Isometric tension curves, made before (I) and after (II) \( P-v \) relation. Levers of different elasticity. Ratio of \( t_4/t_1 \) measured between \( P = 20 \) and 50 g., at intervals of 5 g.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Extensibility of levers: 0-55 and 2-45 mm./100 g. respectively, +0-5 mm./100 g. due to chain.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

From this: \( k + 2.95 \over k + 1.05 \) = 1-55. \( k \) (muscle) = 2-4 mm./100 g. tension.

C. Mean of five isometric tension curves, taking origin at 1-5% \( P_0 \). \( P_0 = 93-5 \) g. Lever + chain stretching 1-05 mm./100 g. \( C \) (muscle + chain + lever) = 3-2 mm.

<table>
<thead>
<tr>
<th>( P/P_0 )</th>
<th>0-2</th>
<th>0-3</th>
<th>0-4</th>
<th>0-5</th>
<th>0-6</th>
<th>0-7</th>
<th>0-8</th>
<th>0-9</th>
<th>0-95</th>
</tr>
</thead>
<tbody>
<tr>
<td>( t_{\text{calc.}} ) (sec.)</td>
<td>0-029</td>
<td>0-042</td>
<td>0-067</td>
<td>0-101</td>
<td>0-148</td>
<td>0-217</td>
<td>0-324</td>
<td>0-525</td>
<td>0-73</td>
</tr>
<tr>
<td>( v_{\text{obs.}} ) (sec.)</td>
<td>0-03</td>
<td>0-045</td>
<td>0-07</td>
<td>0-1</td>
<td>0-14</td>
<td>0-21</td>
<td>0-32</td>
<td>0-55</td>
<td>0-77</td>
</tr>
</tbody>
</table>

Actually, on the frog’s sartorius, the results agree satisfactorily with theory. The value of \( C \) obtained by this method gives an approximate fit to the observed tension curve; the very good agreement in the case of Table III was rather unusual, but in five experiments the value of \( C \) determined in this way did not differ more than 15% from the one which would give the best fit.

At 0° C. the elastic stretch of the muscle (i.e. after deducting the known extension of chain and lever) was on the average 2-2 mm., varying in eleven experiments between 1-3 and 2-8 mm., on a muscle of average length 32 mm. The value of \( C \) tends to increase as a consequence of deterioration or injury (see p. 61 below); this is easy to understand, if
parts of the muscle fibres weaken or become inexcitable and then act like an added piece of passive elastic tissue.

It must be emphasized that the additional assumptions involved in the theoretical tension curve are in some respects over-simplified, and, therefore, while being adequate in the case of the frog's sartorius, may not be expected to apply generally. Clearly the active state does not develop at once; some time is required for the spread of the excitation wave and probably also for the transformation of the contractile substance. Furthermore, it is unlikely that the elastic tissue parts should follow Hooke's law exactly; more probably their extensibility decreases with increasing force, as does that of the resting muscle. For both reasons the rise of tension would be slowed down initially (as is indicated, for instance, in Fig. 3).

The importance of these disturbing factors apparently depends upon the kind of muscle; while, in the frog's sartorius, they can be neglected for a first approximation, in the retractor penis of the tortoise, for these and other reasons (pp. 62, 63), no satisfactory agreement was found between calculated and observed tension curves. The isometric tension of this muscle develops at \( \frac{1}{2} \) to \( \frac{1}{3} \) of the speed calculated, the elastic stretch being determined by a quick release (method (i)). A delayed development of the active state (cf. p. 49 above) and the non-linear tension-length relation of the elastic part, as found in this muscle by quick releases of various extents, are partly responsible for this discrepancy. They cannot explain, however, the protracted approach of the tension curve to its maximum level. This may be due, as will be discussed later, to a "giving" in this muscle of weak parts of the fibres, and consequently to a prolonged shortening of stronger parts in series with them, while the maximum tension is being approached.

(3) The relation between force and speed of lengthening in active muscle

It would be of great interest to decide whether the linear relation between force and rate of total energy production applies also to forces which exceed the isometric tension. While it is certain that the total energy output of a lengthening muscle (i.e. heat minus work), within certain limits of \( P/P_0 \), is less than during isometric contraction [Wyman, 1926; Hill, 1938b], a quantitative study has not yet been possible. As Hill pointed out, it is very difficult to demonstrate a negative "extra heat of lengthening", as required by equation (1), \( (a) \) because the changes to be expected are very small and are superimposed on a large, variable
“basic” heat rate, (b) because with forces considerably greater than the isometric the uniform lengthening (see below) is preceded by a partial “giving” or apparent “relaxing” of the muscle fibres (accompanied by a large outburst of heat) which may leave the muscle, during the subsequent period of “reversible” lengthening, in a state of diminished activity.

It is possible, however, in a frog’s sartorius, to continue the mechanical experiment to loads greater than \( P_0 \), and so to obtain a quantitative test of the theory. The muscle was allowed to shorten several mm. and then, after the isometric tension had developed nearly completely, was loaded either “instantly” (release of a magnet), or gradually (Levin-Wyman apparatus, see p. 47).

**Three components of lengthening.** If the force is suddenly applied, the mechanical record shows three distinct components (Fig. 4):

(i) An immediate downstroke due to the reversible lengthening of the elastic parts of muscle and lever system. This corresponds to the “instantaneous” shortening in a quick release. It is more or less proportional to the increase of tension \((P-P_0)\), usually about 1 mm. for a doubling of \( P_0 \) (0·6 to 1·1 mm. in eight experiments, mean 0·85 mm., on a muscle of average length 34 mm.), after deducting the extension of the chain. The elastic stretch of a stimulated fresh muscle, for a given increase of tension, is distinctly less in this high range of tensions than was found previously in a range between zero and isometric.

(ii) This is followed by a variable amount of initial “give” (Fig. 4), the speed and extent of which become larger the greater the applied
force. If $P$ is only slightly greater than $P_0$, this component is very small and may be imperceptible, especially when the force is applied gradually. It increases with $(P - P_0)$ at accelerating rate and eventually, with $P/P_0$ greater than about 1-8, gives the appearance of a complete mechanical relaxation.

(iii) If the load is not too great, the initial extensions (i) and (ii) are followed by a period of slow, uniform lengthening, which lasts until the end of the stimulus and is apparently the converse phenomenon of the uniform shortening against forces smaller than isometric.

The difference between initial yielding (ii), and slow steady lengthening (iii), is obvious in the cases of relatively large forces ($P/P_0 > 1-5$); with smaller loads, however, the transition is so gradual that the mechanical records alone would not permit a clear distinction between the two phenomena. Simultaneous heat measurements, however [Hill, 1938b], have shown that during the initial, more rapid lengthening, the rate of heat production is always greater, during the prolonged slow lengthening, if anything, less than during isometric contraction. Hill distinguished, therefore, between an initial "irreversible" lengthening in which, analogous to a "giving" wire or to a relaxing muscle, the work done by the falling load is dissipated irreversibly as heat, and (ii) a later "reversible" lengthening during which energy is apparently stored in the muscle, or rather its rate of energy liberation reduced, as predicted by theory. The term "irreversible lengthening" should not be interpreted as implying permanent injury of the muscle; it often does so, but this depends upon other factors (pp. 60 etc. below).

It may be pointed out that the ordinary isotonic relaxation curve (the same applies, though less markedly, to the isometric curve) could also be interpreted as a sequence—in the reverse order—of a period of slow "reversible" lengthening, followed rather suddenly by a breakdown of the contracted state. The sudden change may merely be due to the fact that the muscle relaxes quickly only when its internal force ($P_0$), during its gradual decay, has become less than about 60% of the external tension.

**Speed of "reversible" lengthening.** The speed of the slow, uniform component was measured and compared with the calculated velocity. The result is clear-cut: there is a consistent divergence between the observed and calculated speed of isotonic lengthening (Fig. 5); the actual velocities being several times smaller than the theoretical. This discrepancy is most obvious at high temperature where the $P$-$v$ curve shows a distinct discontinuity at $P_0$. The phenomenon remained unaffected by such alterations as withdrawal of $O_2$ or a large increase of the calcium content of the Ringer solution.

**Effect of temperature on the speed of lengthening.** For a given value of $P/P_0$, the speed of "reversible" lengthening increases with rise of temperature. The effect could not be measured very exactly, because the repeated stretches especially with large loads tended to produce permanent changes. The observations were made at two temperatures (0 and about 15° C.) on the same preparation; to check progressive alterations,
the results obtained at one temperature were compared with the mean results of two series (made before and after) at the other temperature. For a rise of 10° C, the speed of lengthening, at $P/P_0=1.3$, increased in six experiments 1.45–1.63 times, on the average 1.56 times. It changes less than the speed of shortening, which has a temperature coefficient of 2 or more, for a difference of 10° C. [Hill, 1938b].

![Fig. 5. (1) Relation between force and speed of shortening and lengthening. The broken lines give the theoretical $P$-$v$ relation for lengthening, using the constants $a$ and $b$ derived from the speeds of shortening. A. English $R$. temp. (i) 11.8° C.; (ii) 0° C.: B. Hungarian $R$. esc., as in Fig. 2 (2). Note the discontinuity at $P_0$. (2) Inset. Relation between force and size of initial rapid lengthening in the cases of (1) A. Ordinates: initial lengthening in mm. Full circles: elastic lengthening (including chain); hollow circles: total initial lengthening (elastic + "give"). The divergence between observed and predicted speeds of lengthening cannot be explained at present; mechanical analogies, of course, would be easy to think of (a valve offering a greater resistance to motion in one direction than in the other would give this sort of effect). If one considers the equation $v (P + a) = b (P - P_0)$, the reduced speed of lengthening might formally be due to three causes: (i) an enormous increase of $a$ during lengthening, i.e. a "one-way" resistance. This is unlikely, since then the slow lengthening should be accompanied by increased heat production, which is not found: (ii) to an increase of $P_0$ during lengthening (a kind of "stretch response"); (iii) to a reduction of $b$, i.e. of the change of energy output per g. of tension change. Little, however, is gained by such purely formal considerations.
"Irreversible" stretching ("giving") of active muscle. The fact that, with intermediate loads, the muscle "gives" only a little, requires further comment. In order to explain it, we have to assume that, as the load increases, greater and greater portions of the muscle fibres "yield", depending upon a statistical variation of contractile power in their individual linkages. There are several reasons why the muscle may stop relaxing after a short time:

(i) The force developed by the contractile linkages may become greater as they lengthen. This is obviously the case if the load is applied at a very short length at which \( P_0 \) is small (as in Fig. 6).

(ii) Partial giving, especially at a relatively great length (as in Fig. 4), may involve a stretching of portions of the muscle to more than their resting length. Consequently, the inert elastic structures in parallel with the contractile substance (cell membranes, connective tissue) would gradually take up the force and prevent further extension.

(iii) It will be shown below (pp. 58, 59) that the contractile units which yield under a suddenly increased force, readjust themselves and may "adapt" after a short interval to the new level of tension.

Effect of temperature. With a given load \( P/P_0 \), the "irreversible" lengthening becomes greater at higher temperature. With \( P/P_0 = 1.4 \), for example, the size of the initial "give" was 1.33 mm. at 14° C. (varying in five experiments between 1.0 and 1.8 mm.), while only 0.42 mm. (0.33–1.0 mm.) at 0° C. Complete relaxation, i.e. a rapid extension down to the resting length, occurred with \( P/P_0 = 1.7–1.95 \) at 0° C., with somewhat smaller loads (about 1.6–1.8 \( P_0 \)) at the higher temperature.

By loading the muscle gradually, and consequently slowing down the initial "give" (p. 47), the size of the "irreversible" lengthening for a given tension was somewhat reduced. "Complete relaxation" occurred then only at about 2.0–2.1 times the isometric tension.

The difference between instantaneous and gradual loading might be due partly to the inertia of the falling load which acts upon the muscle at the end of the rapid elastic lengthening in the case of an instantan-eous release. To test the possible effect of such a momentary impulse, as distinguished from a permanently increased force, a load was applied, approximately equal to \( P_0 \), and was given a high kinetic energy by letting it fall over a distance of a few mm. before pulling on the muscle. Apart from a transient vibration, this had little effect even if the force under which the muscle would "give" was momentarily exceeded. If, however, the applied load was large enough to cause partial giving, the speed and size of this "give" became greater when initiated with a momentary
"jerk". Apparently, those parts of the muscle which are just at the verge of yielding, are induced to relax by an added brief impulse.

It can be shown that, quite apart from the effects of inertia, a suddenly increased tension exerts an immediate transient effect which declines within several hundredths of a second (0°C) to a steady level. Fig. 6 shows records of an experiment in which a given force (47 g.) was applied to a muscle which had shortened 18.5 mm. and developed 15 g. tension at the new length. The speed of the initial lengthening was limited, in

![Fig. 6. Transient effect of a sudden rise of tension. English R. temp. at 0°C, loaded with 47 g., after shortening 18.5 mm. and developing 15 g. tension. In records 1–3, the speed of initial "giving" was controlled by the Levin-Wyman apparatus, in record 4, free lengthening occurred.](image)

records 1–3, by means of the Levin-Wyman apparatus (p. 47). While the force was the same in all cases, at the end of the initial "give", the effect depended entirely upon the initial speed of lengthening. If the muscle is allowed sufficient time, its internal force $P_0$ increases steadily as it lengthens, until a length is reached at which the load can be held, or lowered slowly at a "reversible" speed (record 1). With greater initial velocities the muscle relaxes well beyond a length at which, in a steady state, it can hold or lift the applied load. After a momentary failure, the muscle reshortens and lifts the load back, as in ordinary isotonic contraction. That this effect (record 4) is in no way due to the inertia of the
recording system was ascertained by repeating the experiment with a stretched spring, instead of the ordinary weights attached to the lever.

There are two alternative possibilities of interpreting this phenomenon: If the "give" is due to a sudden abolition of the active state [Hill, 1938b], one might expect it to continue until the active state is built up again by the next electric shock. This would explain the delayed reshortening and the large effect with high initial speeds. This possibility, however, can be dismissed because the lengthening does not become greater if the interval between the moment of stretching and the next shock is increased (adjustable 2-ring commutator, p. 47), and because reshortening is observed even if the stretch occurs at the end of the stimulus (e.g. 0.09 sec., after the last shock, at 0° C.).

It appears, therefore, that the contractile mechanism requires some little time (at 0° C., judging from the delay of reshortening, several hundredths of a second) to readjust its energy exchanges to the higher level of tension. Although the muscle may be able, at a certain length, to lift, e.g., 50 g., a sudden increase of tension from 2 to 40 g. causes it to relax temporarily beyond that length, until the contractile mechanism has been readjusted. A related phenomenon, though somewhat more complicated (see below), is Gasser & Hill's [1924] observation on the delayed rise of isometric tension following a quick stretch.

Another phenomenon which, on the face of it, seemed to contrast with previous information on the "active state" is easily understood on this basis. A muscle is allowed to shorten a certain distance under a small load then becoming isometric (Fig. 7); then before an appreciable development of tension has taken place, the force is increased suddenly to the full isometric tension. The result is that the muscle gives quickly and soon begins to reshorten to the original length. This seems at first surprising: it is generally agreed [Gasser & Hill, 1924; Fenn & Marsh, 1935; Brown, 1936; Hill, 1938b] that the full active state in muscle is set up soon after the beginning of stimulation, certainly within the 0.65 sec. which preceded the stretch in the case of Fig. 7 (1) (0° C.). One might have expected that the application of the full isometric force, at this moment, would cause no change of length except an immediate stretch of the elastic parts. Actually the muscle yields and reshortens, apparently being unable for a moment to follow the rapid rise from small to full isometric tension.

As to the cause of this temporary failure, no evidence has been obtained yet. It may be, as Hill suggests [1938b], that the sudden rise of tension causes a transient reduction of energy liberation below the level required to maintain the contraction.
After-effects of sudden stretches. Gasser & Hill [1924] found that a quick stretch applied to an active muscle causes its tension after a momentary rise to drop and to redevelop only gradually. No doubt, initially the elastic component alone had been stretched, its tension increasing until it caused the weaker parts of the contractile substance to “relax”. This, in turn, allowed the remainder to shorten; the tension dropped, as in a quick release, and redeveloped slowly. A quantitative comparison would presumably have shown that the tension redeveloped more slowly after an internal “give” than it did originally (cf. Table IV), because some of the overstretched linkages were permanently damaged and acted as additional elastic tissue in series with the contractile elements.

Permanence after-effects indicating a weakening or complete break of some contractile links were regularly found after application of several rapid stretches ($P/P_0 > 1.8$). A variety of changes in form and size of the isometric records were observed (Table IV), which can all be interpreted as due to a partial transformation of active contractile into passive elastic tissue and an increase of the internal shortening $C$ (p. 52). The
A. Effects of injury (due to quick stretches) on the isometric tension records.

<table>
<thead>
<tr>
<th></th>
<th>I (Initial)</th>
<th>II (After repeated stretching)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_0$ (long)/$P_0$ (short) (shortening 5 mm.) (g.)</td>
<td>$44.2 \text{ g.} = 0.79$ 56 g. 30.5 g. 44.2 g.</td>
<td>$46.3 \text{ g.} = 1.24$ 37.4 g. 28 g. 46.5 g.</td>
</tr>
<tr>
<td>Twitch/tetanus ratio</td>
<td>$0.08 \text{ sec.}$ 1.5 mm.</td>
<td>$0.17 \text{ sec.}$ 2.5 mm.</td>
</tr>
<tr>
<td>Elastic shortening (incl. lever system) for quick release from $P_0$ (long) to 7 g.</td>
<td></td>
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</table>

B. After-effects of quick stretches, depending on length of muscle. The Levin-Wyman apparatus was used (p. 47), limiting the speed of "giving". At 5 mm. (third and fifth column, load 134 g.) the initial speed of lengthening was, on the average, 1.7 cm./sec., at 13 mm. (fourth column, load 72 g.), 2.8 cm./sec.

<table>
<thead>
<tr>
<th></th>
<th>After 3 quick stretches from 5 to 0 mm. shortening</th>
<th>After further 3 stretches from 5 to 0 mm.</th>
<th>After 3 stretches from 13 to 5 mm. short</th>
<th>After 3 stretches from 5 to 0 mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_0$ (long) (g.)</td>
<td>69.5</td>
<td>75.5</td>
<td>79.5</td>
<td>77</td>
</tr>
<tr>
<td>$P_0$ (5 mm. short) (g.)</td>
<td>89</td>
<td>73</td>
<td>60.6</td>
<td>62.6</td>
</tr>
<tr>
<td>Twitch (long) (g.)</td>
<td>47.5</td>
<td>38.5</td>
<td>33.2</td>
<td>34.0</td>
</tr>
<tr>
<td>Ratio $P_{\text{A}}(l)/P_{\text{A}}(s)$</td>
<td>0.78</td>
<td>1.04</td>
<td>1.31</td>
<td>1.23</td>
</tr>
<tr>
<td>Tetanus/Twitch ratio</td>
<td>1.46</td>
<td>1.96</td>
<td>2.38</td>
<td>2.28</td>
</tr>
<tr>
<td>Half-time of tetanus (sec.)</td>
<td>0.073</td>
<td>0.16</td>
<td>0.23</td>
<td>0.24</td>
</tr>
</tbody>
</table>

It is obvious that stretching from a length 13 mm. less to one 5 mm. less than the initial length (fourth column) has no damaging effect at all.

(isometric tension)–(length) relation changed, the maximum tension now appearing at a greater length than initially: it often happened that $P_0$ (long) was unaltered or even greater than before, while $P_0$ (short) was considerably reduced. The isometric tetanus tension developed 2–3 times more slowly and, as a consequence, the ratio of twitch to tetanus tension became less. The amount of undamped elastic shortening during a quick release was greater than initially, though it did not increase in proportion to the slowing of tension development. This is not surprising, since some parts of the muscle were probably not completely inactive, but merely weakened; they would gradually lengthen during an isometric contraction, and so protract the development of tension, but would not have undamped elasticity as observed in a quick release.
It is interesting to note that the after-effects of a quick stretch depended upon the length at which the "giving" took place. It was usually observed if the muscle was stretched beyond its length of maximum tension, e.g. from 5 mm. shortening to the initial length (initial load 2 g.), but not if an equally large stretch was applied at a shorter length (e.g. from 13 to 5 mm., see Table IV). In the latter case, the "giving" seems to be due merely to an opening, or "unfolding" of closed linkages, in the former case it involves overstretched and possible breakage of some links.

Fig. 8. Experiment analogous to Fig. 7 made on tortoise muscle at 14°C. Loaded at various stages of tension development (15-6 mm. shortening, about 30% of the resting length) with 73 g. The isometric tension falls somewhat during the experiment so that the applied force was nearly equal to \( P_0 \) in record (1), to \( 1.1 \times P_0 \) in record (4). Lower curve shows development of tension.

**Internal "giving" during isometric contraction.** It was previously mentioned that the development of isometric tension in tortoise muscle is much slower than that calculated from the constants \( a \) and \( b \) and the undamped elastic extension \( C \). An important factor contributing to this divergence is presumably the giving of weak linkages at tensions even less than the isometric. This is suggested by the following observations: Tortoise muscle, in contrast to a frog's sartorius, "gives" even if the applied force is only slightly greater than the isometric tension [see Fig. 4; cf. also Levin & Wyman, 1927; Hill, 1938b]. Furthermore, if during the development of tension, the force is raised quickly from, for example, 0.85 to full isometric tension (Fig. 8), this is followed by a small "give"
which continues for a considerable time before being reversed (in Fig. 8 for 0.5 sec.). The contractile state is fully developed long before then, shown by the equal speeds of initial and delayed shortenings with a large after-load (Table I). Apparently, some parts of the muscle "relax" under a load which at the same time can be lifted by others. The total change of length seems to be made up by (i) a "giving" of gradually diminishing speed, (ii) a slow uniform shortening which eventually reverses the lengthening.

Both observations suggest that, in this muscle, the "isometric" force which can be exerted by each individual linkage varies greatly among the constituents of a contractile chain, and that, therefore, mutual shortening and lengthening is likely to take place during the ordinary isometric contraction.

In frog's muscle, the situation is different: loads which do not considerably exceed the isometric tension cause only a very slow lengthening and, therefore, the development of isometric tension would not normally be slowed by an internal "give". There are, however, three cases in which such "give" is likely to occur: (i) at the beginning of an isometric tetanus, when the full activity has not yet spread uniformly over the whole length of the fibres, (ii) after partial weakening or breakage, (iii) perhaps at a very short length, where a large variation of the force exerted by individual elements of a contractile chain may be expected (the isometric tension changing rather critically with slight changes of length).

**Summary**

The relation between applied force and speed of isotonic shortening was studied in frog and tortoise muscle. The observed relation is satisfactorily described by Hill's hyperbolic equation \((P + a)(v + b) = \text{const.}\) The constant \(b\) (per length of muscle) is about 14 to 40 times, the constant \(a\) (per isometric tension) about 2.5 times greater in frog than in tortoise muscle.

The development of isometric tension can be analysed as a gradual internal shortening of the contractile substance against an elastic, passively extending portion. The isometric tension records were compared with Hill's theoretical relation. A satisfactory agreement between observed and calculated tension records is found in the frog's sartorius. In tortoise muscle large divergences are observed, the reasons of which are discussed.

The relation between a force greater than isometric and the resulting speed of "reversible" lengthening was determined. The observed veloci-
ties are considerably smaller than calculated from theory. If the applied 
force exceeds the isometric tension by 70–100%, the muscle "relaxes" 
rapidly.

A shortened muscle "gives" and later "reshortens" if its tension is 
suddenly increased from small to isometric strength.

Rapid stretching of an active muscle, beyond its optimum length, is 
apt to break or weaken permanently parts of the contractile substance.

My sincere thanks are due to Prof. A. V. Hill for his suggestions and help during this 
work, and to Mr J. L. Parkinson for invaluable technical assistance.

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The relation between force and speed in muscular contraction

Bernhard Katz

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