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THE RELATION BETWEEN VELOCITY OF SHORTENING AND THE TENSION-LENGTH CURVE OF SKELETAL MUSCLE

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Many different types of apparatus have been used in the past by physiologists to study the active shortening of muscle. Isotonic, auxotonic and inertia levers control the force applied to the muscle; other types of apparatus apply a definite pattern of shortening. Fortunately, the wide range of results obtained in these different experimental arrangements can be interpreted in terms of a single property of muscle—that the force of contraction is a function of the velocity of shortening.

The isotonic force-velocity curve of striated muscle was first studied by Fenn & Marsh (1935); three years later Hill derived the equation:

\[(P + a)(V + b) = \text{constant} = (P_0 + a)b\]  \hspace{1cm} (1)

\((a \text{ and } b \text{ are constants, } P_0 \text{ the isometric tension), which describes with remarkable accuracy the force-velocity relation in muscles of the frog (Hill, 1938); tortoise (retractor penis, Katz, 1939; ilio-fibularis, Abbott, 1953); man (Ralston, Polissar, Inman, Close & Feinstein, 1949; Wilkie, 1950); snail (Abbott, 1953); ray (Wilkie, 1952, unpublished), and } Mytilus \text{ (Abbott & Lowy, in preparation).}

The isometric tension developed by a muscle depends on the length at which the muscle is stimulated, being greatest when the muscle has about the same length that it had in the body. Hill's equation can only be applied in the region of this maximum, where the variation of \(P_0\) with length is slight; for \(P_0\) appears in the equation as a constant. In the intact vertebrate body, muscle length changes are more or less limited to this maximal region. The experiments described in this paper were carried out in order to examine the relation between force and velocity in other regions of the tension-length curve.

EXPERIMENTAL METHOD

All experiments were made on sartorii of Rana temporaria kept in oxygenated phosphate Ringer (pH = 7.0) at 0°C; this was drained off before each contraction. The muscle was mounted on a multi-electrode assembly (Hill, 1949) in order to bring all the muscle as quickly as possible to
the state of full activity. It was stimulated maximally by condenser discharges \((RC = 0.1 \text{ msec}, 18 \text{ V}, 5 \text{ stimuli each way per sec})\). The stimulus frequency is not critical so long as it is fast enough to give complete fusion of mechanical response; if the frequency is too high (greater than about 20/sec), tension is not well maintained.

All length measurements are referred to the body length; that is, the length of the sartorius \textit{in situ} when the two legs are pinned out in a straight line. The pelvic end of the muscle was fixed to the multi-electrode assembly and the free (tibial) end attached through a light flexible chain to the recording apparatus. \textit{Isometric} measurements were made by attaching the chain to a single-wire resistance strain gauge of the type devised by Hill (1951); its output was amplified and displayed on a cathode-ray tube. The gauge was moved up and down on a Palmer stand so that the isometric tension developed could be measured at different muscle lengths. \textit{Isotonic}

\[\text{Fig. 1. Circuit used in isotonic experiments to record amount and velocity of shortening.}\]

records were obtained by attaching the chain to a light aluminium lever mounted on ball bearings. The load was suspended from the lever as near as possible to its axle (lever ratio 26 : 1) in order to reduce effective inertia. All contractions were after-loaded and all started from the body length of the muscle. Attached to the lever was an opaque vane situated between a light source and a twin photocell. The output of the photocell, which varied linearly with the deflexion of the lever, was displayed on a cathode-ray tube.

Preliminary experiments revealed two practical difficulties:

(1) \textit{Deterioration of muscle.} Each complete experiment involved measuring on a single muscle both the tension-length curve of the contracting muscle and a set of curves of shortening against various isotonic loads; all under tetanic stimulation. Isotonic records were certainly repeatable with good accuracy throughout the experiment, but repeated isometric records showed a progressive change in the tension-length curve similar to that described by Aubert, Roquet & Van der Elst (1951), and attributed by them to irreversible stretching of series elastic elements. The change consisted in a slight shift of the maximum of the curve towards the region of greater length combined with a diminution in the height of the maximum (see, for example, Fig. 4). It was found that the extent of this irreversible change could be reduced by using winter frogs; by keeping the amount of stimulation down to a minimum; by allowing a 15 min rest between contractions; and by storing the muscle overnight before the experiment in ice-cold Ringer.

(2) \textit{Measurement of shortening velocity.} For purposes of calculation (see below) it was necessary to determine from each isotonic record a curve of shortening velocity against time. This was done at first by measuring the slope of tangents which had been drawn in by eye to the curve of shortening against time. When control measurements were made in this way on the curves of known functions it was found that very large errors could arise, for in drawing the tangent at a point one is much influenced by the shape of the curve as a whole.
In order to avoid error from this source, the velocity of shortening was determined by direct electrical differentiation of the output from the isotonic apparatus, using the circuit shown in Fig. 1. The equation governing the behaviour of the differentiating circuit is

\[ E_r = RC(dE/dt - dE_r/dt), \]

where \( E \) and \( E_r \) are the input and output voltages respectively.

The error term was reduced as far as possible by making \( RC \) small, though a limit is set to this process by the gain available in the amplifiers. With the final time-constant chosen, 4.4 msec, it was possible to follow accurately all except the fastest accelerations. Shortening and velocity were displayed simultaneously on a single beam cathode-ray tube by beam switching with a high-speed relay (Fig. 2).

![Fig. 2. Typical record of isotonic shortening (above) and velocity (below) against a force of 26.7 g wt. Time marks every 20 msec.](image)

![Fig. 3. Semi-logarithmic plot of 'displacement' (above) and 'velocity' (below) obtained from the calibrating input circuit.](image)

In order to scale the velocity record into cm/sec the input of the first amplifier could be switched so that it measured the voltage on a condenser discharging itself through a resistance, a photographic record being obtained of the resulting ‘shortening’ and ‘velocity’. Since the differential of an exponential curve is itself an exponential, both these records should give straight and parallel lines when plotted on semi-logarithmic paper (see Fig. 3), while from the slope and vertical separation of the lines the scaling factor from cm to cm/sec can be easily calculated.
RESULTS

The tension-length curve of the contracting muscle was measured before and after the group of isotonic shortenings in order to estimate and take account of the steady deterioration in isometric tension discussed above. 'Before' (filled circles) and 'after' (open circles) tension-length curves are shown in Fig. 4. A typical isotonic record is reproduced in Fig. 2; it shows how shortening and velocity varied in a contraction against a tension of 26.7 g wt.

\[ \begin{align*} 
\text{(P + a) (V_I + b)} &= \text{(P}\_0\text{)}_I + a \times b, \\
\text{(P}\_0\text{)}_I &= \text{V_I} \times \frac{(P + a)}{b} + P. 
\end{align*} \]

Fig. 4. Tension-length curve of contracting sartorius at beginning (filled circles) and end (open circles) of experiment. Zero on the length scale is the body length of the muscle which was 30 mm long and weighed 97 mg. Shortening negative.

**Method of calculation**

In order to describe this clearly one must anticipate the conclusion which was drawn from the experimental results, i.e. that Hill's equation does apply at all degrees of shortening so long as \( P_0 \) at any length \( l \) at which the velocity \( V_I \) is measured is given the value \( (P_0)_I \) appropriate to that length. Thus

\[ (P + a) (V_I + b) = (P_0)_I + a \times b, \]

or

\[ (P_0)_I = V_I \times \frac{(P + a)}{b} + P. \]

It is shown below how \( a, b \) and \( V_I \) can be determined from experimental isotonic records. The value of \( (P_0)_I \) corresponding to any chosen value of \( l \) can then be calculated by equation (3). By comparing values of \( (P_0)_I \) calculated from isotonic records with those measured directly in isometric experiments the validity of equation (3) is tested. A single experiment only is described in detail, but six others have all given similar results.
Determination of $a$ and $b$. The values of $a$ and $b$ were calculated by fitting Hill's equation to the experimental curve of initial velocity against isotonic load (Fig. 5, circles). The values of $a$ and $b$ giving the fitted curve shown were $a = 18.5$ g wt., $b = 1.19$ cm/sec.

Determination of $V_i$. Each isotonic record, e.g. Fig. 2, gives a length-time and a velocity-time curve. The velocity $V_i$ corresponding to a given length $l$ can thus be read off directly from the record.

Correction for elastic element. It has been pointed out by Dr X. M. Aubert that even isotonic records need to be corrected for the effect of the inert elastic component if isotonic contractions at different tensions are to be compared. A generalized stress-strain curve for the elastic element is given by Hill (1950, fig. 1). By scaling this curve appropriately one can read off the amount of extra shortening, not visible externally, which accompanies isometric or isotonic contraction at a given tension and which must be added if all length measurements are to relate to the same standard, the length of the contractile component at rest and under zero tension. The effect of this correction is small, for at all the tensions used experimentally the passive series compliance has already become small and almost constant; stretching of chain and tension recorder can certainly be neglected. Between 3.8 g wt. and 68 g wt. in the experiment quoted here the elastic element lengthened only 0.9 mm. Fortunately the correcting process does not upset the original calculation of the values of $a$ and $b$, since $(P_0)$, does not vary appreciably over the particular range of lengths at which the initial velocities were measured.

Calculation. Since values of $a$, $b$ and $V_i$ were available at a number of known corrected lengths and for several values of $P$, values of $(P_0)$ could be calculated at these lengths. The result is shown in Fig. 6, open symbols, for five different values of isotonic load. It is clear that the five estimates of the relationship between $(P_0)_i$ and length agree reasonably well with one another.
and with the directly measured curves of isometric tension against length. This agreement justifies the claim that the modified Hill’s equation is valid throughout shortening.

**DISCUSSION**

It has been shown experimentally that Hill’s equation in the form

\[(P + a)(V_l + b) = ((P_0)_l + a)b\]

applies to muscle shortening below its body length so long as \((P_0)_l\) is given, at every instant, the value corresponding to its length \(l\) at that instant. One consequence of this is that the final state of the contracted muscle is the same (see Fig. 7), whether the muscle reaches a given point on the tension-length curve by an after-loaded isotonic contraction (route \(A\)) or by an isometric contraction following passive shortening of the resting muscle (route \(B\)). Whether the modified Hill’s equation applies also to muscles shortening from beyond body length (in the shaded region of Fig. 7) is not yet known. There is evidence (see Buchthal & Kaiser, 1951, p. 121) that when a muscle fibre begins its shortening from beyond body length, for example in a pre-loaded isotonic contraction, shortening ends before the tension-length curve is reached. The same effect sometimes appears with whole muscle when shortening begins at body length, but only at the highest isotonic tensions (see, for example, 45.8 g wt. points in Fig. 6).
Since in the modified form of Hill's equation $a$ and $b$ are still constants, $a/P_0$ and $b/V_0$ must vary with muscle length, both $P_0$ and $V_0$ being zero after complete unloaded shortening. Hill (1939) came to the conclusion that $a/P_0$ was constant at different lengths. His reasoning was based on measurements of the total work done in contractions against a Levin-Wyman ergometer. The disagreement with present findings may have arisen because a substantial fraction of this work was done while the muscle was relaxing and no longer obeying Hill's equation.

![Diagram of tension-length curve](image)

**Fig. 7.** Diagrammatic tension-length curve of muscle. See text.

The fact that $a$ is constant over a wide range of shortening is particularly interesting since it has been shown that the heat of shortening (per cm) is also constant (and numerically and dimensionally equal to $a$) over a wide range of muscle length (Abbott, 1951). Buchthal & Kaiser (1951, p. 178) maintain that the similarity between $a$ and the constant of shortening heat is purely accidental, since the absolute value for $a$ (g/cm²) obtained from mechanical experiments on single fibres of semi-tendinosus is four times greater than that obtained from the whole semi-tendinosus muscle, and both values cannot be equal to the constant of shortening heat. This evidence is too indirect to be acceptable in the absence of parallel thermal experiments, for the method of scaling up from fibre to whole muscle could easily introduce large errors. The conclusion that $a/P_0$ is larger in single fibres than in whole muscle may rest on nothing more than the assumption (p. 177) that the 'natural length' of whole muscle is 35-50% greater than that of the single fibre; it has been indicated above that $a/P_0$ varies steeply with muscle length.
Hill's equation does not directly suggest any particular physico-chemical model of the contractile process: for the time being one must regard the equation as a remarkably accurate but purely descriptive relation between observed facts. Several other 3-constant equations fit the force-velocity curve of muscle satisfactorily, e.g.

\[ P = P_0 e^{-aV} - kV \quad (\text{Fenn & Marsh, 1935}), \]
\[ V = \text{const.} \left( A_1 - P - B^{P-1} \right) \quad (\text{Polissar, 1952}), \]

or

\[ P = P_0 e^{-PV/bP_0} - V a/b \]

(an empirical equation in which \( a \) and \( b \) have the same dimensions and nearly the same values as in Hill's equation).

Some equation other than Hill's may be found whose form is more closely related to the physical chemistry of contraction, but it is clear that any theory which accounts both for the shape of the force-velocity curve and for the occurrence of shortening heat must at the same time be consistent with the known energy turnover:

\[
\text{(Rate of extra energy production in shortening, i.e. shortening heat + work)} \\
\propto [(\text{isometric tension corresponding to instantaneous length}) \\
-(\text{tension on contractile element})].
\]

Several attempts have already been made to explain these experimental facts in theoretical terms. Ramsey (1944) and later Gassner & Reichel (1952) have shown how shortening heat might be accounted for in isotonic contractions by the degradation into heat of that part of the mechanical potential energy (calculated from the area of the tension-length curve) which does not appear externally as mechanical work. Both authors' theories contain many serious defects; for example, both predict the correct amount of shortening heat only under isotonic conditions, whereas experimentally shortening heat is proportional to the distance shortened no matter how much the tension may have varied during shortening. They thus fail to account for the production of extra energy during shortening for the same reason as did the older visco-elastic theories.

Recently, Polissar (1952) has published a theory of the contractile process which is like that of Varga and Szent-Györgyi (discussed by Szent-Györgyi, 1948) in that contraction is held to result from the all-or-none transformation of molecular shortening units from a long (L) to a short (S) form. The degree of shortening of the whole muscle then reflects the state of the dynamic equilibrium \( L \leftrightarrow S \); in Polissar's theory I and II represent different reaction routes. Polissar's model certainly shows some of the properties of living muscle, for example, a force-velocity curve of the correct shape. The theory is weak in its account of the energy relations during change
of length. Thus it wrongly predicts a positive heat of lengthening (p. 800) instead of the negative one found experimentally (Abbott & Aubert, 1951): it cannot account for the constancy of $a$ (thermal) throughout shortenings of large extent (Abbott, 1951) and the explanation given (p. 802) of the source of work in contraction (i.e. that it is mechanical energy stored in the passive elastic element of the muscle) is inadequate, for it fails to account for the production of work in ordinary isotonic contractions where the tension never rises above its isotonic value.

One major stumbling-block in the way of all theories so far suggested has been the fact that the amount of shortening heat is independent of the work done by the muscle. Polissar’s scheme might be improved in this respect by making a clearer distinction between heat and work, and by supposing that in association with the reaction $L \rightarrow S$, chemical means are provided for absorbing any surplus free energy without degrading much of it into heat. It is likely that even mechanical work can be converted by muscle into chemical energy (Abbot, Aubert & Hill, 1951). The heat change accompanying the reaction $L \rightarrow S$ is equal to $\Delta F + T \Delta S - W$, where $F =$ Gibbs’ free energy, $S =$ entropy, $T =$ absolute temperature, $W =$ energy lost from the system either as mechanical work or by chemical transfer. According to the suggested hypothesis $\Delta F - W = 0$, so the residue of heat change is entirely associated with the entropy term, $T \Delta S$. $\Delta S$ might easily be large, because of the great change in molecular configuration and it may be negative (i.e. heat given out during the reaction). $T \Delta S$ has the properties required of a shortening heat, being proportional to the distance shortened (i.e. to the amount of reaction) independent of the work done and nearly independent of the temperature.

Unfortunately, little is known about the kinetics of chemical reactions in which some of the reacting groups are attached to a molecular framework through which they can be influenced by external forces. There thus remains a large gap to be bridged before the microscopic properties of living muscle can be explained fully in terms of the chemical processes associated with contraction, and of the minute and molecular structure of muscle fibres.

SUMMARY

1. Since the isometric tension $P_0$ developed by an active muscle varies with the length at which the muscle is stimulated, Hill’s equation has formerly been applicable only over a restricted range of muscle lengths.

2. It is shown that a simple modification of the equation in which $a$ and $b$ remain as constants is valid throughout the full extent of shortening. The similarity between $a$ and the constant of shortening-heat/cm is thus enhanced.

3. The theoretical interpretation of these facts is still uncertain: several possibilities and suggestions are discussed.
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