J. Physiol. (1958) 143, 104–113

THE DYNAMICS OF MUSCULAR CONTRACTION

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(*Received* 27 *March* 1958)

It is well known that the height of an isotonic after-loaded twitch depends on the load lifted by the muscle; thus the larger the load the less it is lifted. The exact explanation of this fact is not clear. As Fenn (1923) showed, it is not simply that during a twitch a fixed unit of energy is liberated that can be used either to lift a heavy load through a short distance or a light load through a long one; for Fenn, and more recently Hill (1949*a*), have demonstrated that the energy liberated by the muscle varies in a complex way with load and shortening.

A simple qualitative explanation emerges from combining two known facts about muscle: first, that the velocity of shortening of the fully active tetanized muscle is a function of the force (Fenn & Marsh, 1935; Hill, 1938); and secondly, that after a single stimulus the muscle is fully active for a more or less fixed period of time (Hill, 1949*b*; Macpherson & Wilkie, 1954; Ritchie, 1954*a*). Thus, the smaller the load, the higher the velocity and the further the muscle will be able to shorten in that fixed time. If at the end of this time the activity suddenly disappears, the curve of twitch-height against load should have the same shape as the curve of velocity against load, and this is found to be roughly the case. However, the conditions during muscular contraction are much more complicated than this, for the active state following a single stimulus disappears gradually and not suddenly (Hill, 1949*b*). Also, as the muscle shortens it moves to a less powerful region of its tension–length curve. For both these reasons the velocity of shortening falls off gradually throughout the twitch.

A theory which explains both the shape and the size of a muscular contraction under any specified mechanical conditions has to take all these factors into account. We have tried to develop such a theory, but only for the phase of contraction because the mechanics of relaxation are still not understood quantitatively.

THEORY

The problem is to describe the dynamical behaviour of contracting muscle in terms of the known mechanical properties of the contractile substance of active muscle, i.e. to show how muscle length, force and time (x, P and t) are related throughout a contraction. It is assumed that the muscle consists of two elements arranged in series, a contractile element of length x_c and an elastic element of length x_e.

Thus $$x = x_c + x_e.$$

The following four curves must be determined experimentally.

(1) *The load–extension curve of the series elastic component.* This passive element is important because all the experimental records have to be corrected for the distortion which it introduces. The form of this curve is expressed algebraically by saying $x_e = f_1(P)$.

(2) *The tension–length curve.* This can be determined either by tetanizing a muscle at fixed length and measuring the final tension developed, or by allowing a tetanized muscle to shorten fully against a constant load, i.e. $P_0 = f_2(x_c)$ is determined for the condition $\mathrm{d}x_c/\mathrm{d}t = 0$.

(3) *The force–velocity curve.* For a given constant force the initial velocity of shortening of a tetanized muscle is measured at body-length L_0, i.e. $-\mathrm{d}x/\mathrm{d}t = -\mathrm{d}x_c/\mathrm{d}t = f_3(P)$, is determined at x_c corresponding to L_0.

(4) *The active-state curve.* After a stimulus the muscle takes some time to return to its resting state; the ability to develop isometric tension diminishes with time, i.e. $P_0 = f_4(t)$ at a given x_c, for the condition that $\mathrm{d}x_c/\mathrm{d}t = 0$.

These four curves may be accurately determined on a single muscle, but each gives only a partial picture of the active muscle. What happens when P, x and t vary together, as they do in the living body? One approach to this complex problem is to use Hill's equation, which makes it possible under suitable conditions to write for $-\mathrm{d}x_c/\mathrm{d}t = f_3(P)$ the algebraic expression:

$$-\mathrm{d}x_c/\mathrm{d}t = (P_0 - P)\, b/(P + a);$$

a and b being constants. We have allowed for the way in which isometric tension development varies with muscle length by writing for P_0 the expression $f_2(x_c) \cdot f_4(t)/P_0^*$, where P_0^* is the isometric tension when x_c corresponds with L_0. This is the same as the P_0 of Hill's original equation and is a constant for each muscle. The whole equation then becomes:

$$-\frac{\mathrm{d}x}{\mathrm{d}t} = -\frac{\mathrm{d}x_c}{\mathrm{d}t} - \frac{\mathrm{d}x_e}{\mathrm{d}t} = \frac{(f_2(x_c) \cdot f_4(t)/P_0^* - P)\, b}{P + a} - \frac{\mathrm{d}f_1(P)}{\mathrm{d}t}.$$

During isotonic contraction the second term is zero.

Preliminary experiments were in promising agreement with this theory, so the matter was examined more closely.

EXPERIMENTAL TECHNIQUE

The experiments were carried out on frogs' sartorii at 0° C in Ringer's fluid: (mM) NaCl 115·5, KCl 2·0, $CaCl_2$ 1·8, Na phosphate buffer (pH 7) 2. The muscles were maximally stimulated by alternating condenser discharges (time constant 0·1 msec) on a multi-electrode assembly. The arrangements for mechanical recording, the connexions, etc., were essentially similar to those already described (Wilkie, 1956*a*, *b*). Since the calculation depended on maintaining the muscle in a steady condition throughout a long series of measurements, the number of tetani was kept to a minimum in each experiment. Stimuli were given automatically at regular intervals, usually every 2 min, whether records were being taken or not, in order to keep the muscle in a steady state. The four curves required were determined in the following way:

(1) *Load–extension curve of the series elastic component* (Fig. 1*A*). The shape of this curve was determined by the quick-release technique (Aubert, 1956, p. 76; Wilkie, 1956*b*). Unfortunately no method is known of measuring x_e, the actual length of the elastic component. Moreover, x_e becomes indeterminate when the force is very small. We have therefore called x_e zero at the lowest tension with which we are concerned, 1·5 g wt. This is equivalent to subtracting an unknown constant from x_e and adding it to x_c, and does not alter the result of our calculation.

(2) *Tension–length curve* (Fig. 1*B*). Most of the experimental points (open circles) were obtained by adjusting the muscle to various initial lengths and recording the tension developed in an isometric tetanus (30 shocks/sec). This procedure is not satisfactory with short initial lengths (say, less than 23 mm in a 30 mm muscle) because the muscle is so slack that it does not make reliable contact with the electrodes; the points corresponding to short muscle lengths were therefore found by measuring the total shortening in an isotonic tetanus under the required small load. The points obtained by the two methods always cross-checked satisfactorily with one another. All points were then corrected for the change in length in the series elastic component and connexions (solid circles, Fig. 1), in order to determine x_c. The topmost solid circle gives the value of x_c corresponding with L_0.

(3) *Force–velocity curve* (Fig. 1*C*). This was determined from the initial slope of after-loaded isotonic contractions against various loads. Tetani were used for the large, and twitches for the small, loads. Hill's constants *a* and *b* were determined by fitting a theoretical curve to the points in Fig. 1*C*. Although the measurements with different loads were all made with the muscle at L_0, x_c will have been smaller when the tension was higher because the muscle had to contract isometrically before it begins to lift its load. This almost certainly does not matter when, as in Fig. 1, all the relevant values of x_c lie on the flat top of the tension–length curve. In other cases, when the local P_0 was less than its maximum P_0^*, a small approximate correction was made by multiplying the measured velocity by $(P_0^* - P)/(P_0 - P)$.

(4) *Active-state curve* (Fig. 1*D*). This was determined by recording the redevelopment of tension resulting from a 3 mm release at various times after a single shock (Ritchie, 1954*b*). The solid circles represent the active-state curve at the standard length, L_0, and the open circles, the curve at $L_0 - 6$ mm.

Legend to Fig. 1

Fig. 1. The four characteristic curves of a single frog's sartorius at 0° C. $L_0 = 32$ mm, wt. $= 88$ mg. *A*: load–extension curve of series elastic component. *B*: tension–length curve. The open circles are the measured points; the solid circles are the same points corrected for the change in length of the series component, i.e. they give values of x_c. The region to the left of the broken line is the 'reversible zone' (see text). *C*: force–velocity curve. The curve has been drawn from Hill's equation with $a = 13{\cdot}65$ g wt., $b = 16{\cdot}5$ mm/sec, $P_0 = 49$ g wt. *D*: active-state curve. Ordinates, intensity of the active state in %; 100% represents 49 g wt. Abscissae, time in msec measured from the end of the latent period (10 msec after the stimulus). ●, final muscle length $= L_0$; ○, final muscle length $= L_0 - 6$ mm.

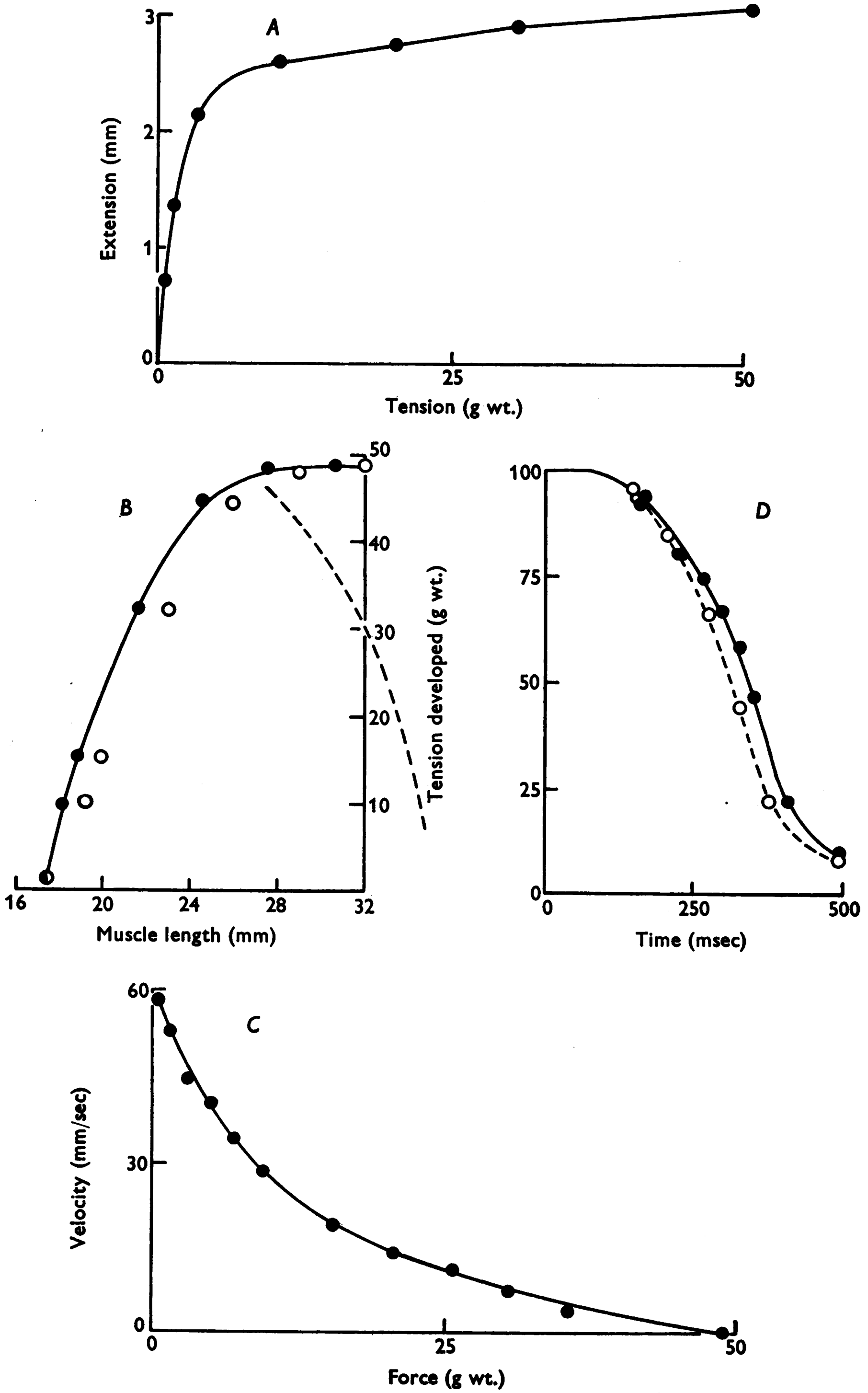
A
Extension (mm)
0
1
2
3
Tension (g wt.)
0
25
50
B
Muscle length (mm)
16
20
24
28
32
Tension developed (g wt.)
10
20
30
40
50
D
Time (msec)
0
250
500
0
25
50
75
100
C
Velocity (mm/sec)
0
30
60
Force (g wt.)
0
25
50

Fig. 1

CALCULATION AND RESULTS

In the equation

$$-\frac{\mathrm{d}x}{\mathrm{d}t}=\frac{(f_2(x_c)\cdot f_4(t)/P_0^*-P)b}{P+a}$$

a, b, $f_2(x_c)$, $f_4(t)$ and P_0^* have been determined experimentally, so that for each chosen value of the isotonic force P, the curve of x against t can be calculated. As the equation cannot be integrated algebraically we tested our equation in the earlier experiments directly in the differential form. Values of $\mathrm{d}x/\mathrm{d}t$ were obtained from experimental curves of x against t by measuring their slopes at chosen values of x or t. Thus we were able to calculate the shape of the function $f_4(t)$ or of $f_2(x_c)$ and to compare the one or the other with the corresponding experimentally determined curves.

A more satisfactory procedure, which was adopted later, was to integrate the equation directly, thus obtaining the amount of shortening x as a function of the time t. This was kindly done for us on a differential analyser by the Department of Mathematics at the National Physical Laboratory. The result is shown in Fig. 2, where theoretical curves (full lines) are compared with experimental ones (circles) for after-loaded isotonic twitches starting at the body length L_0 (Fig. 2*A*) and also for twitches starting at a shorter length, L_0-6 mm (Fig. 2*B*). The general agreement between theory and experiment is quite good, although it should be noted that some of the agreement is arbitrarily imposed by the nature of the mathematical procedure used. Thus the initial slopes of the corresponding experimental and theoretical curves in Fig. 2*A* are obliged to be the same; this restraint does not apply to Fig. 2*B*. Nevertheless, some discrepancies are obvious.

The same degree of agreement between theory and experiment as that seen in the experiment of Fig. 2 was found in the seven complete experiments that were done though the discrepancies did not fall into any perceptible pattern. The agreement has certainly not been improved by the various refinements and elaborations we introduced from time to time in the hope of improving the precision of our result. No great improvement resulted from correcting all lengths carefully for the changes in the series elastic component or changing the active-state curve so as to be a function of muscle length as well as of time (see Ritchie, 1954*b*); both corrections were applied in the calculation of Fig. 2.

DISCUSSION

As a result of the experiments just described it seems to us that the discrepancies between theory and experiment are genuine and are not random experimental uncertainties, as we had at first supposed. Some at least of the discrepancy must arise from properties of muscle that our theory has neglected.

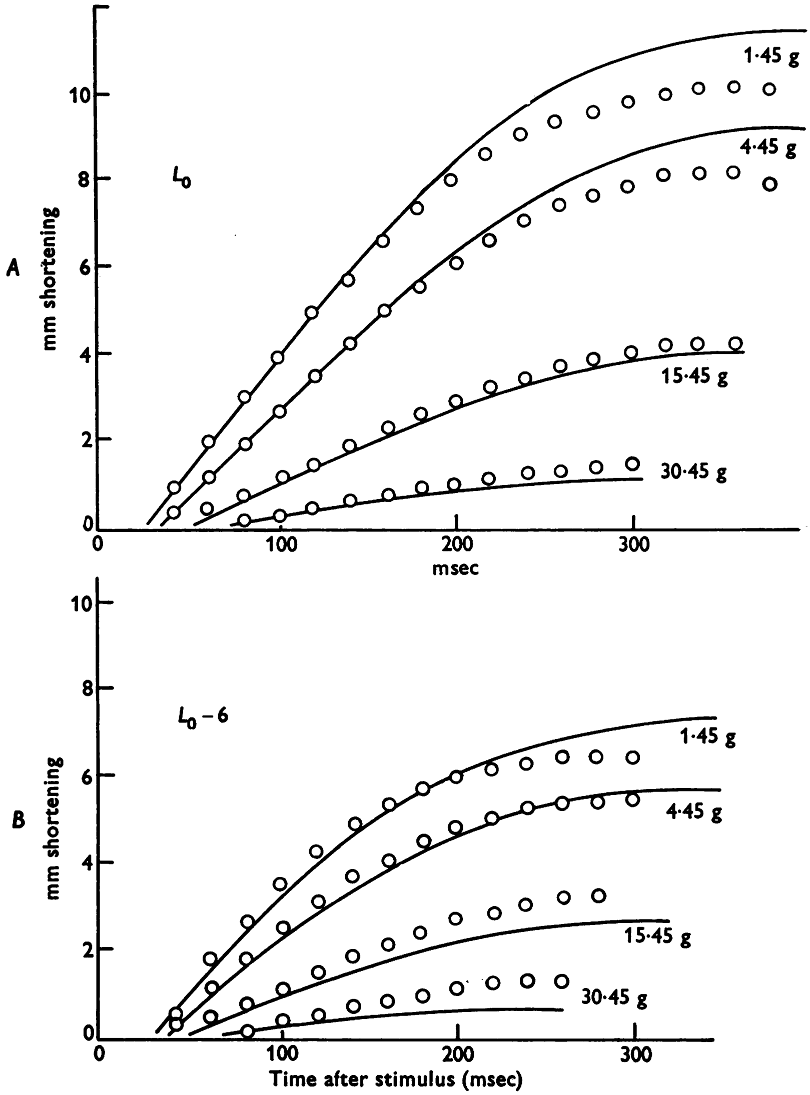

Fig. 2. Theoretical and experimental isotonic twitches compared; same muscle as in Fig. 1. ○, points from the experimental curves; —, theoretical curves derived from Fig. 1. *A*, initial muscle length was L_0 (32 mm); *B*, initial muscle length was $L_0 - 6$ mm. The tension in g wt. is indicated beside each curve.

Our theory supposes that the muscle becomes fully active immediately after the stimulus and that at every instant afterwards its velocity of shortening is a function only of the force acting and of the muscle length, without any reference to its previous history, until the active state begins to decline. The degree of accuracy with which these assumptions are obeyed can be gauged from Fig. 3, which is an experimental record of an isotonic tetanus against a tension of 5 g wt., in which the after-loading stop was moved so as to alter the initial length of the muscle from $L_0 - 4$ mm first to L_0 and then to $L_0 + 4$ mm.

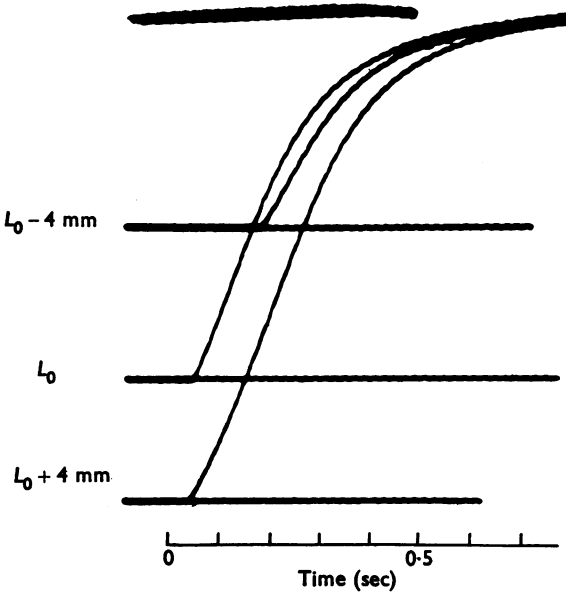

Fig. 3. Isotonic tetani (30 shocks/sec) against a tension of 5 g wt. beginning at $L_0 - 4$ mm (upper line), L_0 (middle line), and $L_0 + 4$ mm (lowest line). Abscissa, time after beginning of stimulus (sec). The system recording length becomes somewhat non-linear at lengths greater than $L_0 + 2$ mm. Sartorius, $L_0 = 32$ mm, wt. = 105 mg.

The final length of the muscle is almost the same in the three cases but during the contractions the curves at any given muscle length are not exactly parallel to one another, though they should be parallel if the theory were strictly obeyed. The discrepancy is most striking in the contraction that begins at $L_0 - 4$ mm, and it can be detected in the one beginning at L_0. This presumably means that the active state takes some time to reach its maximum especially at the shorter length. Even the condition (satisfied in Fig. 3) that the final length of the muscle be independent of the initial length, only applies if the initial length has been kept within the 'reversible zone' whose boundary is indicated by the broken line in Fig. 1 *B*. Otherwise, for example, if the muscle is free-loaded, the final contracted length does depend on the initial length and equations like the one we used cannot be obeyed (Blix, 1895; Buchthal, Kaiser & Rosenfalck, 1951; Maréchal, 1955). A number of other situations are known in which a muscle's behaviour depends on the whole history of the contraction (see, for example, Katz, 1939; Abbott & Aubert, 1952) rather than on the conditions at each instant.

Moreover, as A. V. Hill has frequently pointed out, a muscle is not of perfectly uniform strength along its length. The effect of this non-uniformity will be only partly neutralized by our having measured the four basic curves on the same, non-uniform, muscle.

The equation we used is a development of Hill's well-known equation which has the merit that in it mechanical and thermal parameters are combined. However, in the course of examining many force–velocity curves we have found a fair proportion, about a third, that are not fitted well by Hill's equation, because they have a straight region at the high-force low-velocity end, i.e. the muscle lifts a heavy load faster than is predicted by Hill's equation. In such cases, Aubert's equation (1956, p. 223) often gives a better fit. This discrepancy was not noticed in earlier work probably because of the considerable uncertainty that used to exist about the appropriate value of the isometric tension (see, for example, Abbott & Wilkie, 1953, fig. 3). Here, too, we are not dealing with random errors, for a given muscle consistently gives a force–velocity curve of the same shape.

In this situation there is much to be said for the more empirical approach to the problem adopted by Carlson (1957), which is not tied down to any specific algebraic formula for the force–velocity curve. His equation for the motion of a tetanized muscle is

$$P = F_1(x) + F_2\left(\frac{\mathrm{d}x}{\mathrm{d}t}\right),$$

where $F_1(x)$ and $F_2(\mathrm{d}x/\mathrm{d}t)$ are empirical functions describing the shapes of the tension–length and force–velocity curves respectively. This corresponds to a physical model comprising a non-linear elastic element in parallel with a non-linear viscous one.

For the tetanic case our own equation reduces to

$$-\frac{\mathrm{d}x}{\mathrm{d}t} = \frac{(f_2(x_c) - P)\,b}{P+a},$$

since $f_4(t) = \text{constant} = P_0^*$. This equation was shown by Abbott & Wilkie (1953) to be obeyed with reasonable accuracy. We have tested the two equations side by side against the same experimental results on two occasions when we found somewhat better agreement with Carlson's equation than with ours. However, with both equations the discrepancies between theory and experiment were substantial enough to make it difficult to decide on their relative merits. Aubert's equation, modified so as to take account of the change in isometric tension with length, gave no better result.

The present investigation illustrates a familiar dilemma, that as experimental precision improves it usually becomes harder to fit experimental results into a theory. We think that, at least as far as present theories of muscular contraction are concerned, the precision of our experiments may have reached (or passed) the limit of usefulness. Nevertheless, we are able to draw some general conclusions that bear on the nature of the contractile mechanism. Regardless of the rate at which mechanical work, heat production or shortening takes place, the contractile machinery is switched on for a more or less fixed time following a single shock. The ability to shorten actively and the ability to develop tension run parallel with one another and to a first approximation the dynamical behaviour of the muscle depends on the mechanical conditions at each instant and not on the full history of the whole contraction. The secondary phenomena that are revealed by study in detail are of a kind that cannot easily be allowed for quantitatively and are of such a magnitude that they make it impossible to decide critically between one theory and another.

SUMMARY

1. A mathematical formulation is proposed to account for the mechanical changes in a muscle twitch.

2. This theory has been tested by making an extensive series of different mechanical measurements on a single muscle. Some of these measurements were then used to calculate theoretical values for the other measurements, the comparison providing a test of the theory.

3. The scope and limitations of this theory and of other theories of muscular contractions are discussed.

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