A METHOD OF DETERMINING THE FORCE-VELOCITY RELATION OF MUSCLE FROM TWO ISOMETRIC CONTRACTIONS

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The hyperbolic relation between the developed tension (P) of a muscle and its rate of shortening (v) is well established (Hill, 1938, 1949*a*; Katz, 1939; Wilkie, 1949; Abbott & Wilkie, 1953). In the characteristic equation,

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

P_0 is the maximum tension developed during a maintained isometric contraction, a and b are constants. To determine these constants in the simplest way, a muscle is allowed to contract isotonically with a number of different loads, the velocity of shortening being measured for each. The force-velocity curve is then plotted and the constants found which provide the closest fit. These measurements are independent of the muscle's series elastic component, since its extension is constant at a given load, and the velocity of shortening therefore is that of the contractile element alone.

During an 'isometric' contraction the contractile component shortens and stretches the series elastic component by the same amount. As the latter is stretched its tension rises, so the velocity of shortening gets less according to the characteristic relation. By comparing two isometric contractions, one with and the other without a known compliance added in series, it is possible to calculate (*a*) the force-velocity relation of the contractile component and (*b*) the tension-extension curve of the series elastic one. The sole assumption required is that the velocity of shortening at any moment is a function only of the force at that moment. The fact that relations (*a*) and (*b*) so derived are similar to those obtained by the usual methods is good evidence for the assumption, and confirms the conclusion already reached (Hill, 1938, 1949*b*; Katz, 1939) that the form of the isometric myogram is uniquely determined by these relations.

METHOD

The tension developed by a muscle and the rate of change of tension are recorded simultaneously throughout the growth of a maintained isometric contraction. A similar record is then made with an extra compliance (a small

spiral spring) inserted between muscle and isometric recorder. The muscle must contract within the range of lengths at which P_0 is near its maximum, and the added compliance must not be so large as to allow the muscle to shorten outside that range. It may then be assumed that the rate of shortening of the contractile component throughout both observations is a function of tension only, and the following analysis can be applied.

Let P be the tension developed by time t during the growth of a maintained isometric contraction, and x the amount by which the series elastic component has been stretched by that tension. Since, in an isometric contraction, the total length is constant the velocity of shortening of the contractile component is dx/dt. But the relation between x and P, determined in a quick release (Hill, 1953), does not depend to any important extent on the actual speed of release, so that dx/dP is a function only of P: hence dx/dt can be written $(dx/dP)(dP/dt)_0$, where the suffix 0 refers to the contraction without added compliance. When an extra compliance c (cm/g wt.) is introduced between muscle and recording system the total extension by tension P is $(x+cP)$, so the velocity of shortening is now $(dx/dP+c)(dP/dt)_c$, where the suffix c refers to the contraction with added compliance. But the velocity of shortening is assumed to depend only on the tension P, so at any given P,

$$(dx/dP)(dP/dt)_0 = (dx/dP+c)(dP/dt)_c.$$

Rearranging, this becomes,

$$\frac{dx}{dP} = \frac{c(dP/dt)_c}{(dP/dt)_0 - (dP/dt)_c}. \tag{1}$$

Now $(dP/dt)_0$ and $(dP/dt)_c$ can be read off from the records at a series of values of P, and dx/dP can be calculated for each. The velocity of shortening dx/dt can then be obtained at every value of P by multiplying dx/dP by the observed value of $(dP/dt)_0$: this gives the characteristic force-velocity relation. By plotting dx/dP against P it is simple by numerical integration to obtain the relation between P and x: this is the tension-extension curve. Thus two 'isometric' records, without and with an added compliance, contain in principle the whole of these two fundamental relations; but on one assumption, that the velocity of shortening depends only on the load.

Experimental details

A frog's sartorius was mounted on a multiple electrode assembly (Hill, 1949b) to ensure that it was stimulated simultaneously all over. Its tibial end was joined by a light chain to the anode shaft of a mechano-electronic transducer (R.C.A. 5734) mounted on the vertically adjustable platform of a Palmer stand. The muscle was kept in oxygenated Ringer's solution at 0° C during the experiment. By working the transducer with an anode load resistance of 275 kΩ and a 360 V (dry battery) high-tension supply, a sensitivity of about 0·1 V/g was obtained, the output being fed into one of the Y amplifiers of a double beam oscilloscope. The transducer was also connected to a small triode pre-amplifier, the output of which was fed, via a series condenser, into the other

Y amplifier of the oscilloscope. The condenser, in conjunction with the high input resistance of the Y amplifier, provided a differentiating circuit. One oscilloscope beam recorded the tension P developed by the muscle, the other the rate of tension change dP/dt.

The time constant of the differentiating circuit was about 2 msec which was small in comparison with the time constant of the tension-time curve under consideration. The efficiency of the differentiation was checked by integrating blocks of three or four consecutive differential ordinates from a given record (obtained in the manner described below) and confirming that the integral bore a constant ratio to the corresponding change in the tension ordinate.

In order to reduce pick-up by the transducer of mechanical vibration transmitted along the connecting chain the whole of the apparatus (including muscle holder and Palmer stand) was mounted on a platform separated from the floor by a number of anti-vibration spring mountings. The mass of the apparatus was artificially increased with heavy iron weights in order to give it a longer natural period and attenuate incoming vibration still further. These precautions were extremely effective.

Records of the tension and rate of change of tension were obtained by photographing the oscilloscope trace while the muscle was being stimulated with alternating condenser shocks (time constant = 1 msec) separated by 60 msec intervals. The time base was adjusted to give a single sweep of about 1·3 sec, so the tension was recorded until after it reached its maximum. This procedure was repeated at the same initial length of the muscle with the series compliance ($c = 0·002$ cm/g wt.) inserted. The measurements were all made at muscle lengths about equal to the resting length in the body, where P_0 is a maximum.

The beams were modulated with the 50 c/s a.c., the trace consisting of spots at 20 msec intervals. This arrangement eliminated the disturbing effect of any mains ripple on the differential trace.

The stimulating circuit was locked to the mains frequency, so the first stimulus was always applied in a fixed relation to the timing dots. In consecutive records, therefore, the time spots in one could be directly related to those in another: mean values could thus easily be obtained.

Calculation

Pairs of records were required which had been made at the same initial length of the muscle, one with and the other without the extra series compliance, and in which the final tension was the same. For this purpose the initial length was varied slightly until a pair with the same maximum was obtained. dx/dP was then calculated from equation (1) at a number of tensions P and plotted as a function of tension. By numerical integration of the area under this curve, the extension of the series elastic component plus that of the recording system was calculated at a number of tensions. The extension (which was small) of the recording system itself was determined separately and deducted. The difference gave the tension-length relation of the series elastic body alone. At low tensions the result is rather inaccurate since $(dP/dt)_0$ and $(dP/dt)_c$ are then small and nearly equal (their difference occurs in the denominator of equation (1)): at higher tensions they differ considerably from one another and the result is more precise.

The velocity of shortening was obtained by multiplying dx/dP by the observed value of $(dP/dt)_0$. The result, as before, is more accurate at higher tensions.

A small correction was applied when necessary to allow for the non-linearity of the transducer.

<div align="center">RESULTS</div>

The force-velocity curve always emerged with the expected hyperbolic form. In Fig. 1 the solid circles were obtained by calculation from experiment, and the curve is the nearest fitting hyperbola. From the values of a and b so found, and from P_0 the maximum tension, a/P_0 is calculated as 0·18 and b/l_0 as 0·36 sec^{-1}. These are in reasonable agreement with values usually found by other methods.
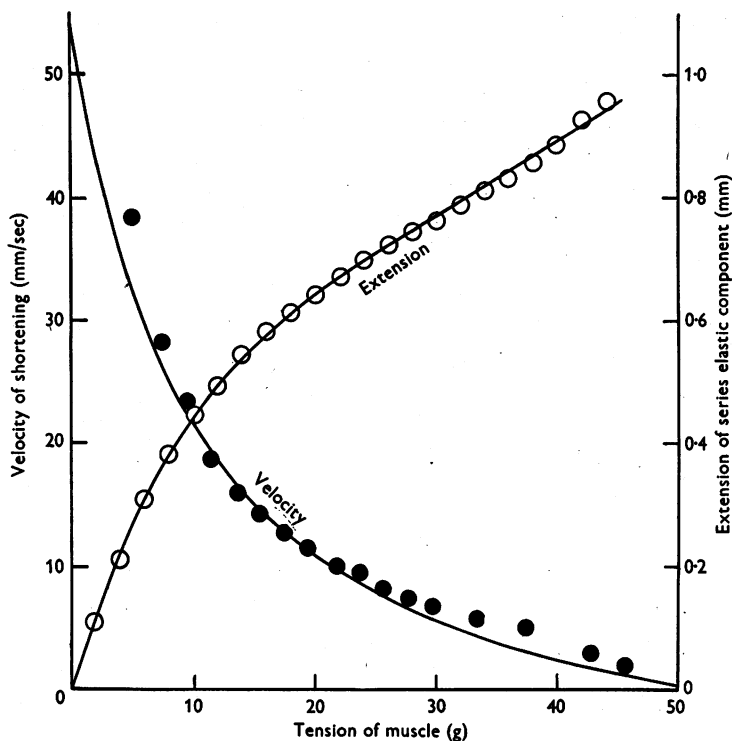

Fig. 1. ●: force-velocity relation calculated from two isometric contractions as described in the text. The line through them is the nearest fitting hyperbola. ○: tension-extension relation similarly calculated. Frog's sartorius, 88 mg, $l_0 = 30$ mm; 0° C.

The tension-extension curves obtained showed the usual curvature at small tensions, gradually becoming linear as the tension and extension increased. They compare well with the curves given by Hill for the series elastic component (1950, fig. 1; 1953, fig. 2), becoming linear at about the same point. The example (hollow circles) in Fig. 1 is derived from the same experiment as the force-velocity relation (solid circles).

DISCUSSION

The fact that the force-velocity curves and the tension-extension curves calculated in this way from pairs of isometric contractions are similar to those obtained by other methods is indirect evidence for the assumption implicit in the calculation that the velocity of shortening is a function only of the load, and alters at once when the load alters. The characteristic equation is still obeyed, even when the force sustained by the muscle is continuously changing.

It had been hoped that the experiments might provide a way of determining the constants of the characteristic equation with only a minimum of stimulation. This information could be useful in various investigations, and would obviate errors which might be introduced by using accepted mean values of a/P_0 and b/l_0. This hope was not fulfilled; the method itself is of interest in confirming predictions and assumptions but its results are not reliable enough, especially at low tensions. The particular requirement that P_0 must have the same value in the two records used for calculation is not easy to meet without several trials, during which the condition of the muscle may change. Possibly the method could be usefully employed with human muscles as investigated by Wilkie (1949, p. 265): in these, repeated trials can be made with consistent results and the initial length can be varied to bring about the equality of the maximum tensions with and without the added compliance. Wilkie's fig. 8 indeed shows such a pair, from which, if the values of dP/dt could be read off accurately enough, the calculations given here could be made.

SUMMARY

1. Two fundamental mechanical properties of muscle are (a) the curve relating the force exerted to the velocity of shortening of the contractile component, and (b) that relating the extension of the series elastic component to the force. Both can be derived from a single pair of isometric contractions, one without and one with an added series compliance, on the assumption that the velocity of shortening depends only on the load.

2. Experiments show that the relations deduced agree with those determined by other methods, and confirm the assumption made. The principle might be usefully applied in human muscles.

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