An analysis of the mechanical components in frog's striated muscle

B. R. Jewell and D. R. Wilkie

*J. Physiol.* 1958;143;515-540

This information is current as of March 19, 2008
AN ANALYSIS OF THE MECHANICAL COMPONENTS IN FROG'S STRIATED MUSCLE

BY B. R. JEWELL AND D. R. WILKIE

From the Department of Physiology, University College London

(Received 27 May 1958)

PART I. The theory of the isometric myogram

A. V. Hill suggested in 1938 that during isometric contraction the actively contractile parts of the muscle shorten at the expense of the passive elastic parts in series with them and thus that the form of the isometric myogram is uniquely determined by the force-velocity curve of the contractile component and the stress-strain curve of the series elastic component. This suggestion has been tested experimentally by Katz (1939), Hill (1949), Wilkie (1950) and Macpherson (1953), whose methods were all variations on the same theme, that of measuring the force-velocity curve and the isometric myogram directly, then calculating the stress-strain curve and showing that this was similar to the estimate currently available from direct measurements. In no case could the underlying theory be rigidly tested, since the three curves had not been determined experimentally on the same muscle. This has led to a somewhat puzzling situation.

Katz, Hill and Wilkie all calculated that the series elastic elements must have been stretched by 6–10% of the muscle length when the tension rose to its full isometric value, and they all noted that this agreed with the direct determination of the series compliance made by Gasser & Hill (1924). However, this early determination must have included an unknown, but presumably large, contribution from the compliance of the mechanical recording lever and its connexion to the muscle; it seems most unlikely that all the later experiments should have included an exactly equal amount of stray compliance. Katz (1939) used similar apparatus and corrected carefully for the stray compliance; nevertheless, his estimate of the series compliance in the muscle itself was double that found later by direct measurement (Hill, 1950, 1953). Hill (1949) did similar experiments using more sophisticated apparatus, but did not correct for the stray compliance. His estimate of the total series compliance (10% of the muscle length for the full isometric tension) is considerably greater than
the direct measurements of the compliance in the muscle alone (3%) made in the following year (Hill, 1950). Although the apparatus used in the two sets of experiments seems to have been roughly the same, it is unfortunately impossible to tell whether all the difference arose from the presence of stray compliance. Wilkie (1950) was working on intact human beings so that his results were in any case not strictly relevant.

Macpherson's (1953) result may have been compatible with the new low estimate of the compliance, but, as he himself pointed out, his method was not very accurate since it depended on small differences. We think that this work should thus not be relied upon as the sole proof of an important theory and that these difficulties can only be resolved by careful determination of all three curves (force–velocity, stress–strain, isometric myogram) on the same muscle. By taking extreme care over details of technique we have been able to make the required long series of records without appreciable deterioration of the muscle.

**METHODS**

The arrangement of the apparatus is shown in Fig. 1. The connexion to the transducer can be hooked into the lever for isometric measurements, or unhooked when the muscle is to be allowed to shorten isotonically. The change in recording conditions is thus made without disturbing the muscle or its connexions. The isotonic load is attached to the lever through a strip of rubber in order to eliminate its effective inertia, as originally suggested by Blix (1895a). In general, the experimental procedure was the same as usual (see, for example, Wilkie, 1956) but many details of technique have received new attention. For example, we have tested the lever and shown it to behave as a pure inertia of 200 mg (equivalent mass referred to the point of attachment of the muscle) up to accelerations of 300 times gravity; we have improved the frequency–response of the photo-electric system used for recording movements of the lever, so that accurate records can be made of very rapid length changes; most of all, we have concentrated on making the connexion from the muscle to the recording apparatus as inextensible as possible while keeping its inertia to a minimum. This is a problem of great importance and some difficulty which will be discussed in a later section. All the experiments were performed in oxygenated Ringer's solution (mm: NaCl 115-5, KCl 2-0, CaCl₂ 1-8, Na phosphate buffer, pH 7-0, 2) and the muscle was stimulated on a platinum multi-electrode assembly. The muscle was automatically tetanized for 1 sec each minute, whether records were being taken or not, in order to keep it in a steady state. These precautions, combined with extreme care in dissection, seem to have prevented the rapid fatigue that has in the past bedevilled measurements of this kind. Our muscles produced very large tensions (up to 2-55 kg/cm²) which declined only gradually throughout the day at rates as low as 0-03% for each second of tetanus. The practical details of all these controls and precautions is described elsewhere (Jewell, 1958).

**RESULTS**

Three complete experiments have been carried out in addition to preliminary investigations. All gave similar results, but only the last of them will be described in detail since it was the most complete and reliable.

The three types of photographic record taken are illustrated in Figs. 2–4. All except Fig. 3b were made at 2° C on the same muscle (L₀ = 30 mm, weight = 64 mg).
(A) After-loaded isotonic contractions from length $L_0$ against various loads (Fig. 2).

(B) Isotonic releases from $L_0$ at 0.7 sec against various loads (Fig. 3). The records show, but with much improved time-resolution, the character previously described (Wilkie, 1956): when the force on the muscle is suddenly reduced by the quick release, there is first a rapid change in length due to passive shortening of the series elastic elements; this is followed by a slower change of length as the contractile component continues to shorten at a constant velocity. The transition from one phase to the other is somewhat obscured by mechanical oscillations. These can be reduced by employing the dashpot ($E$, Fig. 1). Although this introduces some extra inertia, the net effect is to improve the resolution of the method.
(C) Isometric myograms; the initial development of tension at $L_0$ and the redevelopment of tension at $L_0$ after a release from $L_0 + 2$ mm (Fig. 4). In this photograph the two traces happened to be superimposed in a remarkably convenient fashion so that one can see clearly that they coincide only after about 60 msec; before that, the initial rise of tension is somewhat slower than the redevelopment. A similar effect can be discerned in the records published by Hill (1953). This cannot arise because time is taken for the impulse to activate the whole muscle, for the maximum conduction time on our electrode assembly cannot be more than 10 msec, but it could be explained by supposing that the active state does not develop instantaneously to its full value after the first stimulus. If this is truly the case, then the active state cannot quite reach its full tetanic level during a single twitch; for the state of activity

![Graph](image)

Fig. 2. Experimental records on a fast time base (53 msec/sweep) of the early length changes in after-loaded isotonic contractions (1 sec tetanus, 30 shocks/sec) starting at $L_0$. The value of the load is indicated at the point where movement begins. Calibration: 0–5 mm intervals, with beam modulated at 1000 c/s.
certainly begins to decline about 40 msec after a stimulus. In the middle of the third sweep the two traces separate again; this is because the release was made at 0.7 sec in a 1 sec tetanus so that the 'redevelopment' had only 0.3 sec to run while the 'initial' curve had the full second.

Five records were made altogether, in the order ABCBA, so that any deterioration of the muscle would be apparent (none was). This sequence gave us four estimates of the force–velocity curve and two of the stress–strain curve.

![Fig. 3. (a) Experimental records showing the length changes which occur when the force on the muscle is suddenly reduced from the full isometric tension to the value (in g wt.) shown alongside each trace, 0.7 sec after the start of a 1 sec tetanus (30 shocks/sec). The origin of the trace is different for each record and the time base started just before the release catch was operated. Calibration: 0.5 mm intervals with beam modulation at 1000 c/s. The superimposed high-frequency vibration is an artifact produced by the release relay. It is easily remedied, but not in the middle of an experiment. (b) A single record from another experiment (frog sartorius; 31 mm, 76 mg) showing the extrapolation that is made in analysing the trace.](chart)

**ANALYSIS OF THE RECORDS**

**Force–velocity curve**

The records of the early length changes in isotonic contractions (Fig. 2) were made with a fast time base. The early oscillations closely resemble those previously described and analysed (Wilkie, 1950; Hill, 1951b); within 6 msec the velocity has settled to a steady value which is maintained for the full 2 mm of shortening.

No consistent difference could be detected between this velocity (Fig. 2) and the velocity after a release (Fig. 3a), at any given value of the force. This presumably indicates that sufficient time had elapsed before the load was lifted.
for the muscle to become fully active. All four estimates were combined and their means plotted in Fig. 5 together with the range of variation where this exceeds the diameter of the plotted point.

Stress–strain curve

For purposes of calculation it is more convenient to use load (g wt.) and extension (mm) rather than stress (g wt./cm²) and strain (length change/length).

The isotonic quick-release records (Fig. 3a) were analysed as shown in Fig. 3b. In each curve the phase of shortening at constant velocity, xy, was extrapolated back to the instant of release and the height of the intercept, 0z, was taken as the length change in the series elastic elements. In Fig. 6a these length changes have been plotted against the corresponding tensions to give the load–extension curve of the series elastic component and of all the connections up to and including the lever. However, in the arrangement for

Fig. 4. Experimental records of the initial rise of tension in a 1 sec tetanus (30 shocks/sec) and the redevelopment of tension after a quick release at 0-7 sec (the tension rise before the release is not shown; the vibrations are produced by the sudden tightening of the connecting link). After the first 60 msec, during which the initial rise occurs more slowly than the redevelopment, the two traces coincide until the third sweep, when the redeveloped tension begins to decline. This point is indicated by the intersection of the two arrows at the top of the figure. The vertical distance between the two dashed lines corresponds to 20-8 g wt; the dashes occur every 20 msec.
recording isometric contractions, the transducer and the connexion above the lever contributed additional compliance which was estimated by hanging weights on the lever and measuring the corresponding displacements. This gave a linear compliance of 0·0025 mm/g wt., which has been added to the averaged

![Graph](image)

**Fig. 5.** Force–velocity curve at $L_0$. Each point represents the mean of four determinations, two from isotonic afterloaded contractions (Fig. 2) and two from isotonic quick releases (Fig. 3). The maximum range of variation is shown by a vertical line where it exceeds the diameter of the plotted point.

points in Fig. 6a to give the points in Fig. 6b. These show the total load–extension curve of all the elastic elements in series with the contractile component under isometric recording conditions. They have, for convenience in calculation, been fitted empirically by the equations:

$$P = 7e^{x^{0.315}} - 6 \quad \text{when} \quad P < 15 \text{ g wt.}$$

and

$$P = 70x - 9.2 \quad \text{when} \quad P > 15 \text{ g wt.},$$

where $P =$ load in grams and $x =$ extension in millimetres.

**Calculation of the rise in tension in an isometric tetanus**

Our method of calculation is similar in principle to those employed before. At each value of the force, $P$, the velocity of shortening of the contractile component, $dx/dt$, can be read by graphical interpolation from the
Fig. 6. (a) Load–extension curve of the undamped series elastic elements in the muscle and in the connexions below the lever. The points were obtained by analysing two sets of isotonic quick-release records (Fig. 3). (b) Load–extension curve of all the undamped elastic elements in series with the contractile component during isometric recordings. The compliance of the upper connexion (0-0025 mm/g wt.) has been added to the mean of the points in a and the curve drawn from the empirical equations

\[ P = 7e^{0.815} - 6 \quad \text{when} \quad P < 15 \text{ g wt.} \]

and

\[ P = 70x - 9.2 \quad \text{when} \quad P > 15 \text{ g wt.} \]

force–velocity curve (Fig. 5), and \( \frac{dP}{dx} \) is easily obtained by differentiating one of the empirical equations given on p. 521:

when \( P < 15 \text{ g wt.} \), \( \frac{dP}{dx} = 3.18P + 19.1 \text{ g wt./mm} \)

and when \( P > 15 \text{ g wt.} \), \( \frac{dP}{dx} = 70 \text{ g wt./mm} \).

The time required for the tension to rise to a value \( P_i \) is then given by

\[ t = \int_{P=0}^{P=P_i} \frac{1}{(dx/dt) (dP/dx)} \, dP. \]

This integration was performed numerically, using differences up to second order, and the result is shown in Fig. 7 (solid circles). For comparison, the two experimental curves of Fig. 4 have been plotted on the same graph after shifting them so that all curves coincide at the origin. There is a clear discrepancy between theory and experiment, for the muscle actually takes longer to reach a given tension than is predicted by the theory; 80% longer during the initial development of tension and 50% longer during the redevelopment after a release. The whole subject thus demands critical re-examination.
The calculation appears to be based on perfectly sensible premises, and it seems to us that records of the type shown in Fig. 3 can only be interpreted in terms of two separate components whose length and velocity, respectively, are functions of the tension. There are thus three general possibilities to account for the discrepancy:

1. Our estimate of the force–velocity curve may be wrong.
2. Our estimate of the stress–strain curve may be wrong.
3. It may be wrong to represent the muscle by only two undistributed elements; others may be present which are not revealed in isotonic releases, but which are important in isometric tension development. We shall deal with these three possibilities in order.

Fig. 7. Isometric myograms. Solid circles: curve of rise of tension calculated from the force–velocity and load–extension curves. Open circles: observed isometric myograms replotted from Fig. 4; ⨿, initial rise of tension; ◊, redevelopment of tension after a quick release at 0.7 sec. All the curves have been made to coincide at the origin and they all eventually attain the level indicated by the dotted line.

**Force–velocity curve**

Our estimate of this curve is certainly precise enough, as shown by the small scatter of the experimental points in Fig. 5; it is similar to all the previously published curves and could easily have been fitted either by Hill’s equation (1938) or Aubert’s equation (1956). However, the question remains whether this curve, obtained under isotonic conditions, can be used to predict the behaviour of the contractile component under isometric conditions. In formal terms, is the velocity of shortening at each instant a function only of the force
at that instant, or is it influenced, for example, by the previous rate of change of force or some other aspect of the history of the muscle? Such direct evidence as is available supports the original assumption; for the muscle can be seen to achieve a remarkably constant velocity very soon after conditions change from isometric to isotonic, and the velocity at a given force is the same no matter whether the tension has just been rising (Fig. 2) or falling (Fig. 3). Unfortunately, in both types of record the actual moment of transition is obscured by mechanical oscillations which we have not been able to prevent entirely. During the oscillation one cannot say for certain what is happening, but every curve in the two figures could have arisen from a constant velocity and a superimposed damped vibration. There is thus nothing in any of the records to suggest that the velocity does not rise to its final value immediately.

We conclude that the change of velocity follows the change in force very quickly—probably in less than 1 msec and certainly in less than 6 msec. This does not conflict with Hill's (1951b) conclusion that some 8 msec are required in order to reach the full unloaded shortening velocity, for his experiments were made at the onset of activity, ours during full activity in a tetanus. However, our results do contradict A. F. Huxley's prediction that the change in velocity should lag behind the change in force with a time constant of some 28 msec (Huxley, 1957, p. 304).

**Stress–strain curve**

The discrepancy could arise from our having underestimated the compliance of the series elastic component and connexions. Our method of analysis (see Fig. 3b) makes use of an extrapolation which assumes that during the period of elastic shortening and mechanical oscillation the mean velocity of the contractile component is the same as the constant velocity that is achieved after 5–6 msec. However, as discussed above, one cannot be sure that the contractile component does start to shorten immediately at its full velocity: if it does not, the result will be that we do tend to underestimate the compliance. We have thus felt obliged to check our isotonic quick-release method against Hill's (1950) controlled-release method, the principle of which is to measure the variation of tension with length during a single release. This method also leads to an underestimate of the compliance if the shortening of the contractile component is delayed, but the amount of error can be reduced by increasing the speed of release.

**Technique.** For some of the experiments we were fortunately able to borrow Professor Hill's own Levin–Wyman ergometer, to which our electrode assembly and muscle bath could be securely clamped. For others we used a simpler device (Jewell, 1958) consisting of a transducer tube (RCA 5734) fixed to the armature of a relay, which was released by interrupting the current through
MECHANICAL COMPONENTS IN MUSCLE

its coil, whereupon the transducer was pulled rapidly away in the 'release' direction by judiciously chosen and stretched rubber bands. With this device we were able to achieve a speed of release of 500 mm/sec, some three to four times faster than with the Levin–Wyman apparatus. In both cases the movement of the transducer was followed by connecting it to the photo-electric isotonic lever. Tension was displayed on the Y-axis of a cathode ray tube and length on the X-axis, so that the load–extension curve was drawn automatically on the photographic record.

Results. In Fig. 8 are shown a number of stress–strain curves measured on different muscles by either the controlled or the quick-release techniques. The curves have been corrected for the compliance of the connexions, but the correction for active shortening of the contractile component (see Hill, 1953) has not always been applied to the measurements by the controlled release technique, since it is small, e.g. 0.04 mm extension at a stress of 0.164 kg wt./cm² with a release speed of 210 mm/sec. At first we did not understand the full subtleties of the properties of connexions (see Appendix) with the result that we are not certain how big the correction should be in some of the earlier isotonic quick-release experiments. These curves in Fig. 8 (designated 'approximate') have accordingly been corrected for the minimum amount of external compliance that must have been present, though the true correction required may have been somewhat larger and the true stress–strain curve somewhat steeper.

It is evident from Fig. 8 that the isotonic quick-release method is not leading to an underestimate of the series compliance and thus that it cannot be held responsible for the discrepancy apparent in Fig. 7. In one experiment, the series compliance was measured by controlled release and isotonic release methods on the same muscle (Jewell, 1958) with good agreement. All our measurements lead to a somewhat lower estimate for the series compliance that is given by Hill (1950, Fig. 1). His estimate is about 1.4 times ours at stresses above 0.5 kg wt./cm², and more than twice ours below this point.

Elements in the muscle

To explain the discrepancy between theory and experiment, one needs an additional series compliance, for example, a damped elastic element that does not change in length during quick-release determinations but does so during the relatively slow rise of isometric tension. This explanation seems unlikely, since there is still a marked discrepancy between theory and experiment immediately after a quick release, during which there is presumably insufficient time for a damped element to change in length (Fig. 7). The fact that the velocity soon reached the same value, no matter whether the tension had previously been rising (Fig. 2) or falling (Fig. 3), also argues against the participation of a significant damped element. The argument is the same whether one
Fig. 8. The stress–strain curve of the series elastic component. The graph shows the stress–strain curves that have been obtained from a number of frog sartorius muscles by either the quick-release (open circles) or the controlled release (solid circles) techniques. The heavy black line shows the 'standard curve' obtained by Hill (1950) using the second method. For purposes of comparison, the stress has been expressed in kg wt./cm² of muscle cross-section and the strain as a percentage of the muscle length $L_0$. The following table summarizes the details of the experiments made:

<table>
<thead>
<tr>
<th>Curve</th>
<th>Date</th>
<th>$L_0$ (mm)</th>
<th>Weight $M$ (mg)</th>
<th>$P_y L_0/M$ (kg wt./cm²)</th>
<th>Release</th>
<th>Correction for the external compliance</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Feb. 13</td>
<td>31</td>
<td>76-0</td>
<td>2-20</td>
<td>Quick</td>
<td>Approx.</td>
</tr>
<tr>
<td>B</td>
<td>Feb. 13</td>
<td>31</td>
<td>76-0</td>
<td>2-20</td>
<td>Controlled</td>
<td>Approx.</td>
</tr>
<tr>
<td>C</td>
<td>Mar. 12</td>
<td>29</td>
<td>60-0</td>
<td>2-13</td>
<td>Quick</td>
<td>Approx.</td>
</tr>
<tr>
<td>D</td>
<td>May 21</td>
<td>30</td>
<td>64-0</td>
<td>1-62</td>
<td>Quick</td>
<td>Approx.</td>
</tr>
<tr>
<td>E</td>
<td>June 6</td>
<td>32</td>
<td>55-8</td>
<td>2-19</td>
<td>Quick</td>
<td>Accurate</td>
</tr>
<tr>
<td>F</td>
<td>June 28</td>
<td>30</td>
<td>30-6</td>
<td>1-77</td>
<td>Controlled</td>
<td>Accurate</td>
</tr>
<tr>
<td>G</td>
<td>July 2</td>
<td>33</td>
<td>52-0</td>
<td>2-09</td>
<td>Controlled</td>
<td>Accurate</td>
</tr>
</tbody>
</table>

The Levin–Wyman ergometer was used in experiments $F$ and $G$ and the simpler lever system in experiment $B$. In the last column of the table, the term 'accurate' means that the compliance of the connexions and the recording apparatus was carefully measured in the manner specified in the Appendix. In the earlier experiments ('approximate'), this was not satisfactorily done and these curves have been corrected for the minimum amount of external compliance that must have been present. Thus these curves may really be somewhat steeper than is shown in the figure.
supposes that the damped elasticity is passive, or that it consists of weak parts of the muscle being stretched by stronger parts (Blix, 1895b; Fischer, 1926; Katz, 1939; Hill, 1953).

The whole question of inequalities in strength between one part of the muscle and another is very difficult to resolve quantitatively. Professor A. V. Hill has suggested that it might be illuminating to see what happens when two muscles of unequal strength are arranged in series and then stimulated. This is an experiment that we hope eventually to perform.

Thus none of the proposed explanations for the discrepancy is altogether satisfactory, though we favour the view that the velocity depends not only on the force, but on some aspect of the history of the muscle. We doubt whether further improvements in recording technique will shed much light on the matter, as the muscle itself, and the fluid around it, have an appreciable and irreducible inertia and the connexions inevitably add some compliance. Perhaps the tortoise muscle studied by Katz (1939) and Goodall (1957), which is slower and in which the discrepancy is even more marked, would be a more suitable experimental material.

Although Hill’s original theory may not give a quantitatively exact account of the way in which isometric tension develops, there is no doubt that qualitatively, isometric tension rises much more slowly the larger the series compliance (see, for example, Hill, 1951a). The earlier calculations from the isometric myogram that showed a length change of 0·1L₀ in the series elastic structures may well have been correct, for wet threads can easily introduce a large damped compliance which affects the shape of the myogram, but which is deceivingly absent from measurements made by quick-release techniques (see Appendix). Our present experiments certainly show signs of having been made with very inextensible apparatus. For example:

(1) In our isometric myograms the tension rises 2–3 times faster than in comparable ones in the literature (compare our Fig. 7 with Katz (1939), p. 52, Table III; Hill (1953), p. 14, Fig. 6D; Macpherson & Wilkie (1954), p. 293, Fig. 1).

(2) We have obtained high twitch:tetanus ratios of up to 0·92 at 0°C.

(3) A consequence of this has been to cast doubt on the view that the twitch tension gets smaller as the temperature is raised (Hill, 1951d). With our apparatus the twitch tension often increases with rise of temperature, but in all cases the temperature coefficient is close to unity. In muscles where initially the twitch tension rose with increasing temperature, the addition of a small extra compliance to the connexion reversed this effect (see Jewell, 1958, for further details).
APPENDIX TO PART I: PROPERTIES OF CONNEXIONS

In assessing the usefulness of any given type of connexion one is concerned both with its mass per unit length (which determines inertial distortion at high acceleration and greatly influences the occurrence of vibration) and with its elasticity, which is in general complicated by non-linearity and damping. The properties of the three materials that we have used, chain, straightened stainless steel wire and plaited silk are summarized in Table 1. Straightened wire is seen to be light and very inextensible, but it is slightly damped and somewhat non-linear. These defects are only slight if it is straightened by cold-drawing and handled with care. Chain has the disadvantage that it is very heavy, but it is fairly inextensible, linear and undamped; moreover, it is very easy to handle.

### Table 1. Elastic properties of connecting materials

<table>
<thead>
<tr>
<th>Material</th>
<th>Release speed</th>
<th>'Compliance' (%)</th>
<th>'Non-linearity' (%)</th>
<th>Weight (mg/cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silver chain</td>
<td>Fast</td>
<td>0.071</td>
<td>8.0</td>
<td>25-600</td>
</tr>
<tr>
<td></td>
<td>Slow</td>
<td>0.075</td>
<td>8.5</td>
<td>—</td>
</tr>
<tr>
<td>36 s.w.g. wire (stainless steel)</td>
<td>Fast</td>
<td>0.036</td>
<td>39.0</td>
<td>2-240</td>
</tr>
<tr>
<td></td>
<td>Slow</td>
<td>0.050</td>
<td>44.0</td>
<td>—</td>
</tr>
<tr>
<td>Plaited silk (Weiss Gauge 1)</td>
<td>Fast</td>
<td>0.490</td>
<td>58.3</td>
<td>0-693</td>
</tr>
<tr>
<td></td>
<td>Slow</td>
<td>0.560</td>
<td>63.0</td>
<td>—</td>
</tr>
<tr>
<td>Wet</td>
<td>Fast</td>
<td>0.660</td>
<td>29.7</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Slow</td>
<td>1.560</td>
<td>44.6</td>
<td>—</td>
</tr>
<tr>
<td>Complete connexion (3% silk, 97% 36 s.w.g. wire)</td>
<td>Fast</td>
<td>0.044</td>
<td>45.4</td>
<td>2-200</td>
</tr>
<tr>
<td></td>
<td>Slow</td>
<td>0.057</td>
<td>52.0</td>
<td>—</td>
</tr>
<tr>
<td>Wet</td>
<td>Fast</td>
<td>0.036</td>
<td>13.7</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Slow</td>
<td>0.079</td>
<td>52.6</td>
<td>—</td>
</tr>
</tbody>
</table>

After stretching the connexion to produce a tension of 50 g wt., the tension-length curve was measured by making a controlled release at the required speed. The straight part of each curve (extending from 50 g wt. down to about 25 g wt.) was extrapolated to zero tension, producing an intercept a on the length axis. If b is length change actually required to drop the tension to zero and L is the length of the connexion, then the ‘compliance’ is taken as b/L × 100 % and the ‘non-linearity’ as (b - a/b) × 100 %.

Silk thread, of which a small quantity must be used for tying muscle to wire or chain, is the main source of confusion since it is very compliant and non-linear, and its properties are critically dependent on whether it is wet or dry. When wet, as it normally is in use, its stress-strain curve varies considerably with speed. At high speed it is very inextensible, presumably because the water cannot move about rapidly in the pores of the material. We have therefore kept the length of the silk so short that its contribution as a damped elastic element is small, approximately 5 % of that of the whole connexion.

Because of these complications it is by no means a simple matter to correct for the stretch that takes place in the connexions. We have come to the conclusion that the only valid way to do this is to perform a dummy experiment similar in speed and other respects to the one on the muscle, but in which the muscle itself has been cut away and the knot from its tendon slipped on to a hook held rigidly in the clamp that formerly held the pelvis. The corrections designated ‘accurate’ in Fig. 8 have all been based on this procedure.
PART II. Further observations on the elastic properties of muscle

Since we had been obliged to improve the technique for estimating the compliance of the series elastic component, we thought that we should try to extend our knowledge of this element of the muscle by making measurements at various muscle lengths, at various times after a single stimulus and at different temperatures.

*The effect of muscle length on the series elastic component*

Measurements have been made by both the quick-release and the controlled-release methods. Both give the same result but only those obtained by the latter method will be given here.

![Load-extension curves of the series elastic component at various muscle lengths](image)

**Fig. 9.** Load–extension curves of the series elastic component at various muscle lengths. (Frog sartorius: 80·3 mg, \(L_0=32\) mm, 0° C.) (a) Muscle lengths below \(L_0\); (b) Muscle lengths above \(L_0\). In both graphs the curve at \(L_0\) is the mean of five curves at 0° C. The load–extension curves obtained at other muscle lengths have been shifted horizontally to make their highest points lie on this curve. Not corrected for the compliance of the connexions.

Fig. 9a shows that reducing the muscle length from \(L_0\) to \(L_0-10\) mm produces very little change in the load–extension curve of the series elastic component. Stretching the muscle to about \(L_0+4\) mm also leaves the curve unaffected (Fig. 9b), but at greater lengths, e.g. \(L_0+8\) mm, a characteristic change takes place in the shape of the curve. It becomes flatter, especially at low tension; that is, a larger release is needed to produce a given fall of tension.

The length at which the change occurs is that at which the resting muscle begins to show long-lasting tension, suggesting that at this point the parallel
elastic components in the muscle somehow begin to contribute to the measured series elasticity of the muscle.

Before explaining how this comes about, it will be necessary to review briefly what is known of the parallel elastic components in muscle. That such structures must exist is clear from the fact that resting muscle can bear tension, though it has long been known that resting muscle is a very imperfect elastic body. Blix (1893) demonstrated that it did not obey Hooke's law and that its elastic properties were markedly time-dependent, leading to hysteresis and after-extension. He attributed this behaviour to internal viscosity and experimented with visco-elastic model systems, but despaired of a quantitative solution to the problem. Later authors (Banus & Zetlin, 1938; Buchthal, Kaiser & Rosenfalek, 1951; Hill, 1952) have shown that the stress-strain curve is, to a first approximation, exponential. The time-dependent property has been analysed in two ways: either by supposing that the resting muscle contains a number of linearly damped elements with different time constants (Buchthal et al. 1951; Abbott & Lowy, 1957), or that it can be treated as a single damped element with highly non-linear properties (Stacy, 1957).

With fairly slow stretch and release, say 10 min each way, hysteresis is not very great. We have obtained sets of stress-strain curves from the whole muscle that are similar in appearance to those obtained from single fibres (Buchthal et al. 1951, Fig. 12). If the muscle is held extended, the stress-strain curve shifts along the length axis in the direction of increasing length. Accordingly, the tension measured at any given extension falls off with time. Similar behaviour is shown, but to a more striking degree, by smooth muscle (Abbott & Lowy, 1957).

These secondary phenomena make accurate prediction difficult, but they can be turned to some use. When a muscle is held at such a length that it exhibits resting tension, its series elasticity is affected (see Fig. 9). If the muscle is held continuously at this length, the resting tension falls progressively, and the change in the series elastic curve progressively disappears. This proves that it is the mechanical contribution of the parallel elastic component and not the length of the muscle as such that modifies the series elastic properties of the highly extended muscle. The exact way in which the series and parallel elements act together must depend on the way in which these structures are arranged in the muscle. Two simple arrangements that have been suggested in the past are shown in Fig. 10, I and II (Hill, 1951c, p. 346, Fig. 6; Aubert, 1956, Fig. 19, respectively).

We have made the following assumptions:

1, that at rest the contractile component is freely extensible;
2, that in quick-release experiments on the active muscle there is not time for appreciable shortening of the contractile component to occur; and
3, that the active contractile component can go slack if its ends are approximated, i.e. that it has no rigidity in compression.

It is then possible to work out the quantitative relation between the load-extension curves of the two elements and that of the whole muscle, for each of the two proposed models (see Jewell, 1958, for details). Fig. 10 shows load-extension curves made by the controlled-release technique on active muscle at $L_0$ (curve A), resting muscle at $L_0 + 10$ mm (curve B) and active muscle at $L_0 + 10$ mm (curve C), all corrected for the compliance of the connexions. The first two experimental curves have been used to calculate theoretical values for the third; these are shown as open circles for model I and filled circles for model II. Both sets of symbols fall so close to curve C that one cannot exclude either model. Considering the complex structure of the actual muscle it is very satisfactory that this analysis in terms of three undistributed elements works out as well as it does.
The series elastic component at various times after a stimulus

We have found that the controlled-release technique is more suitable for investigating this problem than the quick-release technique previously used (Wilkie, 1956). Our Fig. 11 is similar to Fig. 1 of the earlier paper, but the difference between curves which is found now is almost certainly significant, whereas that in the earlier paper could be, and was, discounted as being due to experimental scatter. Our conclusion is that the series elastic component does become slightly more compliant during relaxation.

![Graph](image-url)

Fig. 11. Load–extension curves of the series elastic component at various times after a single shock. Frog sartorius: 60 mg, \( L_0 = 29 \) mm, \( 0^\circ \) C. If the curves are moved along the horizontal axis until their highest points coincide with the stress–strain curve obtained at 0.2 sec, then the shifted curves fall more and more to the right of this curve as the releases are made at later times after the stimulus. The dashed line indicates the position of the shifted 0.6 sec curve; all the others fall in the envelope bounded by this line and the 0.2 sec curve.
The effect of temperature on the series elastic component

A set of measurements on a single muscle at various temperatures is shown in Fig. 12. Measurements at room temperature are difficult to make and probably not very accurate, for even using the fastest attainable speed of release, the active shortening of the contractile component is rather large; also

Fig. 12. Load–extension curves of the series elastic component at various temperatures. Frog sartorius: 80·3 mg, $L_0$ 32 mm; the same muscle as in Fig. 9. The load–extension curve at 0°C is the mean of five determinations and the range of variation is shown by a horizontal bar at each point. The curves obtained at 10·8 and 21·7°C have been shifted horizontally to make their highest points lie on the 0°C curve. Not corrected for the compliance of the connexions or for active shortening.

at the high speed there are uncertainties about inertial reaction, frequency response of photocell system, etc., that make the labour of correcting for active shortening seem scarcely worth while. However, all the difference between the curves probably does not arise from these causes, so that the series compliance may be slightly greater at the higher temperature.
The effect of hypertonic Ringer's solution on the series elastic component

This is shown in Fig. 13. Soaking for 30 min in double-strength Ringer's solution reduces the series compliance almost to one half its normal value. The change is reversed on replacing in normal Ringer's fluid. Hypertonic solutions greatly reduce the intrinsic speed of the muscle (Howarth, 1957) and may have the effect of damping any parts of the series elastic component that are distributed along the muscle fibre, so that their compliance cannot be detected during quick changes of the length of the muscle.

Fig. 13. The effect of hypertonic Ringer's fluid on the series elastic component. Frog sartorius 0° C; 32 mm, 74 mg; controlled release technique at 300–400 mm/sec; all curves corrected for compliance of connexions. ○, normal Ringer's fluid, mean of 4 determinations. ●, in 2 × Ringer's fluid; concentration of all solutes except phosphate has been doubled; mean of 3. ○, control determinations after return to normal Ringer's fluid, mean of 3.
MECHANICAL COMPONENTS IN MUSCLE

THE ANATOMICAL SITES OF THE SERIES AND PARALLEL ELASTIC COMPONENTS

Series component

The question has often been posed whether the series elastic component is all in the tendinous ends of the muscle or whether part of it may be located within the microstructure of the muscle fibres (see e.g. Buchthal et al. 1951, p. 168; Wilkie, 1950). These two possibilities correspond roughly with models II and I, respectively, in Fig. 10, so that it is a pity that mechanical analysis did not lead to a clear decision between them. The failure of the series component to change substantially with muscle length, temperature or time after a single shock points to its being in an inert region of the muscle and probably excludes the possibility that it is in the A or I filaments or the bonded region between them (see Hanson & Huxley, 1955). This leaves only the Z disk, as suggested earlier by Szent-Györgyi (1953).

Some indication of the amount of stretch in the tendon during isometric contraction can be obtained by direct observation of the contracting muscle. By recording the movement of marks on the muscle (either pieces of black thread or spots of fluorescent dye) Fischer (1926) and Csapo & Mashima (1957, and private communication) have shown that the middle of the muscle shortens and stretches out the ends. However, the stretched ends are not the same thing as the series elastic component, for the movements of the former must be highly damped by the contracted muscle fibres that they contain. As explained above, such damped elements will not contribute to the measurements of the series elastic component. In order to locate the site of the undamped elastic regions one would have to record the length changes in different parts of the muscle during the actual course of a quick release from one tension to another. This would certainly be very difficult to do, for the total length change is only about 0.5 mm and it takes place in less than 5 msec. A simpler experiment that gives almost as much information is to examine a muscle microscopically during a tetanus. If the contraction were perfectly isometric, the muscle perfectly uniform in strength and the series elastic component uniformly distributed along the length of the muscle fibres, no movement would be detected. From the movements that do occur it is possible to assess how accurately the above conditions are satisfied and, in particular, whether much of the stretch takes place in the anatomical tendons. The muscle was mounted on the usual multi-electrode assembly in Ringer's fluid and tetanized for 1 sec each minute. At room temperature the tetanic plateau lasts quite long enough to permit one to make measurements of the movements of marks on the surface of the muscle through a binocular microscope. Carborundum particles (J. R. Hill, 1957), scattered on the surface from a fine brush, are very suitable for the purpose. The results of three such experiments are
shown in Fig. 14, from which it is clear that there is a good deal of variation from one muscle to another.

Less than 0.2 mm of tendon is normally visible at the tibial end of the muscle between the knot and the muscle fibres, and although the distal part of the muscle does stretch slightly, it is clear that only a negligible amount of this stretch takes place in the tendon proper. At the pelvic end the muscle fibres are inserted into a sheet of tendon attached to the pelvic bone and this stretches appreciably, up to 0.25 mm, under full tetanic tension. Even so, the

Fig. 14. The movement of marks on the surface of a frog’s sartorius muscle during a 1 sec tetanus at 18–20°C. Abscissae: Original position of mark in mm from pelvic end. Ordinates: Movement of mark in mm, measured along the mid line, to left or right (i.e. towards pelvic or tibial end). Positive slope indicates local shortening and negative slope indicates local stretching; unit slope (45°) corresponds to 10% local length change. The ordinate at the extreme right-hand end of each curve shows the movement of the knot, that is, the stretch in the connexions. Solid lines, muscle at body length; dashed lines, muscle extended. A. 53.0 mg muscle, seen from skin side \( L_0 = 32 \) mm. B. 140.0 mg muscle, seen from skin side, \( L_0 = 35 \) mm. C. 67.4 mg muscle, seen from bone side, \( L_0 = 32 \) mm.

total stretch in the anatomical tendons accounts for only about one half the measured series compliance, the remainder probably being distributed along the muscle. The same conclusion is strongly, though indirectly, suggested by the demonstration that hypertonic solutions reduce the measured series compliance to about one half of its normal value.

The maximum local shortening encountered was 25% (Fig. 14 C, 5 mm from pelvic end); but this took place in only 1 mm of the muscle. Elsewhere, as in
most of $A$ and $B$, the length changes were much smaller. The most striking movements to be seen are those between the middle of the muscle and its edges, which sometimes move in opposite directions.

If the muscle is extended by 8–10 mm before stimulation, the movements are smaller and more uniform from one muscle to another, and in every case the pelvic end shortens somewhat, stretching out the remainder of the muscle. There is certainly no sign that instability results from stretching the muscle, as was predicted earlier (Hill, 1953).

**Parallel component**

If Fig. 10 has been interpreted correctly, the parallel elastic component is the same in resting and in active muscle. This helps to justify what has often been assumed implicitly, that in the tension–length curve one may subtract the resting tension from the total tension in order to determine the active contribution of the contractile mechanism (see Hill, 1953; Banus & Zetlin, 1938). Banus & Zetlin were able to show that the connective tissue sheath, when present, was the most important site of parallel elasticity in whole muscle and that it determined whether the tension–length curve of the active muscle had a hump and dip (as in the frog’s sartorius) or was monatonic (as in the frog’s gastrocnemius).

In the case of single isolated fibres the situation is less clear since there appears to be a conflict of evidence between Ramsey & Street (1940) and Casella (1951) over the question whether the sarcolemma can support the full resting tension. It seems likely to us that both parties may have been right but that their techniques of dissection were slightly different, for Ramsey and Street’s active tension–length curves show a very pronounced hump and dip, indicating weak parallel elastic structures, in contrast to those of the Buchthal school (see e.g. Buchthal et al. 1951, Fig. 50) which have no dip at all, indicating that stronger structures had been spared by the dissection. Whether the contents of the resting muscle fibre have any tensile strength is not known for certain. One attractive hypothesis is that resting tension is borne by the H filaments that link together the ends of the myosin filaments. However, these appear to be too flimsy for the purpose (H. E. Huxley, private communication).

**SUMMARY**

1. An attempt has been made to test the theory that the form of the isometric myogram is governed by the isotonic force–velocity curve and the stress–strain curve of the series elastic elements. In order to do this, all three curves have been accurately measured on the same muscle at the same time, at 2° C.

2. It is found that the theory predicts a faster rise of tension than is actually observed experimentally.
3. It is shown experimentally that the initial development of tension is slower than redevelopment of tension after a release. This probably indicates that the active state takes some time, approximately 60 msec, to become fully established.

4. The theory of the myogram is based on the assumption that the force-velocity relation is instantaneously obeyed. Our experiments show that the velocity of active shortening does change very quickly when the tension on the muscle alters. The change is seen to be complete within 6 msec, though the actual delay in the muscle may well be much less.

5. We have also examined critically the other assumption, that the isotonic quick-release method does measure the effective series elasticity. Comparable measurements by the more familiar controlled-release method give similar results and all lead to a lower estimate of the series compliance than the currently accepted value (2% length change instead of 3% for the full isometric tension).

6. Great care was taken to eliminate stray compliance from the connexions and to correct for whatever compliance remained. The correction is greatly facilitated by choosing suitable materials for the connexions. This problem is dealt with in an appendix.

7. If the recording apparatus and connexions are made sufficiently inextensible, the twitch tension varies only slightly with change in temperature. Usually the twitch tension decreases with rise in temperature, but sometimes it increases.

8. As the muscle length is changed from 10 mm below to about 4 mm above body length, the measured series elasticity hardly alters. However, at still greater lengths the measured compliance increases; this can be quantitatively accounted for by supposing that parallel elastic components have begun to participate.

9. At late times after a single shock, the series elastic component becomes slightly more compliant.

10. Measurements at higher temperatures are not very reliable, but they indicate that the series compliance increases when the temperature is raised.

11. In hypertonic Ringer’s solution the series compliance is reduced almost to half its usual value.

12. The anatomical sites of the series and parallel elastic components are discussed. Direct microscopic observation of the contracting muscle shows that about half the series compliance is in the pelvic tendon. The remainder is probably distributed along the muscle fibres.

We wish to thank Professor A. V. Hill for lending us his Levin-Wyman ergometer, for encouraging us to look for non-uniformities in the muscle and, in general, for refusing to believe our results until our experiments actually showed what we claimed they did.
REFERENCES


B. R. JEWELL AND D. R. WILKIE


An analysis of the mechanical components in frog's striated muscle
B. R. Jewell and D. R. Wilkie

*J. Physiol.* 1958;143;515-540

This information is current as of March 19, 2008

<table>
<thead>
<tr>
<th>Updated Information &amp; Services</th>
<th>including high-resolution figures, can be found at: <a href="http://jp.physoc.org">http://jp.physoc.org</a></th>
</tr>
</thead>
<tbody>
<tr>
<td>Permissions &amp; Licensing</td>
<td>Information about reproducing this article in parts (figures, tables) or in its entirety can be found online at: <a href="http://jp.physoc.org/misc/Permissions.shtml">http://jp.physoc.org/misc/Permissions.shtml</a></td>
</tr>
<tr>
<td>Reprints</td>
<td>Information about ordering reprints can be found online: <a href="http://jp.physoc.org/misc/reprints.shtml">http://jp.physoc.org/misc/reprints.shtml</a></td>
</tr>
</tbody>
</table>