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The Viscous Elastic Properties of Muscle.

A. Levin* and J. Wyman.†

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(From the Department of Physiology and Biochemistry, University College, London.)

I. Introduction.

Towards the middle of the last century Weber (1) investigated the problem of muscular contraction from the physical and mechanical points of view. He thought it possible to express the activity of the muscle solely in terms of a change in its elastic condition in response to stimulation. In other words, he assumed that the active muscle behaved as a stretched spring and that the tension-length curve of a given muscle, under a definite set of external conditions, was invariable and independent of the particular way in which it was obtained. This assumption was shown to be erroneous by Blix (2), with the help of his myographion, by means of which tension-length diagrams both of shortening, and of stretched, muscle could be automatically recorded. Blix showed that, at any length, tension developed during stretch was greater than corresponding tension developed during release. This observation was confirmed and extended by Fick (3, 4), who at first assumed an increased "physiological" response in stretch as the cause of this effect. In order to measure this response he determined the total energy of a contraction, this term denoting the algebraic sum of mechanical work and heat produced by the muscle. This quantity was found to be smaller in the case of a stretched muscle, and no satisfactory explanation was available capable of fitting the more elaborate picture which had emerged, largely from Fick's hands.‡

A new aspect of the problem was created by the work of A. V. Hill (5) and his associates (6, 7) from twenty to thirty years later. These investigators introduced the concept of friction and viscosity, irreversibility in the thermodynamic sense, into the study of muscle. The effect of this point of view was immediate. In Hill's paper of 1922 experiments were described which promised to clear away a substantial part of the difficulties presented by the work of Fick (and others). Hartree and Hill (8), in a paper on thermoelastic phenomena in muscle,

* Working for the Medical Research Council.
† Fellow of the National Research Council, U.S.A.
‡ We have omitted any account of the work of various other investigators in order to emphasize the main trend of the problem with which we are concerned in this paper.
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had previously shown that "when the length of a muscle is altered passively, a considerable quantity of heat is evolved, which is greater the more sudden the change of length." They had attributed this phenomenon to the degradation of a portion of the mechanical energy of the system into heat as a result of frictional and viscous processes accompanying deformation; and Hill expressed the view that deviations from the theoretical maximum work (as calculated from isometric tensions developed at various lengths) and the actual work obtained when a frog's muscle was allowed to shorten by means of a maximum work device (see Doi (9)) were to be ascribed to the same cause, i.e., wastage of work in the viscous material of the muscle itself. In 1922 Hill (5) investigated the matter in the case of human arm muscles by having the arm to work against the inertial reaction of a heavy fly-wheel, the mechanical advantage and, consequently, the speed at contraction being variable. It was found that the work decreased with increase in the speed of shortening, as expressed by the formula

$$W = W_0 \left[1 - \frac{k}{t}\right],$$

where $W$ is the work, $t$ is the time occupied by the shortening, and $W_0$ and $k$ are constants. Now this is precisely the expression for the work done by a simple viscous-elastic system shortening at any constant speed $1/t$ (see below). In this case $W_0$ gives the ideal work which the system is capable of doing as the speed of shortening approaches zero, and $k$ is a constant depending on the viscosity.

A wider development of this idea was contained in the paper by Gasser and Hill (10). In this paper the results obtained with human arm muscles were confirmed in general by experiments on the directly stimulated sartorius of the frog. Further experiments also were carried out on the effects of sudden stretches and releases on the tension registered by frog's muscle. It was found that after an "instantaneous" release of an isometrically stimulated muscle, there was a drop of tension below the normal isometric value for the new length, proportional to the percentage shortening. A 15 per cent. shortening caused complete disappearance of tension. Such a drop of tension was followed by a redevelopment along the same curve (when tension was plotted against time) as that for the development of an isometric contraction. When the shortening was carried out more slowly, the drop of tension was less marked, until, for very low speeds, the tension fell gradually from the isometric value for the initial to that for the final length. If, on the other hand, the muscle was stretched, there was a momentary rise of tension depending on the extent
and suddenness of the stretch. If the stretch was very sudden, the rise was
followed by a fall, and that in turn by a redevelopment to the tension character-
istic of the new length along the usual curve for an isometric contraction. If
the stretch was less sudden, the tension rose above the value for the new length
and approached equilibrium from above. When a quick release was followed
by a quick stretch, the initial tension was at once restored, and similarly for a
quick stretch followed by a release. All these rather complicated results
Gasser and Hill attributed to the viscous properties of the muscle system, which
prevented the immediate attainment of equilibrium when its length was
changed. They also made direct determinations of changes in viscosity conse-
quent upon stimulation by means of recording the damping effects of muscles
on the oscillations of a flat steel spring. Finally they concluded their experi-
ments by showing that, qualitatively at least, their results could be repro-
duced with a viscous-elastic model described in their paper.*

If, thus, the introduction of the concept of viscosity removed many of the
objections arising from the work of Fick and others, there still remained the
question of the total energy liberated by the muscle. Fick's experiments
dealing with this matter did not admit any such simple interpretation. His
heat measurements have been recently substantiated by the researches of
Fenn (11, 12) and Wyman (13). Fenn had, it is true, confined his attention in
the main to cases of shortening muscles; but Wyman had made a careful study
of stretches as well, using the improved thermal methods of Hill for measuring
heat and a new and very accurate form of myograph for recording work. He
found, just as Fick had done, that the muscle liberated more total energy when
it shortened and did external work than when it was stretched and work was
done on it. Wyman, however, pointed out that the values of the total energy
calculated from the protocols of all these experiments were based on a certain
assumption, which, though plausible, was by no means assured. It was taken
for granted in the calculations that the chemical energy liberated in contraction
(the measure of the physiological response) all appeared either as work or heat;
in particular it was assumed that any mechanical potential energy present at
the moment of relaxation would be degraded quantitatively into heat. Unless
this assumption were granted (if, for example, it were supposed that part of the
mechanical energy disappeared directly as chemical energy in relaxation), it
was wholly impossible to say, from the results of these experiments, whether
more energy was liberated in a stretch or in a shortening, and it was quite

* Hill himself has recently repeated and confirmed in the case of Holothuria nigra and
tortoise the part of these experiments dealing with stretches and releases. See Hill (19).
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reasonable to assume that it was the same for both. It appeared possible, therefore, that the total energy liberated by the muscle was independent of the conditions of work under which contraction took place, and that the simple viscous-elastic view of muscle was, after all, correct.

What was needed, in the opinion of the writers, in view of the complexity of the situation, was further work along two lines. In the first place it was important to carry out fresh and more searching experiments on the viscous-elastic properties of muscle, following the lead taken by Hill. In the second place it was necessary to find independent ways of studying the energy liberation of muscle under different conditions of shortening and lengthening in order to determine whether or not there really are corresponding differences in "physiological" response. Experiments of the first type form the subject of the remainder of this paper.

II. Method.

The general plan of the experiments on the mechanical properties of muscle has been to obtain really accurate tension-length curves for stretches and releases at different constant speeds, and to study these curves quantitatively as far as possible, subjecting them to careful analysis with the aid of various types of viscous-elastic models. In this way it was hoped to throw further light on the real nature of muscle regarded as a viscous-elastic system.

In order to attain this end we have made use of a new type of myograph, previously described in another connection (13), but for this purpose somewhat modified and entirely overhauled. This instrument differs substantially in design from the Blix's myographion. Whereas in the latter it is the rate of change of tension which is within the control of the experimenter and is kept approximately constant (so far as this can be done by merely manual means), the corresponding change of length being recorded by the muscle itself, in the instrument described below it is the length which is changed at a constant rate (this being achieved by mechanical means), the corresponding change of tension being recorded by the muscle. The final result for both instruments is the tension-length diagram. In such a diagram the work done by, or on, the muscle is given by the area enclosed by the curve. Curves obtained by our instrument are given below in fig. 2 and others.

The construction of the machine, with the latest improvements, is represented in fig. 1. The muscle M is supported in a vertical position, its lower end held immovable by the clamp C and its upper end connected by an inextensible wire with an isometric lever L. This lever is mounted on a bar B, which may be rotated in the vertical plane about the axis A. In this way, by suitably
suspended weights \( W \), either a stretch or a shortening may be carried out. The extent of movement is controlled by adjustable stops \( S \). The speed is regulated by the needle valve \( V \) in the piston of the dashpot \( P \), and may be varied from zero to about 50 cm. per second; it is measured by recording on the indicator diagrams the vibrations of a pneumatic tambour (not shown on the diagram) mounted on the bar and reproducing the oscillations of a vertical pendulum of period \( 1/3 \) to \( 1/50 \) sec. The arrangement of the dashpot ensures that constant speed is reached almost instantaneously and maintained throughout the movement. Release of the bar at any desired moment is effected by closing the circuit of the electromagnet \( E \), which controls a catch mechanism consisting of a tooth \( T \) gripping a notched plate \( N \) mounted in the end of the bar \( B \). It is essential that both shortening and lengthening take place between the same limits, and this is ensured by having the bar move always the full distance between the stops.

In the course of the experiments it soon became evident that special precautions were required in order to obtain records free from mechanical distortion. Even a very small amount of "give" in the arrangement, for example, in the lever \( L \), due to its not being perfectly isometric, or in the clamp \( C \), was found to influence the shape of the curves and make analysis uncertain, on account of the difficulty of allowing for effects extraneous to the muscle. Accordingly special attention was given to making the lever as isometric as possible. Moreover, to obtain the greatest possible rigidity combined with the least moment of inertia, the rocking bar \( B \) was made of a straight piece of hollow steel tubing. In order that the tension-length axes of the diagrams should be perpendicular, the arm of the lever \( L \) was set obliquely to the bar. The arm itself was designed according to the principle of girder construction and given
the shape of a triangle, of which the two long sides were formed of thin bamboo fibre and the short base was a light brass rider mounted directly on the spring of the lever. This arrangement possesses the advantage of having the smallest possible moment of inertia combined with the greatest rigidity in the plane of recording, at the same time being very flexible at right angles to that plane so that the friction of the tracing point is small. In order further to reduce the period of oscillation of the lever, the arm was made comparatively short (5 cm.).

The recording itself was done on an immobile smoked glass surface with a fine glass point. The curves obtained in this manner could be magnified and copied with great accuracy by means of a projection lantern, so that no inconvenience was experienced due to the small size of the records, whilst advantage was derived from almost complete absence of oscillations of the lever.

With this arrangement it has been possible to obtain very accurate tension-length curves for stretches and releases of various muscles under definitely reproducible conditions. The muscle to be studied is carefully dissected out of the animal and fixed in the clamp C. It is tied directly at its upper end by a stout thread to the wire rod, which connects it with the isometric lever of the instrument. Great care is taken to ensure that there is no length of tendon or thread intervening between the muscle and the wire, which might confuse the results by the introduction of extraneous elastic effects. The stimulus used consists of a moderately strong tetanising current passed through the entire length of the muscle. A “Harvard” induction coil was used with a 2-volt battery and the secondary coil slightly overlapping the primary. When, and not until, the muscle has developed maximum tension in response to the stimulus, the bar B is released by the tooth device T and the stretch or shortening is carried out. If the experiment extends over any considerable time, care is taken to provide that the temperature is maintained constant: in the case of the experiments on tortoise, the muscle was kept in a Dewar flask brought up from below and supported by the clamp bearing the muscle. In most cases an experiment consists of a series of operations at different speeds, starting with quick releases, proceeding to quick stretches, and then returning to quick releases. In this way the effects of fatigue, if present, can be observed and allowed for.

* This type of lever arm proved useful to one of us (A. L.) in connection with work on recording the form of the pulse-wave (unpublished). It appears to us that it might be found applicable in all cases where good mechanical properties of the lever arm are of particular importance.
III. Results on Dog-Fish.

Studies have been carried out on various types of muscle with results which, in the light of theory, appear very consistent. We begin our discussion with what has proved to be the simplest case, the jaw muscle of the dog-fish. The results obtained with this muscle are best described in connection with the actual curves taken from the protocol of an experiment. Fig. 2 gives a set of tension-length curves, magnified and copied in the way we have described above,

![Diagram](image)

Fig. 2.—Tension-length curves from the jaw muscle of the Dog-Fish. Numbers indicate the order in which the observations were made. The corresponding speeds (arbitrary units) are as follows:

<table>
<thead>
<tr>
<th></th>
<th>Speed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6.15</td>
</tr>
<tr>
<td>2</td>
<td>7.07</td>
</tr>
<tr>
<td>3</td>
<td>2.72</td>
</tr>
<tr>
<td>4</td>
<td>1.19</td>
</tr>
<tr>
<td>5</td>
<td>1.17</td>
</tr>
<tr>
<td>6</td>
<td>0.35</td>
</tr>
<tr>
<td>7</td>
<td>0.59</td>
</tr>
<tr>
<td>8</td>
<td>0.71</td>
</tr>
</tbody>
</table>

obtained from a single muscle. The individual curves were superimposed so as to bring the axis of ordinates and abscissae into coincidence. Each curve represents a stretch or release (right- and left-hand groups respectively) at a definite constant speed. The quickest release is the curve farthest to the left; the quickest stretch that farthest to the right; the other curves lie between in the order of speed. The broken line represents the ideal curve for zero speed; the curve for the slowest release has been corrected for fatigue, as shown by the shorter broken line. The line AB, corresponding to a stretch or release at zero tension, is obtained by joining the points of zero tension at the two lengths between which movement takes place. It is evident at once that these curves afford a striking confirmation of the observations of Blixt and Fick that at any given length a muscle exerts greater forces when it is being stretched than when it is shortening. Moreover, it appears that this effect is the greater the greater the speed of movement; the curves for the stretches migrate always
to the right as the speed of movement increases; those for the releases to the left. But beyond this the form of the curves is very definite and, as we shall see, significant. In the first place they are not straight lines, but are exponential in character; there is a large initial rise or drop of tension at the beginning of movement, which falls off as the movement goes on; and in their subsequent course curves for different speeds of stretch or release tend to become parallel. In the second place the curves for the stretches or releases all start out in coincidence, cutting the line of isometric development of tension at a definite finite angle. (See also fig. 105.)

Fig. 3 contains results of a more indirect kind, but no less important. In this curve work done by the muscle, or in practice values proportional to this work, obtained by measuring the areas of the tension-length curves of fig. 2, are plotted against speed of movement. Since we are interested only in absolute values, we neglect the difference in sign for work done in stretches and releases. On the other hand, in plotting speed we preserve differences in sign and take stretches as positive (displacement increasing with time) and releases as negative. The resulting curve is S-shaped; it is continuous through the axis of ordinates and it appears to have an upper and a lower asymptote, the

* It must be pointed out that in these experiments the recording arm of the lever was not always adjusted so as to give rectangular co-ordinates, but since we are only interested in relative values of force and work, we may neglect this.
former for the right and the latter for the left-hand branch, both parallel to the axis of abscissae. This indicates the presence of an upper and a lower value for the work done by or on the system, approached as the speed of movement becomes very great.

IV. Models.

These results are of considerable interest as they suggest the presence in muscle of an element of free or undamped elasticity, a point which will be discussed at length below. At the same time they render untenable Hill's view in its original form. For the equation given above (p. 219) used by Hill to describe the behaviour of human arm muscles, and on which the original viscous-elastic theory was based, implies that muscle is, mechanically, a system of the type illustrated by Model I, i.e., a single spring damped at its free end by a vane surrounded by a viscous fluid (fig. 4); whereas, in fact, this system may be shown to give results quite different from those we have just described for muscle. For example, it is obvious that Model I, when being stretched or allowed to shorten, will exert forces greater than or less than those due to the spring alone by an amount proportional to the speed of movement. From this it follows that at the beginning of a release at any finite speed the tension should drop (or rise in the case of a stretch) instantaneously, an effect which is not found in the case of muscle. Furthermore, the tension-length curves for stretches
and releases should be throughout strictly parallel to one another and to the ideal curve corresponding to zero speed of movement; but this latter curve is for muscle as well as for Model I approximately a straight line, as may be inferred from tensions developed isometrically at intermediate lengths and as has indeed been shown directly for tortoise muscle by actually carrying out very slow releases or stretches (see fig. 105). The curves of our tension-length diagrams, on the other hand, are far from being straight lines. Moreover, since work is simply the integral of force with respect to the distance passed through, the work done by Model I or any system of the same type will be a linear function of the speed. We have seen that this is not the case for muscle.

It might be supposed that this discrepancy between the results actually recorded for muscle and those predicted for a system similar to Model I arises from methodical errors on our part rather than any fundamental differences of structure. It is to be expected, for instance, that any element of free elasticity, even very small, introduced into the arrangement will of itself give rise to effects of the kind observed (see below). Great care in the preparation of the muscle makes it possible to eliminate at once the question of elasticity of the tendons or of the thread used in fastening the muscle to the wire. It would, however, be difficult to rule out the possibility of effects due to "give" in the recording instrument itself or in the clamp without an experimental test of the matter. For this purpose an actual model of the type we have just been discussing (Model I) was constructed and substituted for the muscle. The results obtained in this way are shown in fig. 5. The tension-length curves for greater speeds

\[\text{Fig. 5.—Tension-length and work-speed curves from Model I.}\]
are somewhat marred by oscillations which were very difficult to avoid with this arrangement, but both they and the work-speed curves obey exactly the behaviour we have predicted above. This makes it clear that the discrepancy we have been discussing is genuine, and that the effects observed in the case of muscle are inherent in its structure.

We have already remarked that the tension-length and work-speed curves suggest the presence in muscle of an undamped elastic element in addition to a viscous-elastic structure of the type of Model I. We now propose to examine and justify this hypothesis with the aid of a second mechanical model (II) represented in fig. 4. This model differs from Model I in having another spring attached above the damping vane. We thus have a two-part viscous-elastic system of which one elastic element is free and the other damped. We shall show the essential identity of behaviour of this model and muscle.

It is not difficult to deduce from mechanical considerations the behaviour of Model II when it is subjected to stretches and releases of the type carried out with muscle. What we desire is an expression for \( F \), the force exerted by the free end of the top spring, as a function of its displacement, up or down, from the initial position, for any given velocity of movement. From this we may determine the character of the tension-length curves for the system. In the treatment which follows it is to be noted that since we are dealing with a system which is capable of compression as well as extension, unlike many analogous systems which buckle (such as muscle), the results hold for positive and negative values of all the variables.

Let \( \alpha_1 \) and \( \alpha_2 \) refer to the elastic coefficients of the lower and upper springs (lengths \( l_1 \) and \( l_2 \)) respectively, similarly \( x_1 \) and \( x_2 \) to the extensions of the same when the system is stretched; let \( \eta \) be the viscosity, or, strictly speaking, the total damping effect of the vane. We assume that the inertia of the arrangement is negligible; consequently we may equate the opposing forces acting at the point of attachment of the vane and write as the fundamental equation describing the motion of the system

\[
\frac{\alpha_1}{l_1} x_1 + \eta \frac{dx_1}{dt} - \frac{\alpha_2}{l_2} x_2 = 0,
\]

* These oscillations are not due to the recording lever, as might be supposed. The connection between the lever and the damping vane being absolutely inextensible and the lever itself very isometric, any minute vibrations of the steel bar supporting the lever, set up in the moment of stretch, were reproduced on a magnified scale.

† This model has been discussed by Poole in connection with natural fibres (14). The paper of Shorter (15) is also of interest in this connection.
which gives, when we differentiate with respect to the time,

\[ \frac{\alpha_1}{l_1} \frac{dx_1}{dt} + \eta \frac{d^2x_1}{dt^2} - \frac{\alpha_2}{l_2} \frac{dx_2}{dt} = 0. \]  

Now the net force \( F \) exerted by the free end of the top spring, which would be recorded by our instrument if the model were substituted for the muscle, is

\[ F = \frac{\alpha_2}{l_2} x_0. \]  

Furthermore, during any stretch or shortening carried out at constant speed \( v \), we have

\[ \frac{dx_1}{dt} + \frac{dx_2}{dt} = v. \]  

Eliminating \( x_1 \) and \( x_2 \) between equations (2), (3) and (4) we obtain

\[ \frac{d^2F}{dx^2} = \frac{\alpha_1 / l_1 + \alpha_2 / l_2}{\eta} \cdot \frac{dF}{dt} = \frac{\alpha_2 \alpha_1}{l_1 l_2} \cdot \frac{v}{\eta}, \]  

of which the complete solution is, as may be shown by substitution,

\[ F = A + B \left( 1 - e^{-\frac{\alpha_1 \alpha_2 / l_1 l_2}{\eta} y} \right) + \frac{\alpha_1 \alpha_2}{l_1 l_2 + \alpha_2 \alpha_1} \cdot \frac{v}{\eta}. \]  

The value of the constants \( A \) and \( B \) may be obtained from the two relations

(i) that when \( t = 0 \), \( F = F_0 \), where \( F_0 \) is the tension exerted by the system in equilibrium at the initial length; and (ii) that also, when \( t = 0 \), the velocity of the vane is zero, i.e., from equation (4),

\[ \frac{dx_1}{dt} = 0 = v - \frac{dx_2}{dt}, \]

whence from equation (3)

\[ v = \frac{l_2}{\alpha_2} \frac{dF}{dx}. \]

When \( A \) and \( B \) are worked out and we substitute for \( t \) the quantity \( y/v \), where \( y \) is the displacement of the free end of the top spring, positive or negative according to the sign of \( v \), from the initial position, we arrive at the result

\[ F = F_0 + \frac{(\alpha_2^2/l_2^2) \eta v}{(\alpha_1/l_1 + \alpha_2/l_2)^2} \left( 1 - e^{-\frac{(\alpha_1 \alpha_2 / l_1 l_2) v}{\eta} y} \right) + \frac{\alpha_1 \alpha_2 / l_1 l_2}{\alpha_1 / l_1 + \alpha_2 / l_2} \cdot \frac{v}{\eta}, \]

or, since the sum of the first and last term on the right gives the "reversible" tension \( \overline{F} \) corresponding to infinitely slow movement,

\[ F = \overline{F} + \frac{(\alpha_2^2/l_2^2) \eta v}{(\alpha_1/l_1 + \alpha_2/l_2)^2} \left( 1 - e^{-\frac{(\alpha_1 \alpha_2 / l_1 l_2) v}{\eta} y} \right). \]
It is obvious that the relation between $\bar{F}$ and $y$ is linear. Consequently the tension-length curves of the model are of an exponential character, when referred to a base line corresponding to infinitely slow movement, and agree in type with those obtained from muscle. The theoretical case differs, however, from the case of muscle in so far as it includes negative tension (compression) of either or both of the springs, the analogue of which is obviously impossible in muscle. But in the actual model there is no such discrepancy, provided the connections between the springs and the recording lever, etc., are flexible and therefore liable to buckle, or provided the springs themselves are represented by rubber bands.

We may emphasise two points of very definite agreement between two sets of curves. (a) In the first place it is seen that the force $F$ exerted by the model drops or rises along an exponential curve as shortening or lengthening proceeds. As $y$ increases $F - \bar{F}$ approaches $\frac{(\alpha_2^2/l_2^2)}{(\alpha_1/l_1 + \alpha_2/l_2)^2}$ as a limit and the curve tends to become a straight line parallel to the line $F = \bar{F}$. This is just what we observed in the case of muscle. (b) In the second place

\begin{equation}
\frac{dF}{dy} = \frac{d\bar{F}}{dy} + \frac{\alpha_2^2/l_2^2}{\alpha_1/l_1 + \alpha_2/l_2} e^{-\frac{y l_1}{\alpha_1} + \frac{y l_2}{\alpha_2}} y.
\end{equation}

When $y = 0$ this reduces to

\begin{equation}
\frac{dF}{dy} = \frac{d\bar{F}}{dy} + \frac{\alpha_2^2/l_2^2}{\alpha_1/l_1 + \alpha_2/l_2},
\end{equation}

which, since $\bar{F} = F_0 + \frac{\alpha_2}{\alpha_1/l_1 + \alpha_2/l_2} y$ and therefore $\frac{d\bar{F}}{dy} = \frac{\alpha_2}{\alpha_1/l_1 + \alpha_2/l_2}$, gives

\begin{equation}
\left(\frac{dF}{dy}\right)_{y=0} = \frac{\alpha_2}{l_2},
\end{equation}

which is independent of the values of $\alpha$ and $\eta$. This shows that curves for different speeds all coincide at the start, intersecting the "isometric" tension line at an angle $\phi = \tan^{-1} \frac{l_2}{\alpha_2}$, just as in the case of muscle. Moreover, this angle is independent of any changes in viscosity such as those produced by changes of temperature. This, too, was found to be the case with muscle.

In three different sets of releases carried out with the same tortoise muscle at three different temperatures, the following values of $\phi$ were obtained:

$T = 13 \cdot 6^\circ C., \phi = 12 \cdot 4^\circ; \ T = 7 \cdot 5^\circ C., \phi = 12 \cdot 4^\circ; \ T = 21 \cdot 5^\circ C., \phi = 12 \cdot 3^\circ$.

Similar agreement in the behaviour of the model and the muscle is observed when we turn to the relation of work to speed. The work done by, or on, the
model in a stretch or release of extent $\Delta y$ may be obtained by integration of the expression for $F$ in equation (6) with respect to $y$ and is given by

\begin{equation}
W = \bar{W} \pm \frac{(s_2/2)^2 \eta y}{(s_1/l_1 + s_2/l_2)^2} \left[ \Delta y - \frac{\eta y}{\alpha_1(l_1 + \alpha_2/l_2)} (1 - e^{-\frac{\alpha_1 l_1 + \alpha_2 l_2}{\eta y}} \Delta y) \right].
\end{equation}

The graph from this equation, relating $W$ and $\eta$, is an $S$-shaped curve of the type obtained from muscle, crossing the axis of ordinates (zero speed) at a value of $W = \bar{W}$ and having an upper and lower asymptote corresponding to the speeds of movement so great that the lower spring has no time to change its length at all. Both the upper and the lower limiting values of $W$ are thus determined solely by the properties of the upper spring. The right and left branches of the curve (referred to the axis of ordinates) are strictly analogous, and either may be obtained by rotation of the other in the plane of the figure through $180^\circ$ about the point ($W = \bar{W}$, $\eta = 0$).

In regard to this latter property alone there seems to be some divergence between the dog-fish and the model. In the work-speed curve for the dog-fish the two branches are not strictly analogous; the right-hand branch (stretches) rises more above the line $W = \bar{W}$ than the left-hand branch falls below it. But this is easily explained when we recall that in the case of muscle we are dealing with a system in which the tension can never become negative, whereas equation (9) is valid without restriction only for systems capable of compression; and it is easy to see that any discrepancy between the two branches of the work-speed curve for a system which buckles must be in the direction observed in the case of muscle. It may be objected here that the discrepancy in question prevails over a range of speeds within which the tension of the muscle does not actually at any point of the shortening fall to zero (see fig. 2), so that this argument cannot apply. But we must remember that in muscle we are dealing with a system of very complex microscopic structure, which may be expected to represent not a single model of the type under discussion, but rather a whole family of them arranged in parallel like the fibres, with constants distributed about certain mean values. It is then to be expected that as the speed of shortening increases the more viscous elements will be unable to follow and will buckle, though the tension exerted by the muscle as a whole is not zero. In this way it is possible for the discrepancy in question to arise without the tension of the muscle vanishing. With the removal of this difficulty, therefore, we are entitled to regard dog-fish muscle, from a mechanical point of view, as a system of the type represented by Model II.

For purposes of illustration, and to render the matter more convincing, we
have actually constructed a working model like that shown in fig. 4 (II), and curves obtained from this model with our recording instrument are given in fig. 6. The general agreement in the behaviour of muscle and model is apparent by comparison of these with figs. 2 and 3.

Fig. 6.—Tension-length and work-speed curves from Model II.

(An adjustment of the scale of speed and of the relative lengths of the two springs would turn the work-speed curve of fig. 6 into that of fig. 3.)

V. Further Experimental Results.

We now pass on to results obtained with other muscles. Fig. 7 refers to the longitudinal body-wall muscles of Holothuria nigra, and fig. 8 to the lantern muscles of Echinus. In both cases we are dealing with smooth muscles, which are many (perhaps 100) times slower in their response than the jaw muscle of the dog-fish; consequently the speed scale in the work-speed curves is of a different order from that of fig. 3. Both muscles are very fragile and frequently gave trouble by actually tearing during the course of an experiment. Allowance had to be made for this as for fatigue in plotting the curves, and for this reason the results are less reliable than those for the other muscles. Nevertheless, they are in very good qualitative agreement with what we have found for dog-fish.

On the other hand, the results obtained in the case of the biceps cruris muscle
of the tortoise (fig. 10) and the claw muscle of the spider crab (fig. 9) are at first sight very perplexing. It is evident both from the work-speed and tension-length curves that speed is far less effective in increasing the tension during a

![Graph](image1)

**Fig. 7.—Work-speed curve from longitudinal body muscle of Holothuria nigra**

![Graph](image2)

**Fig. 8.—Work-speed curve from lantern muscle of Echinus.**

stretch than in lowering it during a shortening. The discrepancy in form between the two branches of the work-speed curve is, in fact, just the opposite of what we observed for dog-fish muscle. The phenomenon cannot possibly be accounted for in terms of buckling. On the other hand, the appearance of
the tension-length curves for the stretches suggests a rupture of some of the contractile elements soon after the beginning of movement and consequent rise of tension. After a rapid initial rise of tension the curves for the stretches

![Graph](image)

**Fig. 9.**—Tension-length and work-speed curves from Spider Crab.

![Graph](image)

**Fig. 10.**—Tension-length and work-speed curves from Tortoise.

become somewhat irregular and frequently show oscillations. This corresponds to a point of discontinuity beyond which stretching produces comparatively small further rise of tension. The muscle behaves as if it were unable to develop more than a certain limited amount of tension, and as if slipping
or breaking of some elements occurred each time it was stretched beyond this limit. The breaking or slipping may be supposed to go on as stretching proceeds; it cannot, however, result in any permanent, irreversible damage to the muscle, for tensions developed in subsequent contractions are as high as ever. Such breaking possibly involves certain molecular arrangements formed in response to the stimulus such as those proposed by Garner (17), but it would be idle to attempt any precise molecular interpretation. The residual effects of speed on stretches may be referred to the elements which are not ruptured.

VI. Correlation with Results of Gasser and Hill.

It is relevant to this discussion to recall the results of Gasser and Hill on the effects of sudden stretches on frog's muscle. There, if the stretch was too great, the tension of the muscle was momentarily partially destroyed, but recovered again to its usual value. This suggests also a separable rupture of certain muscle elements. On the other hand, in the case of Holothuria, where the phenomenon under discussion does not appear, sudden stretches (provided they do not actually tear the gross structure of the muscle) produce no such fall of tension (see Hill (19)). It is all the more reasonable to suppose, therefore, that the anomaly in the case of tortoise and crab is due to breaking or slipping of a part of the contractile elements and not to any fundamental difference of structure between them and dog-fish. We regard this structure as of the same type as the Model II.

The case for this view of muscle which we have been advocating is further strengthened by a more extended consideration of the results of Gasser and Hill. In the first place it is of interest to observe that, quite apart from any mechanical interpretation, our own results are in close accord with theirs. It is possible, indeed, without hypothesis to deduce one set of observations from the other. For example, if we accept the results of Gasser and Hill on the effects of a quick release, we can predict, for a muscle shortening at finite speed, tension-length curves of the same form as those we have actually observed. Let us assume that the continuous process of shortening is the limiting case of a discontinuous process consisting of a large number (n) of quick releases, \( \Delta y \), occurring at times \( t_1, t_2, \ldots, t_n \) after the beginning of movement, the limit being approached as the value of \( n \) becomes infinite. We now apply the results of Gasser and Hill to each quick release. They have shown that a release of extent \( \Delta y \) is followed by a drop of tension \( \Delta F = k \Delta y/y_0 \), where \( k \) is a constant and \( y_0 \) is the resting length of the muscle, and that this drop is followed by a recovery along a curve like that for the development of tension in an isometric
contraction. This curve is well known to be approximately exponential in character, so that we may write for the force $F$ exerted by the muscle at any time $t$ after a single quick release $\Delta y$

$$F = F_0 - \Delta F e^{-at} = F_0 - \frac{k}{y_0} \Delta y e^{-at}.$$  

Here $F_0$ is the equilibrium value of the tension for the new length and $a$ is a constant. We now consider a discontinuous process of shortening consisting of a large number of quick releases. We suppose for simplicity that $F_0$ has the same value for all lengths covered (which is approximately the case for the range considered). Then at any time $t$ after the first quick release the tension exerted by the muscle will be

$$F = F_0 - \frac{k}{y_0} \sum_{k=1}^{n} \Delta y_k e^{-a(t-t_0)}.$$  

As $n$ becomes infinite, corresponding to the case of the continuous shortening carried out in our experiments, this expression becomes

$$F = F_0 - \frac{k}{y_0} \int_{t_0}^{t} e^{-a(t-t_0)} dy/dt \, dt.$$  

If, as in our experiments, the shortening proceeds at constant speed

$$v = \frac{y - y_0}{t},$$

the value of this integral is

$$F = F_0 - \frac{k v}{y_0} \left(1 - e^{-\frac{2}{a} (y-y_0)}\right),$$

i.e., precisely the expression (equation (6)) which we have shown to describe the behaviour of muscle in our experiments in the case of shortening. The same expression might likewise be deduced for stretches in cases like dog-fish or Holothuria, where the complicating effects of breaking or slipping do not occur.

Now that we have shown the fundamental identity of our own and the results of Gasser and Hill, it is of interest to observe that the latter agree very closely with the mechanical interpretation we have given the former. In the first place the fact that a quick release of extent not greater than 15 per cent. of the resting length of the muscle leads not to the abolition, but only to a drop, of tension roughly proportional to the amount of shortening, shows that muscle cannot be a system like Model I, containing no element of free elasticity. In such a system any quick release, however small, leads to a temporary total disappearance of tension. On the other hand, this result is quite in accord
with the behaviour of a system like Model II. If Model II, at equilibrium under a certain tension, be suddenly released, the top spring, undamped, will alone shorten; the lower spring will be unable immediately to change its length on account of the damping vane. In this way equilibrium between the two springs will be destroyed; the top spring will shorten by an amount greater than corresponds to equilibrium at the new length, and the tension exerted by the system, though not zero, will be less than the normal value for this length. At the same time a force will be brought to bear on the vane, causing it to move downward, so as to stretch the top spring and allow the lower spring to shorten until the new equilibrium is reached. The rate of this movement, which is the rate of attainment of the final tension for the new length, is proportional to the difference in tension between the two springs. From this it is clear that recovery from the initial drop must take place along an exponential curve. It may, in fact, be deduced from the equations describing the motion of the system that the tension $F$ exerted at any time $t$ after a sudden change of length (stretch or release) of extent $\Delta y$ is given by the expression

$$F = F_0 + \frac{\Delta y^2/l_2^2}{\alpha_1/l_1 + \alpha_2/l_2} \Delta y^2 \left( \frac{\alpha_1 + \alpha_2}{\alpha_1} \right),$$

where $F_0$ is the equilibrium tension for the new length. If the release be of such an extent that the top spring shortens to its unstretched length, we have a temporary disappearance of tension, just as in the case of muscle when the shortening is more than 15 per cent. of the resting length.

These results, therefore, of Gasser and Hill and of Hill confirm, both directly of themselves and indirectly by implying our own results, the amended viscous-elastic interpretation we have given to muscle.

In accordance with this interpretation it would, in fact, be possible to work out the absolute values of the three constants $\alpha_1/l_1$, $\alpha_2/l_2$, and $\eta$, for any given muscle, from its tension-length and work-speed curves. We have not actually carried out any such calculations, and it is doubtful if just how much value they would be, for it is obvious from the meanings we have assigned to $\alpha_1$, $\alpha_2$, and $\eta$ that they depend on the size and shape as well as on the intrinsic character of the muscle. In order to calculate significant figures in this way it would be necessary to reduce them to values for 1 c.c. of muscle tissue referred to an axis parallel to the direction of the fibres.

VII. A Theoretical Derivation of the Contraction Curve.

A further point of interest arises in connection with the view advanced by Gasser and Hill that the development of tension in the isometric contraction is governed by the same factors as the redevelopment of tension after a sudden release. The view is based on the close similarity of the tension-time curves
for both processes. This is precisely what would be expected if it were assumed that the muscle consists of two sets of elastic elements, one free and the other damped, the damped elements being the contractile part of the structure. In this case stimulation may be supposed to bring about a sudden change in the elastic properties of the contractile structures, which in consequence begin to shorten and stretch the purely elastic elements. Shortening of the contractile parts falls off logarithmically as the system approaches its new equilibrium, so that the change of tension with time will be the same as during recovery after a sudden release. The process of contraction could be simulated with the model we have been discussing by giving the lower spring a sudden extension without allowing the vessel containing the damping liquid to move. It is obvious that the effect of such a stretch would be strictly analogous to the effect of a sudden release of the upper spring. A similar comparison might be made with the effects of a sudden stretch. It is plain that quite a different result would follow if it were the free elastic elements which were responsible for contraction. In this case there would be a sudden initial rise of tension at the moment of contraction, followed by a drop to the equilibrium value, quite the contrary of what is actually observed.

Not only does this view explain the fundamental similarity of an isometric contraction and a redevelopment of tension after a release, but it enables us to see why a sudden shortening of 15 per cent. should lead to an abolition of all tension in the muscle. For this purpose we have only to suppose that when the isometrically contracting muscle attains its maximum tension, the free elastic elements are stretched by an amount equal to 15 per cent. of the length of the muscle.

These free elastic elements may indeed be regarded as "buffers." They protect the muscle in case of sudden changes of length. If the muscle were a simple viscous-elastic system like Model I, any sudden extension such as might occur in the case of certain movements of the animal would produce a tremendous immediate rise of tension which would result in shock if not in actual rupture of the muscle. On the other hand, the viscous character of the contractile elements serves to prevent too sudden changes of tension when the muscle contracts isometrically or when it shortens; great strains would be introduced by the immediate development of maximum tension. Here, again, the elastic buffers play their rôle, for without them any rapid shortening of small extent might lead to an immediate disappearance of tension, and the efficiency of the muscle would be greatly reduced. We seem, therefore, to be dealing with a highly effective and adaptive arrangement.
It might be maintained that an objection to this point of view lies in the fact that in reality the curves for the isometric development of tension are not strictly logarithmic but contain a point of inflection near the start. It is, however, very simple to explain this apparent inconsistency as due to finite time (small, to be sure, when compared with the time required for the development of maximal tension) occupied by the chemical events determining the change in the elastic properties, and in general in the colloidal state, of the contractile elements. Certainly this change cannot occur instantaneously, even though Gasser and Hill have shown, by suitably timed stretches, that there is a great rise in viscosity before there is any appreciable development of tension on the part of the muscle in response to stimulation.

It is important to remark here that in the foregoing analysis we have made use of concrete models simply as illustration of types of mechanical systems and to facilitate the deduction of the mathematical description of the behaviour of these systems. We do not in the least suggest any actual resemblance between the muscle and these arbitrary structures. It might have been supposed that certain histological elements in the structure of the muscle were the counterparts of the two different elastic components of Model II, e.g., the isotropic and the anisotropic bands in the fibres might be indentified with the free and damped elastic elements of the model. The fact that both smooth and striped muscle display similar behaviour makes any such procedure very dangerous. It is far more likely that the behaviour of the muscle is correlated with a much finer, molecular structure.

VIII. Effect of Fatigue.

Some experiments also have been performed with a view to investigate the effects of fatigue on viscosity. They are of importance in the question of the relation of the viscosity to the contraction. It is a well-known fact that as a muscle becomes fatigued the speed of its response to stimulation is decreased, i.e., the time taken to develop maximal tension isometrically is increased. This may be explained in accordance with our view as due to an increase in the viscosity of the contractile elements, owing possibly to the accumulation in the muscle of some breakdown products of contraction. This explanation implies, however, a corresponding increase with fatigue in the "viscous" loss of work when the muscle shortens at a given speed, for we have shown above that both phenomena—the development of tension along an exponential course and the loss of work for any shortening at finite speed—can be ascribed to the same cause, namely, viscosity, or its analogue, in muscle. In order to test this
point we therefore carried with dog-fish muscle a large number of releases at a
given speed until fatigue was well established. When we measured the ratio
of the "viscous" loss to the ideal work at zero speed in successive shortenings
at a given speed, we found a large increase (from 47 to 77 per cent.) between
the first and the last observations. The actual experimental results are shown
in fig. 11. This all provides additional evidence (a) that the factor determining
the rate of the initial development of tension isometrically is the same as that
governing the irreversible loss of work in any shortening at finite speed, viz.,
"viscosity," and (b) that fatigue is intimately connected with an increase of
the "viscosity" of the contractile elements.

**FIG. 11.—Effect of fatigue on "viscosity" in Dog-fish muscle.** The muscle was stimulated
and released at the same constant speed consecutively, 25 times (numbers on the
horizontal axis). "Viscosity" (upper curve) is plotted in terms of the ratio:
"viscous" loss of work
ideal work at zero speed
(fatigue) (lower curve) is represented in terms of decrease
(per cent.) of the initial ideal work in the consecutive contractions.

**IX. Conclusion.**

We referred above briefly to a proposed molecular picture of the type of
structure involved in muscular contraction. Garner has suggested that
contraction may be due to a rearrangement of the molecular pattern of lipoid
molecules oriented in an anisotropic film on the surface of the contractile ele-
ments. Recent work on the area covered by the lipoid substances contained
in muscle makes it probable that the elements in question are fibris rather
than fibres. But in any case it is of considerable interest in this connection to
observe the analogy between the hysteresis curves obtained by Adam with
contracting and expanding films and the results obtained with muscle (see
Hill (16), p. 105). The curve shown in fig. 4 of Hill’s paper, taken from the
paper of Adam and Dyer (18), is quite similar to the tension-length curves for
muscle with ordinates and abscissae interchanged. It must, of course, be
remembered Adam's films show pressures not tensions. The films tend to expand, not contract. Certainly, however, the analogy is suggestive.

But whatever be the intimate structure postulated for muscle, the facts and arguments presented in this paper make it very probable that we are dealing with a system which is, mechanically considered, of the type represented by Model II. Muscle behaves, in fact, with a few easily explained deviations, precisely like this model; and it is reasonable to suppose that its structure contains viscous and elastic elements which are the counterparts of those of the model, the contractile elements being probably those showing the property of viscosity.

X. Summary.

(1) By means of an improved form of myograph very accurate tension-length curves were obtained for stretches and releases carried out on various types of muscles, smooth and striated, at any desired constant speed. A description is given of the characteristics of these curves, as well as of others derived from them, showing the relation of external work done to the speed of stretch or release.

(2) These curves confirm the observations of Fick and of Hill that tension developed in isometric contraction is reduced by release and increased by stretch and that the effect increases with the speed. They also confirm the views, advanced by Hill, that this effect is caused by "viscosity." At the same time the fact contained in our curves, that tension never falls or rises instantaneously at the moment when release or stretch commences, suggests the presence of free elasticity undamped by "viscosity."

(3) A mechanical model was constructed to investigate this (fig. 4 (II)) in which the three factors concerned were represented separately, namely, damped elasticity, viscosity producing the damping, and free undamped elasticity. A mathematical treatment of this model is given and a careful analysis of the behaviour of the muscle in the light of this model leads to the conclusion that muscle is, mechanically considered, a system of this type.

(4) Our results suggest the following explanation of the phenomena (see figs. 2 and 10). When the muscle is stimulated isometrically, tension is set up in it, which is shared by the viscous-elastic and by the purely elastic elements. When the muscle is then released (or stretched) at a constant speed, the viscous-elastic elements lag behind and only the purely elastic elements contract (or are stretched) at the first instant, the presence of the latter preventing the tension from dropping (rising) instantaneously; the tension-length curve, therefore, starts at an angle which is determined solely by the elastic coefficient.
of the purely elastic elements and is the same for all speeds of the release or stretch. Subsequently the viscous-elastic elements also gradually shorten (lengthen), thereby diverting the curve from the initial direction along an exponential course. Finally a steady state of lag is reached and the tension remains reduced (increased) throughout the movement by a constant amount, which is greater with greater speeds. In other words, the curves for all speeds tend to become parallel to each other and to the line of infinitely slow release or stretch. When the release (stretch) stops, the viscous-elastic elements continue to shorten (lengthen), stretching (being stretched by) the purely elastic elements until the equilibrium tension is reached.

(5) The exponential form of the isometric tension-time curve showing the initial development of tension on stimulation and its similarity to the curve of redevelopment after release (Gasser and Hill) are easily explained on the basis of our theory. We have only to assume that the viscous-elastic elements are the actual contractile structures and that they change their elastic properties suddenly on stimulation and start thereupon to shorten and to stretch the elastic elements until a new equilibrium is reached along an exponential curve.

(6) The purely elastic elements may be regarded as “buffers,” which take up any sudden stresses produced by the contraction of the viscous elements, or by quick movements of the animal, and which also prevent an immediate disappearance of tension when the muscle rapidly shortens by a small amount.

(7) In the model, the tension is as much reduced by a release as it is raised by a stretch at the same speed, provided (a) that no buckling occurs at quicker releases, so that negative tension (compression) is also transmitted, and (b) that no slipping or breaking occurs at quicker stretches when the tension is raised beyond a certain limit. In some muscles the tension drops less for releases than it rises for stretches, suggesting buckling of some of the slowest fibres. In some other muscles, on the contrary, the rise of tension in stretches is less than corresponds to the drop in releases, the tension appearing to be cut short at a certain limit, suggesting slipping or breaking (reparable) of some of the elements of the active muscle.

(8) Fatigue has the effect of increasing the “viscosity” as well as of decreasing the tension.

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