ISOTONIC EXTENSION OF UNSTRIATED MUSCLE

BY INDERJIT SINGH

(From the Physiological Laboratory, Cambridge, and the Haffkine Institute, Bombay)

Received November 2, 1942

(Communicated by Lt.-Col. S. S. Sokhey, C.M.G., F.A.SC)

ISOTONIC extension of unstriated muscle has been described by Jordan (1929); Winton (1930, 1937); Singh (1938, 1940, 1942 a, b). Unstriated muscle when stretched gives three kinds of curves. In the first kind there is a continuous curvature throughout and there is no linear phase (Fig. 1). In the second there is a point of inflexion with the curvature now in the opposite direction, followed by another point of inflexion with the curvature returning to the original direction (Fig. 2). The third curve is intermediate between the two, there being a linear phase (Fig. 3).

In this paper the curve with the linear phase is taken as the standard curve and variations from it are discussed.

Fig. 1. Isotonic extension of Mytilus muscle
Magnification 7 times, load 19 grams
Two equations fit the time extension curves with the linear phase (Singh, 1942 a, b).

\[ x = \frac{c}{p} \left(1 - e^{-\frac{pt}{k}}\right) + At, \]

where \( x \) = extension, \( t \) = time, \( c \) = constant force of the undamped spring, \( p \) = restoring force proportionate to the modulus of elasticity, \( k \) = coefficient of inner friction or viscosity, \( A \) is a constant.

\[ x = m \left(\frac{\gamma}{k} - \frac{mg - T}{k^2}\right) \left(1 - e^{-\frac{kt}{m}}\right) + \frac{mg - T}{k} \cdot t, \]
where \( m \) = extending weight, \( g \) = force of gravitation, \( v \) = initial velocity of the damped phase, \( k \) = coefficient of viscosity, \( T \) = force of tone. In this equation \( v \), the initial velocity, like the final velocity, will be proportional to \( mg - T/k \), so that the equation reduces to

\[
\frac{m(mg - T)}{k^2} (c - 1) (1 - e^{-\frac{kt}{m}}) + \frac{mg - T}{k} \cdot t, \tag{3}
\]

where \( c \) is a constant proportional to the impulse received by the damped phase.

The first equation fits majority of the curves, but has no theoretical basis, so that it is difficult to explain the variations of the linear phase. The second equation explains the linear phase in majority of the curves, but its exponential factor fits only a small number of curves. The exponential factor increases with viscosity, as is found in some experiments. In one experiment, a diminution of the exponential factor with increase in weight has been recorded, as demanded by the equation; this is probably due to the response to stretch (Singh, 1938 b). The second equation will therefore be used to explain the variations in the linear phase of the time extension curves.

**Effect of adaptation.**—When to the muscle is added a substance that causes contraction, to which it subsequently adapts, then the curve is of the kind shown in Fig. 2. The increase in the velocity of extension prior to the exponential diminution is thus due to adaptation. The equation that represents these curves is of the form

\[
x = At + B (1 - e^{-\frac{kt}{m}}) - ct + bt^2, \tag{4}
\]

where \( c \), \( b \) and \( k \) are constants.

\[
x = At + B (1 - e^{-\frac{kt}{m}}) - ct + de^{bt}. \tag{5}
\]

Adaptation is a process by means of which the force causing contraction, diminishes with time. The simplest assumptions are that the force diminishes linearly or exponentially with time. The equation for the motion of the system will then be

\[
m \frac{d^2x}{dt^2} + k \frac{dx}{dt} = mg - T - (F - bt) \tag{6}
\]

\[
m \frac{d^2x}{dt^2} + k \frac{dx}{dt} = mg - T - (F - he^{bt}), \tag{7}
\]

where \( F \) is the force of contraction and \( b \) is the coefficient of adaptation, and \( h \) a constant.

\[
m \frac{d^2x}{dt^2} + k \frac{dx}{dt} = mg - T - Fe^{-ht}. \tag{8}
\]
Isotonic Extension of Unstriated Muscle

When the equations 6 and 7 are integrated, the solutions are similar to equations 4 and 5 respectively, so that the assumption about adaptation is probably correct. The solutions of the equations 6, 7 and 8 respectively are

\[ x = \frac{m}{k} \left( v^0 - \frac{mg - T - F}{k} + \frac{bm}{k^2} \right) \left( 1 - e^{-\frac{kt}{m}} \right) - \]
\[ \frac{m}{k} \left( \frac{b}{k^2} - \frac{mg - T - F}{k} \right) t + \frac{k}{2b} t^2 \]  
(9)

\[ x = \frac{m}{k} \left( v^0 - \frac{mg - T - F}{k} - \frac{1}{mb + k} \right) \left( 1 - e^{-\frac{kt}{m}} \right) + \frac{mg - T - F}{k} \cdot t - \frac{h}{b(mb + k)} (1 - e^{kt}) \]  
(10)

\[ x = \frac{m}{k} \left( v^0 - \frac{mg - T}{k} + \frac{F}{k - mb} \right) \left( 1 - e^{-\frac{kt}{m}} \right) + \frac{F}{k} \left( 1 - e^{KT} \right) + \frac{mg - T}{k} \cdot t \]  
(11)

In equations 6 and 7, the value of \( x \) is only valid till \( F = at \), or \( F = he^{kt} \). But if the substance produces adaptation to tone also, such as happens with adrenaline, veratrine, then the equation is valid for greater values of \( F \).

Effect of initial length.—When the muscle is stimulated with potassium, with increase in initial length, the tension may increase linearly for a considerable period, follow a parabolic course, or diminish exponentially (Singh, 1938 b). The equations for extension will therefore be

\[ m \frac{d^2x}{dt^2} + k \frac{dx}{dt} + Fx = mg \]  
(12)

\[ m \frac{d^2x}{dt^2} + k \frac{dx}{dt} = mg - Fe^{-rt}, \]  
(13)

where \( r \) is a constant

\[ m \frac{d^2x}{dt^2} + k \frac{dx}{dt} = mg - ax + bx^2. \]  
(14)

The solution of equation 12 is

\[ x = \frac{1}{a - b} \left\{ v^0 \left( e^{kt} - e^{-at} \right) + \frac{amg}{F} \left( 1 - e^{kt} \right) - \frac{bmg}{F} \left( 1 - e^{-at} \right) \right\}, \]  
(15)

where \( a = \frac{k}{2m} + \sqrt{\frac{k^2}{4m^2} \cdot \frac{F}{m}} \), \( b = \frac{k}{2m} - \sqrt{\frac{k^2}{4m^2} \cdot \frac{F}{m}} \).

The damping is such that the motion is aperiodic. \( Fx \) acts like the restoring force; if the latter is not neglected then the solution will be similar.
There will be a continuous curvature in the time extension curves, as in Fig. 1.

Effect of viscosity.—If the viscosity decreases then the linear velocity will be reached later than when the viscosity is high, as in Fig. 4. Adaptation will reduce the viscosity, as well as change in length; change in viscosity with change in length is also shown in striated muscle (Bouckaert, Capellan and de Blende, 1935). The equations will be

\[ m \frac{d^2x}{dt^2} + (p - kt) \frac{dx}{dt} = mg - T - (F - at) \] (16)

\[ m \frac{d^2x}{dt^2} \pm ax \frac{dx}{dt} = mg - T. \] (17)

Effect of stretch.—This will oppose the extending force, and may even temporarily exceed it, but the muscle soon adapts. The equation will be of the form

\[ m \frac{d^2x}{dt^2} + k \frac{dx}{dt} = mg - T - (F - bt) \text{ or } mg - T - Fe^{-bt}. \] (18)

Effect of spontaneous contractions.—The stretch curves of frog stomach are complicated by spontaneous contractions. These can be represented by a Fourier's series. The simplest rhythmic spontaneous contractions of plain muscle are represented by a sine curve, the equation being of the form \( a + b \sin ct \). The spontaneous contractions of the guinea pig uterus are
more complicated and can be approximately represented by a limited number of the terms of the series

\[ 2 \left[ \sin t - \frac{1}{3} \sin 2t + \frac{1}{5} \sin 3t - \frac{1}{7} \sin 4t + \frac{1}{9} \sin 5t \ldots \right] \]  

(19)

\[ a + \sin t + \frac{1}{3} \sin 3t + \frac{1}{5} \sin 5t \ldots \]  

(20)

The force causing extension would be periodic and the equation of the extension curve would be of the form

\[ At + B (1 - e^{-kt}) - \left( a \sin \frac{\pi}{c} t + a_2 \sin \frac{\pi}{c} 2t \ldots \right) \]  

(21)

the differential equation being

\[ m \frac{d^2x}{dt^2} + k \frac{dx}{dt} = mg - T - b (a_1 \sin t + a_2 \sin 2t \ldots). \]  

(22)

**Crossing of curves.**—When time extension curves cross each other (Fig. 5), then it is evident that two factors in the muscle have been oppositely affected;

![Graph showing isotonic extension of Mytilus muscle](image)

**Fig 5.** Isotonic extension of Mytilus muscle
Curve 1, in 0.5 M NaNO\textsubscript{3}; Curve 2, in 0.5 M NaI

the exponential and linear factors, if oppositely affected will produce such a result.

**Partial contraction of muscle.**—The question arises as to how the partial contraction of plain muscle is affected. Is it due to contraction of a partial number of fibres, or is it due to contraction of portions of fibres, or does it affect the whole fibre? Whatever happens it appears that the remaining uncontracted element is thereby strained if the length is fixed. This is seen from Fig. 6. The successive spontaneous contractions increase in magnitude, corresponding to increase in tension with the initial length. The contracted and non-contracted elements will have different viscosity producing two points of discontinuity instead of one, one at the junction of the undamped and the damped phases, and the other at the junction of phases of lesser and
greater viscosities (Fig. 7). The undamped phase may be regarded as damped by very low viscosity.

**Discussion**

During extension of plain muscle the following variables are involved: (1) tone, (2) viscosity, (3) extending force, (4) tonic contraction, (5) adaptation, (6) change of contraction with length, (7) change of viscosity with length, (8) change of viscosity with time, (9) stretch response. But most of these factors can be eliminated and so the analysis simplified. By prolonged soaking adaptation can be eliminated. Substances can be used to which adaptation is very slow. Thus Mytilus muscle adapts to 0.1 M KCl in about 16 hours; it adapts to barium extremely slowly. Effect of length can be eliminated if partial extension only is taken into account (Singh, 1942 a, b), or solutions can be used in which length has no effect on tension. The linear phase should thus be studied just after the exponential phase emerges into it (Singh, 1942 b). Attention is drawn to other papers on the subject (Singh, 1938 a, b, c, d, e, f; 1939 a, b; 1940; 1942 a, b, c; Rao and Singh, 1940).

**Summary**

There are many variables involved in the extension of plain muscle. These are (1) tone, (2) viscosity, (3) extending force, (4) tonic contraction, (5) adaptation, (6) change of contraction with length, (7) change of viscosity with length, (8) change of viscosity with time, (9) stretch, (10) restoring force.

**REFERENCES**

Fig. 6
Spontaneous contractions in Mytilus saline

Fig. 7
Isotonic extension of Mytilus muscle in 0.5 M KCl