

Theoretical Series Elastic Element Length in *Rana pipiens* Sartorius Muscles

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ABSTRACT Assuming a two component system for the muscle, a series elastic element and a contractile component, the analyses of the isotonic and isometric data points were related to obtain the series elastic stiffness, dP/dl_s , from the relation,

$$\frac{dP}{dl_s} = \frac{dP}{dt} \cdot \frac{dt}{dl_s} = \frac{dP}{dt} \cdot \frac{1}{v}.$$

From the isometric data, dP/dt was obtained and shortening velocity, v , was a result of the isotonic experiments. Substituting $(P_0 - P)/T$ for dP/dt and $(P_0 - P)/(P + a)$ times b for v , $dP/dl_s = (P + a) / bT$, where $P \leq P_0$, and a , b are constants for any lengths $l \leq l_0$ (Matsumoto, 1965). If the isometric tension and the shortening velocity are recorded for a given muscle length, l_0 , although the series elastic, l_s , and the contractile component, l_c , are changing, the total muscle length, l_0 remains fixed and therefore the time constant, T . Integrating,

$$\int_{P_0}^P \frac{dP}{P + a} = \frac{1}{bT} \int_{l_{s0}}^{l_s} dl_s,$$

the stress-strain relation for the series elastic element,

$$\frac{P}{P_0} = 1 - \left(1 + \frac{a}{P_0}\right) \left[1 - \exp\left(-\frac{1 - \frac{l_{sc0}}{l_0}}{\frac{bT}{l_0}}\right)\right],$$

is obtained; $l_{sc0} = l_s + l_{c0}$ where l_{c0} equals the contractile component length for a muscle exerting a tension of P_0 . For a given P/P_0 , l_s is uniquely determined and must be the same whether on the isotonic or isometric length-tension-time curve. In fact, a locus on one surface curve can be associated with the corresponding locus on the other.

INTRODUCTION

The studies by Fenn and Marsh (1935), Hill (1938, 1953), Katz (1939), Wilkie (1950), and Aubert (1956) have defined the mechanical behavior of the active striated muscle as a two component system of active contractile components in series with passive elastic ones. Hill (1950) and Wilkie (1956) have described the undamped series elastic component, showing it to be independent of time. When the contractile component is stimulated and develops a force, it can do so only by shortening and stretching its series elastic elements. Were the contractile component directly attached to the skeleton at both ends, the movements would be uncontrollably sudden and jerky. There would be no way of accumulating mechanical energy for jumping. The extremely rapid movement of the contractile component is buffered by the action of the series elastic component resulting in smoother and slower muscular shortening.

SERIES ELASTIC STIFFNESS

The observable variables involved in the study of muscle mechanics whether isotonic or isometric can be represented by tension, length, and time (P , l , t) of the active contractile system. To simplify a complicated problem, all other variables are assumed to be or kept constant, e.g. temperature, Ringer's solution composition, etc. Then the relation of the physical variables of the muscle is represented as.

$$P = f(l, t),$$

and

$$dP = \left(\frac{\partial P}{\partial t}\right)_l dt + \left(\frac{\partial P}{\partial l}\right)_t dl. \quad (1)$$

If this relation were differentiated with respect to l , holding P constant,

$$\left(\frac{dP}{dl}\right)_P = \left(\frac{\partial P}{\partial t}\right)_l \left(\frac{dt}{dl}\right)_P + \left(\frac{\partial P}{\partial l}\right)_t \left(\frac{dl}{dl}\right)_P.$$

When P is held fast, P does not change so that

$$\left(\frac{dP}{dl}\right)_P = 0$$

Furthermore,

$$\left(\frac{dl}{dl}\right)_P = 1$$

Therefore,

$$\left(\frac{dP}{dl}\right)_t = - \left(\frac{\partial P}{\partial t}\right)_l \cdot \frac{1}{\left(\frac{dt}{dt}\right)_P}. \quad (2)$$

The muscle length is equal to the sum of the contractile component and the series elastic element length for a two component contractile model,

$$l = l_c + l_s.$$

For isometric contraction, l remains fixed, hence

$$\left(\frac{dl}{dt}\right)_i = \frac{dl_c}{dt} + \frac{dl_s}{dt} = 0$$

and
$$\frac{dl_c}{dt} = -\frac{dl_s}{dt}. \quad (3)$$

The shortening velocity of the contractile component equals the stretching velocity of the series elastic element when the muscle is developing tension isometrically, $\left(\frac{dP}{dt}\right)_i$. In the afterloaded isotonic contraction, the load the muscle lifts is constant and therefore the series elastic length remains unaltered during shortening.

$$\left(\frac{dl}{dt}\right)_P = \frac{dl_c}{dt}. \quad (4)$$

The quantity, $\left(\frac{dl}{dt}\right)_P$, refers to the rate of change of l of the contractile component itself, $\frac{dl_c}{dt}$. Consider the situation at time, t , during the rise of the isometric tetanus, when tension reaches the value, P . Then at that time the velocity of the contractile component must be exactly the same as the velocity with which the muscle would be shortening under the same load P , and at exactly the same muscle length, l , if it were isotonic (Fig. 1).

Then

$$\left(\frac{dP}{dl}\right)_i = -\frac{\left(\frac{dP}{dt}\right)_i}{\frac{dl_c}{dt}} = \frac{\left(\frac{dP}{dt}\right)_i}{\frac{dl_s}{dt}} = \left(\frac{dP}{dl_s}\right)_i. \quad (5)$$

This analysis, under the condition of constant l , shows that $\left(\frac{dP}{dl}\right)_i$ is actually the series elastic stiffness $\left(\frac{dP}{dl_s}\right)_i$. Hence

$$\left(\frac{dP}{dl_s}\right)_i = -\left(\frac{dP}{dt}\right)_i \cdot \frac{1}{\left(\frac{dl}{dt}\right)_P}. \quad (6)$$

Let
$$-\left(\frac{dl}{dt}\right)_p = \left(\frac{P_0 - P}{P + a}\right) b \tag{7}$$

according to the Hill equation.

The isometric tension rise is assumed to be an exponential function of time based on the results shown in this paper. If we can express the isometric tension rise as an exponential function of time, then we can represent

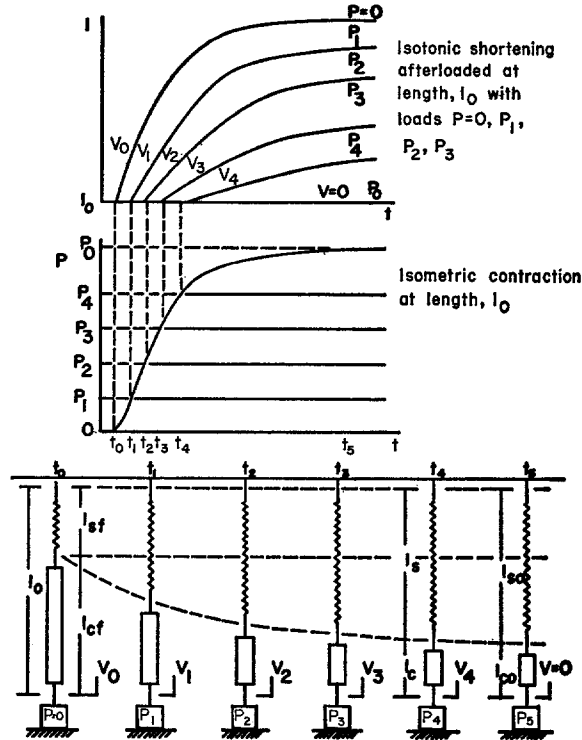


FIGURE 1. Diagrammatic representation of the two component muscle model for the condition of determining dP/dl_s , series elastic stiffness. The load, P , is symbolically defined as constant.

$$P = P_0 \left[1 - \exp - \left(\frac{t}{T} \right) \right] \tag{8}$$

where T is a characteristic time constant for that muscle length. Then

$$\left(\frac{dP}{dt}\right)_l = \frac{P_0 - P}{T} \tag{9}$$

Substituting in the series elastic stiffness equation, the result is

$$\frac{dP}{dl_s} = \frac{P + a}{bT} \tag{10}$$

¹ Negative velocity means decrease in length with respect to time.

If the elastic stiffness relation is experimentally valid, knowing a , b , and T , one would expect to find a straight line relation between $\frac{dP}{dl_s}$ and P . Another method of experimental test is to plot $\left(\frac{dP}{dt}\right)_l$ vs. P (assumed straight line), obtain v from the force-velocity relation, and determine $\frac{dP}{dl_s}$ (Fig. 7). For both curves, the initial length at which contraction begins must be the same. The series elastic stress-strain equation can be developed by integrating the s.e. stiffness relation.

Let

l_s = length of series elastic element for muscle length l_0 exerting tension, P at time, t , during active contraction.

l_c = length of contractile component for muscle length l_0 exerting tension, P at time, t , during contraction when $l_0 = l_s + l_c$.

l_{s0} = length of series elastic element for muscle length l_0 exerting tension, P_0 .

l_{c0} = length of contractile element for muscle length l_0 exerting tension, P_0 , when $l_0 = l_{s0} + l_{c0}$.

l_{sf} = length of series elastic element for muscle length l_0 exerting tension, $P = 0$ during contraction.

l_{cf} = length of contractile component for muscle length l_0 exerting tension, $P = 0$, during contraction ($l_0 = l_{s0} + l_{c0}$).

Rearranging and integrating the expression for the series elastic stiffness,

$$\int_{P_0}^P \frac{dP}{P+a} = \int_{l_{s0}}^{l_s} \frac{dl_s}{bT},$$

and

$$\ln \frac{P+a}{P_0+a} = \frac{l_s - l_{s0}}{bT},$$

which is equivalent to

$$\frac{P}{P_0} = 1 - \left(1 + \frac{a}{P_0}\right) \left[1 - \exp\left(-\frac{l_{s0} - l_s}{bT}\right)\right]. \quad (11)$$

But

$$l_0 = l_{s0} + l_{c0}$$

and

$$l_0 = l_s + l_c.$$

Therefore

$$l_{s0} + l_{c0} = l_s + l_c$$

and

$$l_{s0} - l_s = l_c - l_{c0}.$$

Also

$$(l_{s0} + l_{c0}) - (l_s + l_{c0}) = (l_c - l_{c0}) = l_{s0} - l_s.$$

Therefore

$$l_0 - (l_s + l_{c0}) = l_{s0} - l_s.$$

Let $l_{sc0} = l_s + l_{c0}$, a measurable quantity in quick release experiments,

and

$$l_{sfc0} = l_{sf} + l_{c0}.$$

Then

$$\frac{P}{P_0} = 1 - \left(1 + \frac{a}{P_0}\right) \left[1 - \exp\left(-\frac{1 - \frac{l_{sc0}}{l_0}}{\frac{bT}{l_0}}\right)\right], \quad (12)$$

the series elastic stress-strain relation for $l_{sfc0} \leq l_{sc0} \leq l_{s0c0}$. Thus, this result shows that P/P_0 is only a function of the change in series elastic element length, l_s , independent of time and that the stress-strain characteristic is an exponential.

When $P = 0$, $l_{sc0} = l_{sfc0}$ and

$$\frac{l_{sfc0}}{l_0} = 1 - \frac{bT}{l_0} \ln \frac{P_0 + a}{a}, \quad (13)$$

where l_{sfc0} equals the sum of the unstressed series elastic element length and the contractile component length when $P = P_0$. The results of these equations should be compatible with the findings of quick release experiments, transient change being too rapid for the contractile component length to be altered.

EXPERIMENTAL

Frog-Ringer's solution made up of 95 mM NaCl, 2.5 mM KCl, 1.34 mM CaCl₂ and 1.0 mM MgSO₄ buffered at pH 7.2 with 1.0 mM Na₂HPO₄ and 1.0 mM NaH₂PO₄ was used for all the experiments conducted in this research. The excised muscled stored in oxygenated Ringer's of the above composition at 0°C still contracted 5 days after dissection. The experiments were carried out on whole sartorius muscle of *Rana pipiens* isolated in ice cold Ringer's solution. The *in situ* muscle length varied from 42 to 50 mm and wet weight ranged from 161 to 210 mg. The preparation was equilibrated for at least 1 hr in oxygenated Ringer's in the muscle chamber at 0°C before contraction measurements were made. The sartorius was stimulated in air by rectangular pulses. The stimulus, which proved adequate to maintain isometric tetanic

tension at a plateau for at least 30 sec, had a pulse duration of 5.0 msec and strength of 10 v at 12.5 pulses/sec.

Isotonic contractions were studied with a series of afterloads and the shortenings were imposed at intervals no shorter than 10 min. For each muscle, a whole family of shortening vs. time curves was obtained, each curve within the series differing from the others in the amount of afterload (Matsumoto, 1965, 1967).

For the isometric condition, tension-time course records were taken over the range of muscle length from the smallest length at which tension could be just recorded to the extreme length at which active tension disappeared. Tension and length (P/P_0 ,

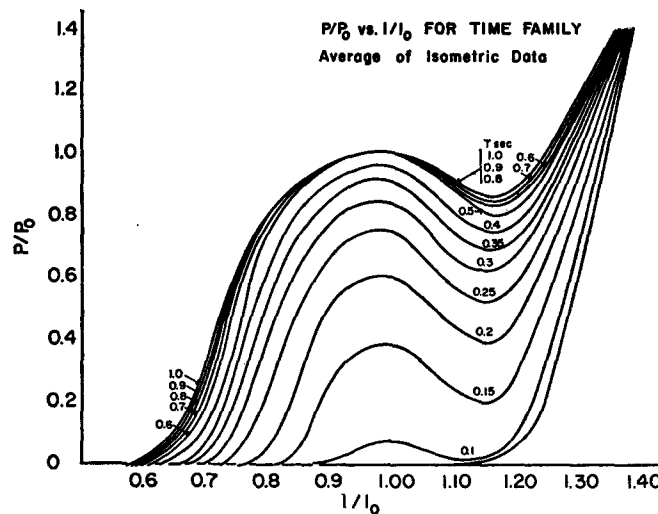


FIGURE 2. Tension-length curves for time family. From the tension-time course records tension-length plot was constructed for a series of selected times during activity (see text)

l/l_0) were normalized and a family of tension development curves was obtained for different isometric lengths. A length-tension plot was first constructed for a series of selected times during activity. The family of curves resulting from four experiments was averaged to give Fig. 2.

EXPERIMENTAL IDENTIFICATION

Exp. 45	$P_0 = 1.94 \text{ kg/cm}^2$	$l_0 = 45.0 \text{ mm}$	$M = 185 \text{ mg}$
Exp. 46	$P_0 = 1.45 \text{ kg/cm}^2$	$l_0 = 42.0 \text{ mm}$	$M = 184 \text{ mg}$
Exp. 48	$P_0 = 2.16 \text{ kg/cm}^2$	$l_0 = 50.0 \text{ mm}$	$M = 185 \text{ mg}$
Exp. 49	$P_0 = 1.94 \text{ kg/cm}^2$	$l_0 = 50.0 \text{ mm}$	$M = 184 \text{ mg}$

The standard deviation for point P_0 , l_0 , and $t = 1.00$ sec of Fig. 2 is zero since this was the selected point of reference in the normalization procedure. As l is increased or decreased and also decreased in t , standard deviation of P increased. For example, at $t = 1.00$ sec and $\frac{l}{l_0} = 0.900$, standard deviation of

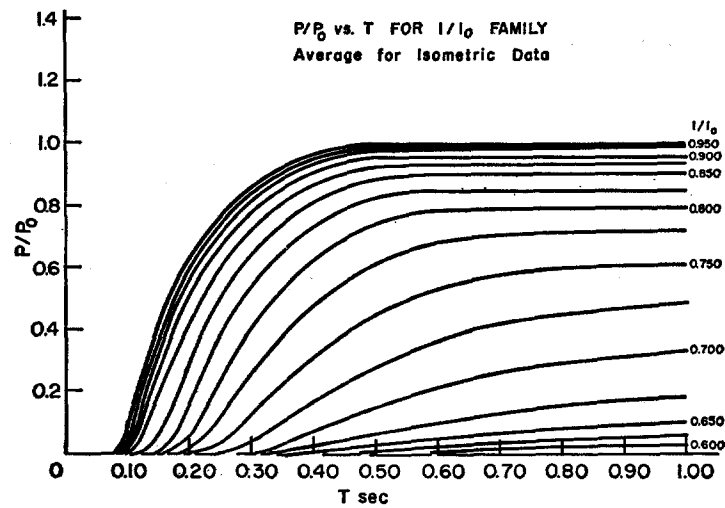


FIGURE 3 a

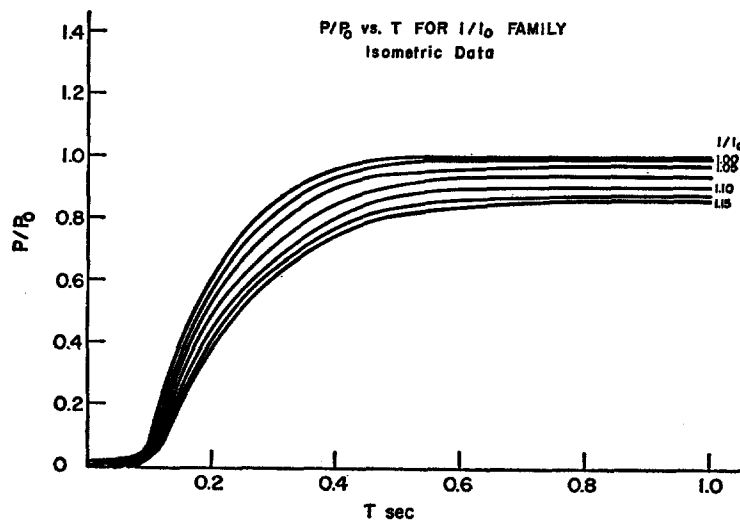


FIGURE 3 b

FIGURE 3 a and b. Tension-time curves for l/l_0 family. The tension-time plot was obtained from Fig. 2.

P is $\pm 1.3\%$ P_0 ; for $\frac{l}{l_0} = 0.700$, $\Delta P = \pm 5\%$ P_0 . At $t = 0.40$ sec, standard deviation was found to be $\pm 3.4\%$ P_0 for $\frac{l}{l_0} = 0.900$ and $\Delta P = \pm 2.7\%$ P_0 for $\frac{l}{l_0} = 0.700$.

From this graph of the isometric tension-length profile, a normalized

tension-time plot was reconstructed, but now averaged and interpolated for equal l/l_0 intervals (Fig. 3).

From the resulting normalized tension-time plot, values of P/P_0 were taken at a series of times. These coordinate points were then used to construct

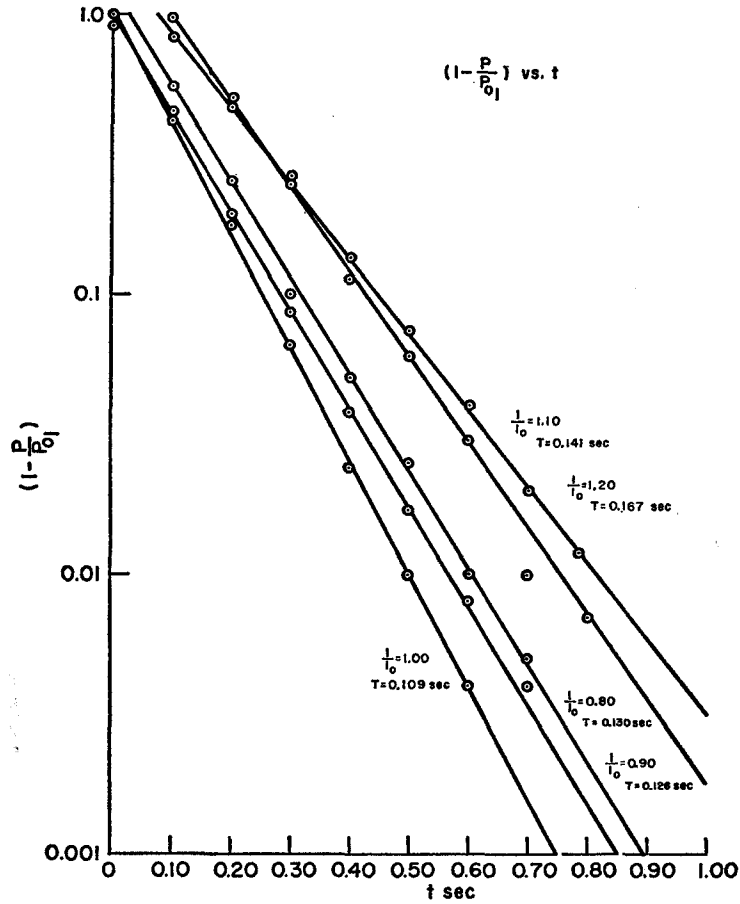


FIGURE 4. Semilog plots of $(1 - P/P_0)$ vs. t for the respective isometric lengths. Time constant, T , was graphically determined for the corresponding isometric length. The data points were obtained from Figs. 3 *a* and *b*.

semilog plots of $(1 - P/P_0)$ vs. t for the respective isometric lengths (Fig. 4). Time constant, T , was graphically determined for the corresponding isometric length.

The normalized tension-time curves were also used to construct $\frac{1}{P_0 t} \frac{dP}{dt}$ vs. t curves. The rates of normalized tension rise against time plots were obtained

by graphical analyses (Fig. 5). This procedure was necessary to evaluate eventually the series elastic stiffness.

RESULTS

The time course of tension development for $l < l_0$ falls short of linearity in the semilog plots. Once T is obtained, the tension-time course can be com-

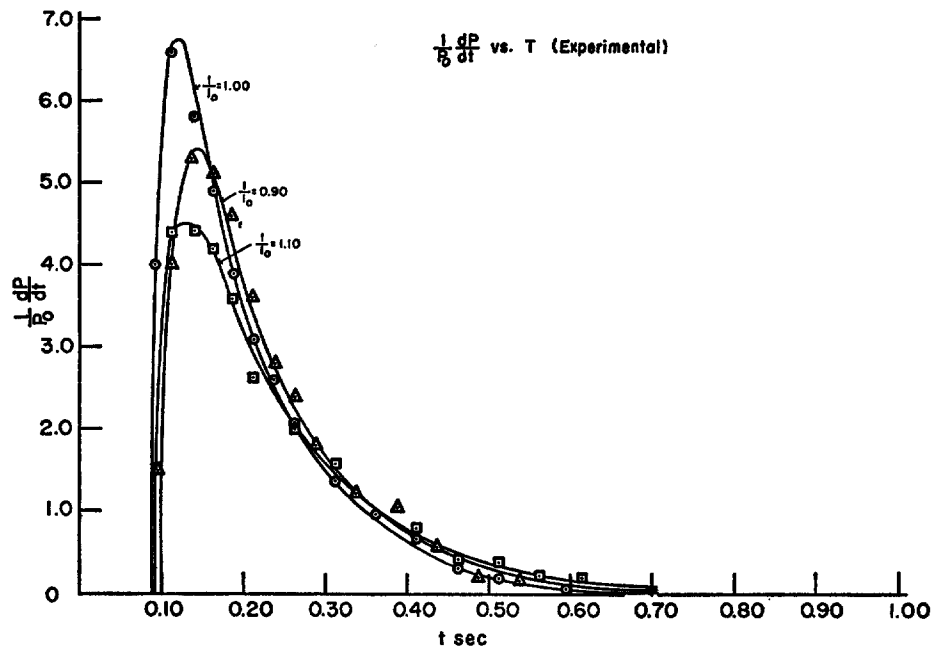


FIGURE 5. Normalized tension rate vs. time curves. Data points were obtained by graphical analyses from Figs. 3 *a* and *b*.

puted from $P/P_0 = \left[1 - \exp\left(-\frac{t}{T}\right) \right]$ and compared with the corresponding curve of Fig. 3. Knowing T , $\frac{1}{P_0} \frac{dP}{dt}$ can be calculated and compared with the direct graphically analyzed values of $\frac{1}{P_0} \frac{dP}{dt}$ (Fig. 6).

The P/P_0 time course does not show an abrupt change of tension from $P/P_0 = 0$ to $P/P_0 > 0$ but progresses up an initial sigmoid path. At the onset of a contraction, the rate of tension rise does not show a discontinuity. This obviously is because propagation time is finite and the active state takes a certain time to reach its full value. Macpherson and Wilkie (1954) believed that a plateau of active state lagged 45 msec after stimulus, whereas Jewell and Wilkie (1958) have presented evidence for tetanically stimulated muscle

that activation requires 60 msec. This rise in dP/dt reflects the mobilization events, but no detailed attention is given to them here. $\frac{1}{P_0} \frac{dP}{dt}$ initially starts at zero and increases approximately exponentially. The present analysis does

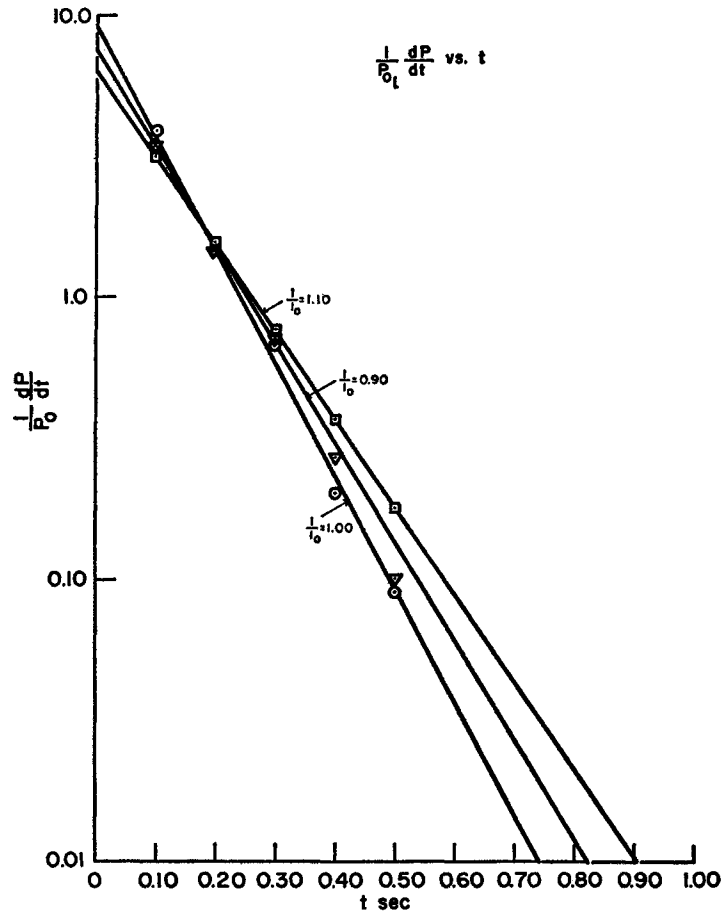


FIGURE 6. Semilog plots of $\frac{1}{P_0} \frac{dP}{dt}$ vs. t . The data points were obtained from Fig. 5. If the exponential tension-time course is approximately correct, $(1 - P/P_{0i})$ vs. t is expected to be a straight line in the semilog plot (Fig. 4). Also $\frac{1}{P_0} \frac{dP}{dt}$ vs. t must be a straight line in the semilog plot and with the same time constant, T , as in Fig. 4.

not consider this first phase of tension development and the main exponential rise of tension therefore is extrapolated to $P/P_0 = 0$ giving the intercept, T_1 as the reference time for the present consideration.

The series elastic stiffness relation, dP/dl_s , results from the analyses of iso-

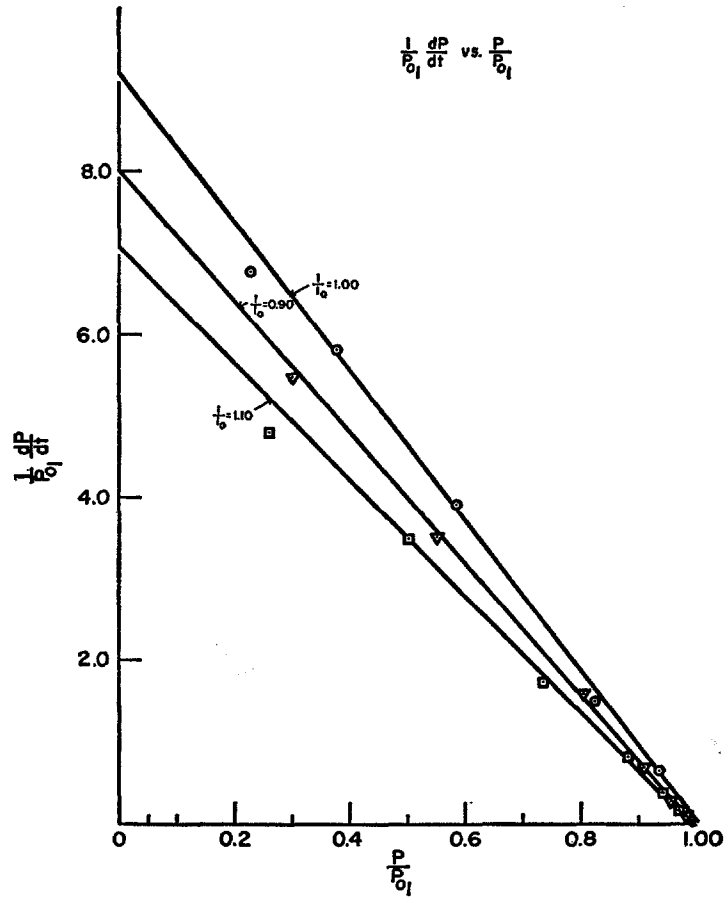


FIGURE 7. $\frac{1}{P_{0i}} \frac{dP}{dt}$ vs. $\frac{P}{P_{0i}}$. Straight lines are obtained from the equation $\frac{1}{P_{0i}} \frac{dP}{dt} = -\frac{1}{T} \frac{P}{P_{0i}} + \frac{1}{T}$. The data points are from Figs. 2 and 5.

metric data coupled to isotonic contraction. If equation,

$$\frac{dP}{dl_s} = \frac{P + a}{bT},$$

is normalized,

$$\frac{d\left(\frac{P}{P_0}\right)}{d\left(\frac{l_s}{l_0}\right)} = \frac{l_0}{P_0} \frac{dP}{dl_s} = \frac{P}{P_0} + \frac{a}{P_0}. \tag{14}$$

For isometric tension developed at length, l_0 , and isotonic contraction after-

loaded at muscle length, l_0 , the values of the constants are $a/P_0 = 0.25$, $b/l_0 = 0.30$ per sec (Matsumoto, 1967), and $T = 0.109$ sec when $l/l_0 = 1.0$. Substituting these values in the above equation,

$$\frac{l_0}{P_0} \frac{dP}{dl_s} = 30.6 \frac{P}{P_0} + 7.65 \text{ (see Fig. 8).} \tag{15}$$

One can also obtain $\frac{l_0}{P_0} \frac{dP}{dl_s}$ by dividing $\frac{1}{P_0} \frac{dP}{dt}$ by $\frac{1}{l_0} \frac{dl}{dt}$ (Sonnenblick, 1962).

Both methods have been used to tabulate the following:

TABLE I

$\frac{P}{P_0}$	$\frac{l_0}{P_0} \frac{dP^*}{dl_s}$	$\frac{1}{P_0} \frac{dP}{dt}$		$\frac{1}{l_0} \frac{dl}{dt}$		$\frac{l_0}{P_0} \frac{dP}{dl_s}$		Diff.
		Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.	
0.0	7.6	9.2		1.2		7.7		
0.10	10.7	8.2	6.3	0.77	0.75	10.7	8.4	-2.3
0.20	13.8	7.3	6.6	0.53	0.53	13.8	12.4	-1.4
0.30	16.8	6.4	6.1	0.38	0.38	16.8	16	-0.8
0.40	19.9	5.5	5.4	0.28	0.26	19.7	20.8	+1.1
0.50	22.9	4.6	4.5	0.20	0.20	23	22.5	-0.5
0.60	26.0	3.7	3.6	0.14	0.15	26	24	-2.0
0.70	29.1	2.8	2.8	0.09	0.09	29	29	0
0.80	32.1	1.8	2.0	0.06	0.06	30	33	+3.0
0.90	35.2	0.9	1.2	0.03	0.03	35	40	+5.0
1.00	38.2	0	0.2	0	0			

* From Equation 15.

The $\frac{l_0}{P_0} \frac{dP}{dl_s}$ of a muscle is a measure of that part of the system which depends upon the length for a corresponding tension. Extension of that length has a one to one correspondence with tension. This is then a measure of the stiffness of the series elastic element.

Integrating the elastic stiffness relation,

$$\frac{P}{P_0} = 1 - \left(1 + \frac{a}{P_0}\right) \left[1 - \exp\left(-\frac{1 - \frac{l_{sc0}}{l_0}}{\frac{bT}{l_0}}\right)\right] \text{ for } l_{sfco} \leq l_{sc0} \leq l_{s0c0}$$

where l_{sc0} is the series elastic element length plus the muscle contractile component length, l_{c0} , the contractile component length corresponding to a muscle exerting a tension, P_0 (i.e., $l_{sc0} = l_s + l_{c0}$). This then is the curve for the tension extension of the elastic element. The plot of this equation compared to an equivalent plot of Wilkie's experiment (1956) shows an approximate agreement.

However, the difference that does exist between curves in Figs. 9 and 10 is such that for the same $\frac{P}{P_0}$, the curve obtained from Wilkie's data is at longer $\frac{l_{sc0}}{l_0}$ than the curve obtained by our analysis. Since Wilkie's muscle was stimu-

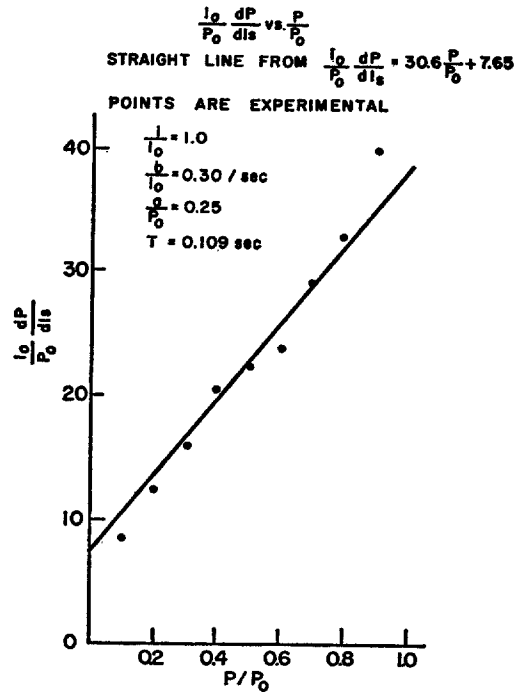


FIGURE 8. $\frac{l_0}{P_0} \frac{dP}{dl_s}$ vs. $\frac{P}{P_0}$. Straight line is obtained from the equation,

$$\frac{l_0}{P} \frac{dP}{dl_s} = 30.6 \frac{P}{P_0} + 7.65.$$

The data points were obtained by division of $\frac{1}{P_0} \frac{dP}{dt}$ by $\frac{1}{l_0} \frac{dl}{dt}$ (Matsumoto, 1965).

lated with a single shock, contractile length for P_0 , l_{c0} , is longer than for our l_{c0} which was obtained by tetanically stimulating the preparation. Also, the divergence of the two curves becomes greater with lighter load. This may indicate the change of l_{c0} during the quick release time in Wilkie's experiment.

For $P = 0$, let $l_{sc0} = l_{sfc0}$, then

$$\frac{l_{sfc0}}{l_0} = 1 - \frac{bT}{l_0} \ln \frac{P_0 + a}{a}$$

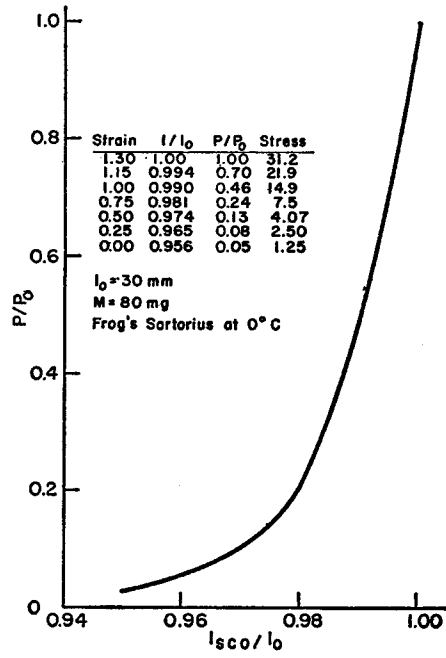


FIGURE 9. Series elastic element stress-strain curve. Series elastic data were obtained from Wilkie (1956) and variables were normalized.

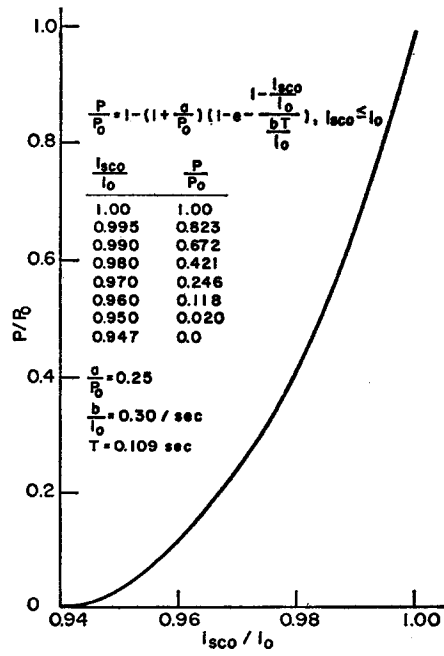


FIGURE 10. Series elastic element stress-strain curve using the equation derived in the text.

and

$$1 - \frac{l_{sfc0}}{l_0} = \frac{bT}{l_0} \ln \frac{P_0 + a}{a}$$

But

$$l_{sfc0} = l_{sf} + l_{c0},$$

and

$$\frac{l_{s0c0}}{l_0} = \frac{l_{s0} + l_{c0}}{l_0} = \frac{l_0}{l_0} = 1;$$

Therefore

$$\frac{l_{s0} + l_{c0}}{l_0} - \frac{l_{sf} + l_{c0}}{l_0} = \frac{l_{s0} - l_{sf}}{l_0} = \frac{bT}{l_0} \ln \frac{P_0 + a}{a}.$$

Since l_{s0} equals the series elastic element length for a muscle exerting a tension, P_0 , and l_{sf} is the series elastic element length for an active muscle exerting zero tension,

$$\frac{l_{s0} - l_{sf}}{l_0} = \frac{bT}{l_0} \ln \frac{P_0 + a}{a} \quad (16)$$

is a method to obtain the total change in series elastic element length corresponding to tension change of zero to P_0 .

$$\frac{l_{s0} - l_{sf}}{l_0} = 5.3\%$$

for $a/P_0 = 0.25$, $b/l_0 = 0.30$ per sec, and $T = 0.109$ sec. Wilkie's direct measurement shows approximately 4 to 5% of l_0 extension.

DISCUSSION

An effort has been made in the present research to correlate the isotonic data with the isometric observations. For the length region greater than l_0 , the parallel elastic element is irreversibly stretched and the unique correspondence of tension to length in active muscle cannot be shown. The length region less than l_0 is adequately reproducible for length-tension-time relations. Conceptually the series elastic element is defined as that part of the muscle which possesses the property of a unique correspondence between tension and length. For the same tension, whether isometric or isotonic, the series elastic element must then have equal length and therefore the difference in the two conditions resides in the contractile component length for a two element system. The consequence of this model system is that the series elastic element is identical in the isometric and isotonic P, l, t surface curves. If this is the case, for the state of the series elastic element (P, l_s, t), the knowledge of two of the three variables should determine the other, viz. $P = f(l_s, t)$. But since the series elastic element is independent of time, for a given tension, the length, l_s is uniquely determined and converse. Therefore $P = f(l_s)$. Then $dP =$

$\frac{df(l_s)}{dl_s} dl_s$ and $\frac{df(l_s)}{dl_s}$ is descriptively defined as the series elastic stiffness. Since this transfer function exists identically in the constant load condition as well as for constant length, it must then have a point on the isometric surface correlative to an isotonic point on its curve in the same state.

In order to integrate the relation,

$$\int_{P_0}^P \frac{dP}{P+a} = \int_{l_0}^{l_s} \frac{dl_s}{bT},$$

the expression on the left must be independent of length and that on the right must be independent of P . It is necessary to establish the constancy of a , b , and T , or determine explicitly their relation to P and l for the evaluation of the integral. If the results of the isotonic analysis are accepted (Matsumoto, 1965), i.e. a , b is not a function of l and t , and since a and b remain unaltered with respect to P and v , according to the force-velocity relation, it must maintain its constancy for dP/dl_s .

T is the characteristic time of isometric contraction but varies with muscle length. It is fixed, however, for the isometric tension time course. If the integral is restricted to one isometric length, l_0 , the corresponding time constant will not change. Knowing the property of the series elastic element and having the knowledge of both isometric and isotonic P , l , t curves, a point on one can be related to a point on the other.

It must be emphasized, however, that the exponential approximation of the isometric tension time rise seriously weakens the extension equation,

$$\frac{P}{P_0} = 1 - \left(1 + \frac{a}{P_0}\right) \left[1 - \exp\left(-\frac{1 - \frac{l_{ec0}}{l_0}}{\frac{bT}{l_0}}\right)\right]$$

in the neighborhood of $P \rightarrow 0$, which will be manifested in the constant value of T .

The total series elastic extension equation,

$$\frac{l_{s0} - l_{sf}}{l_0} = \frac{bT}{l_0} \ln \frac{P_0 + a}{a},$$

results in approximately 5.3% l_0 for *Rana pipiens* using the data of this research. Corresponding values using Wilkie's data show about 4 to 5% l_0 for *Rana temporaria*. Sandow (1958) reports 6.3% l_0 according to his calculation. A. V. Hill (1953) has a figure of 3 to 4% l_0 for frog's or toad's sartorius. The equation offers a simple method of evaluating $(l_{s0} - l_{sf})$ independent of quick release.

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