

Validity of the Force-Velocity Relation for Muscle Contraction in the Length Region, $l \leq l_0$

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ABSTRACT Considerable attention has been directed to the characteristic force-velocity relation discovered by A. V. Hill in the study of muscle kinematics. Models of contractile process were tested on the basis of their compatibility with the Hill equation. However, almost all the isotonic data have been restricted to one length, l_0 , the maximum length with almost no resting tension; the velocities measured are those initial values when the load begins to move. The force-velocity curve extrapolates to zero velocity for isometric tension, but only for the tension at that one length. Very few efforts have been made to study the profiles of the curves throughout the range of lengths over which shortening takes place. In examining the length region, $l \leq l_0$, for an isotonically contracting muscle, not only is the force-velocity relation valid for the initial reference length, l_0 , but also for any other length. The analysis in this report indicates that the constants a/P_0 and b/l_0 remain fixed throughout the length change of afterloaded isotonic shortening in the *Rana pipiens* sartorius muscles.

INTRODUCTION

3 yr after Fenn and Marsh (1935) established the "Fenn effect," Hill suggested that the isotonic force-velocity equation of the striated muscle could be described accurately in terms of a simple hyperbolic relation:

$$(P + a)(v + b) = (P_0 + a)b,$$

where a and b are constants and P_0 equals isometric tension at l_0 . Hill achieved this result by means of study involving heat measurements in the frog sartorius muscles during contraction (A. V. Hill, 1938).

Independent of heat data, the force-velocity relation can also be derived from mechanical measurements. This characteristic relation found for mechanical movement, though differing in the time factor, is similar in character

in the cross-striated muscles of man (Wilkie, 1950), frog (A. V. Hill, 1938), and tortoise (Katz, 1939; Abbott, 1953) as well as in the smooth muscles of marine invertebrates (Abbott, 1953; Abbott and Lowy, 1956).

The force-velocity relation has in general been derived only for the initial length of the muscle corresponding to l_0 . Whether this simple equation holds for any other lengths requires examination. One approach is to test the constancy of a and b for P_{0l} corresponding to that length. P_{0l} is the maximum isometric tension developed by a muscle at length l . The equation can be rearranged as:

$$P = b \left(\frac{P_{0l} - P}{v_l} \right) - a, \quad (\text{Katz, 1939})$$

and the relation tested by plotting the values P vs. $\left(\frac{P_{0l} - P}{v_l} \right)$ at different lengths (Fig. 1). Fig. 1 *a* is a straight line plot of the isotonic data points to determine the constants $\frac{a}{P_0}$ and $\frac{b}{l_0}$ subsequently employed in testing the validity of the force-velocity relation during muscle contraction. Throughout the length region $l \leq l_0$, the equation in Fig. 1 *a*,

$$\frac{P}{P_0} = \frac{1 - \frac{P}{P_0}}{\frac{v_l}{l_0}} \frac{b}{l_0} - \frac{a}{P_0}, \text{ for } P \leq P_0$$

and

$$\frac{P}{P_0} = \frac{\frac{P_{0l}}{P_0} - \frac{P}{P_0}}{\frac{v_l}{l_0}} \frac{b}{l_0} - \frac{a}{P_0}, \text{ for } P \leq P_{0l}$$

should have data points falling on the same line, since the slopes and the $\frac{P}{P_0}$ intercepts are the same. P_0 is the maximum isometric tension developed by a contracting muscle at length, l_0 . Fig. 1 *b* is a family of straight lines to test the possibility of maximum speed of shortening, v_{\max} , being constant. In this case, for each length of the muscle, $l \leq l_0$, a straight line is expected in the $\frac{P}{P_0}$ vs. $\frac{\frac{P_{0l}}{P_0} - \frac{P}{P_0}}{\frac{v_l}{l_0}}$ graph, and $\frac{b}{l_0}$ changes with test muscle length.

The test for the validity of the force-velocity relation in the isotonic length

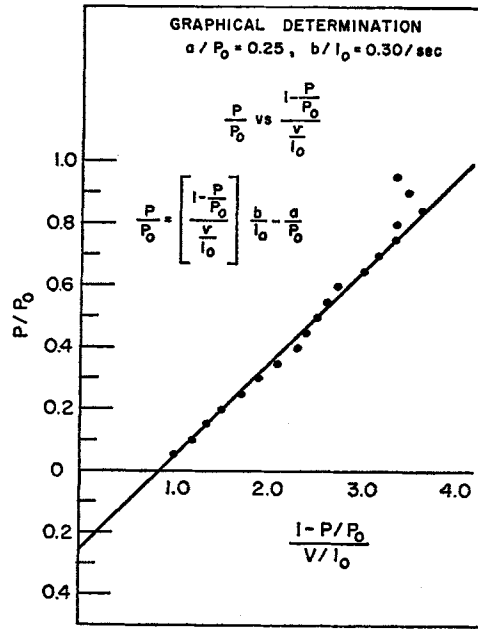


FIGURE 1 a

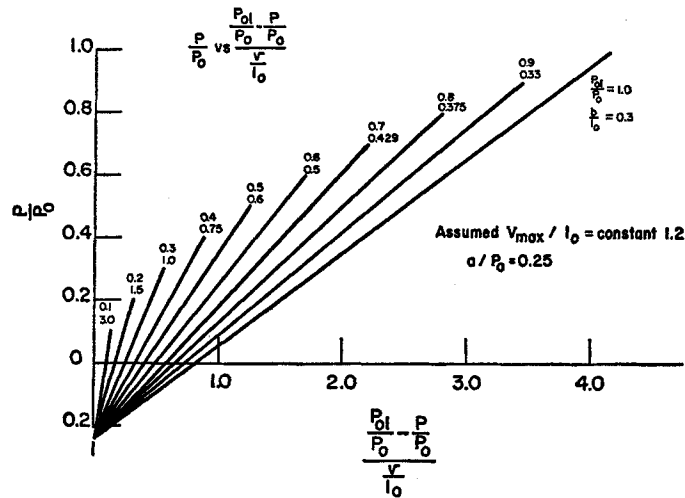


FIGURE 1 b

FIGURE 1. The above equation is obtained by rearranging the force-velocity relation (Katz, 1939). The variables of the axes are chosen to determine the constants a/P_0 and b/l_0 by a straight line relation. Fig. 1 a shows the data points are in agreement with the constant $a/P_0, b/l_0$. Fig. 1 b shows the theoretical linear relation when v_{\max}/l_0 and a/P_0 are fixed.

region of contraction, $l \leq l_0$, was made by imposing two different but plausible conditions on the Hill equation and determining the significance of the data point fits. For the first condition, v_{\max}/l_0 and a/P_0 were held constant for any length of contraction, $l \leq l_0$. The second condition fixes a/P_0 and b/l_0 as constants throughout the isotonic lengths of shortening, $l \leq l_0$. The first condition differs from the second in that b/l_0 is not a constant independent of the contractile length. Corresponding to each length of the muscle (i.e., for $l \leq l_0$), there is a normalized load P_{0l}/P_0 that the muscle cannot shorten. For that length, load P_{0l}/P_0 is therefore the "isometric tension." For $P/P_0 < P_{0l}/P_0$, the muscle then shortens with a given velocity as a function of load. The first condition was selected for analysis of the force-velocity property as indicated in Sonnenblick's papillary muscles (1962). The selection of the second condition was to question the validity of the force-velocity relation for muscle lengths other than l_0 .

THEORY

From the analysis of the imposition of condition (1) on the Hill equation, the following result is formulated:

Let $v_{\max}/l_0 = \text{constant}$.

Assume $(P + a)(v_l + b) = (P_{0l} + a)b$ is the force-velocity relation corresponding to isotonic length, l .

Then
$$v_l = \left(\frac{P_{0l} - P}{P + a} \right) b,$$

and
$$\frac{v_l}{l_0} = \frac{\left(\frac{P_{0l}}{P_0} - \frac{P}{P_0} \right)}{\left(\frac{P}{P_0} + \frac{a}{P_0} \right)} \cdot \frac{b}{l_0}.$$

For
$$\frac{P}{P_0} = 0, \quad \frac{v_l}{l_0} = \frac{v_{\max}}{l_0}$$

and therefore
$$\frac{v_{\max}}{l_0} = \frac{P_{0l}}{a} \cdot \frac{b}{l_0}$$

or
$$\frac{b}{l_0} = \frac{v_{\max}}{l_0} \cdot \frac{a}{P_{0l}} = \frac{\frac{a}{P_0}}{\frac{P_{0l}}{P_0}} \cdot \frac{v_{\max}}{l_0}.$$

Then
$$\frac{v_l}{l_0} = \frac{\left(\frac{P_{0l}}{P_0} - \frac{P}{P_0} \right) \left(\frac{a}{P_0} \right)}{\left(\frac{P}{P_0} + \frac{a}{P_0} \right) \left(\frac{P_{0l}}{P_0} \right)} \cdot \left(\frac{v_{\max}}{l_0} \right), \quad \text{condition (1) equation.}$$

This equation was then used to plot the force-velocity relation of Fig. 2.

Imposing condition (2) when a/P_0 and b/l_0 are fixed throughout the duration of shortening,

$$(P + a)(v_l + b) = (P_{0l} + a)b$$

and rearranging

$$V_l = \left(\frac{P_{0l} - P}{P + a} \right) b$$

or

$$\frac{V_l}{l_0} = \frac{\frac{P_{0l}}{P_0} - \frac{P}{P_0}}{\frac{P}{P_0} + \frac{a}{P_0}} \frac{b}{l_0}$$

condition (2) equation.

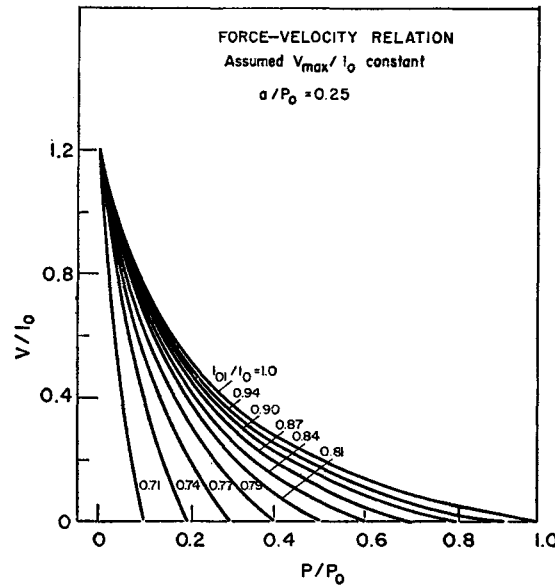


FIGURE 2. Theoretical force-velocity relations assuming v_{max}/l_0 and a/P_0 are constants.

The condition (2) equation was then tabulated and graphed in Fig. 3. For a given constant P/P_0 line in Figs. 2 and 3, the intersecting $(v/l_0, l/l_0)$ points describe a velocity-length relation for that load. Families of velocity-length curves are shown in Fig. 4 for different loads.

EXPERIMENTAL

For the experiments conducted in this research, 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

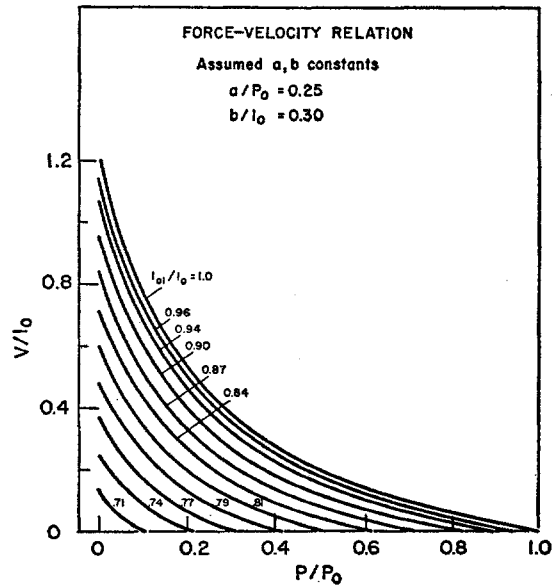


FIGURE 3. Theoretical force-velocity relations assuming a/P_0 and b/l_0 are constants.

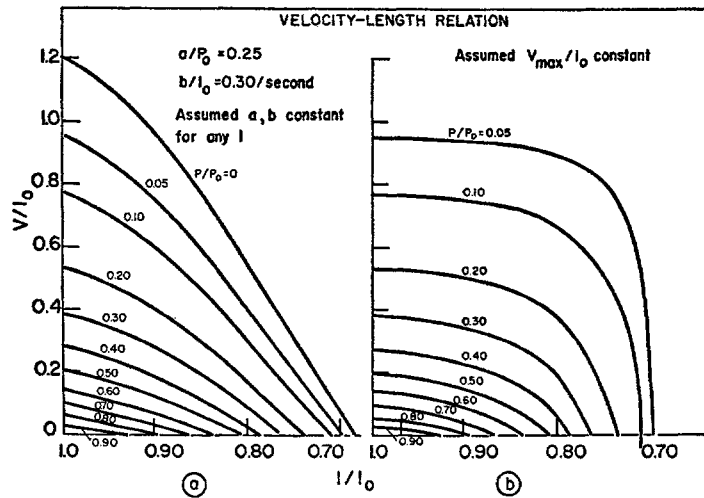


FIGURE 4. *a* and *b*. The velocity-length profiles are obtained respectively from Figs. 2 and 3 (see text).

1.0 mM Na_2HPO_4 and 1.0 mM NaH_2PO_4 was used. The experiments were carried out on whole sartorius muscles of *Rana pipiens* isolated in ice cold Ringer's solution. 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, whose strength, duration, and frequency could be varied. The duration and frequency were adjusted to give fused tetanic response at the operating temperature. The strength was at least double the threshold value. For all the experiments conducted, 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.

At the beginning of each experiment on afterloaded isotonic tetanic contraction, the muscle was tested isometrically in order to determine maximal isometric tension

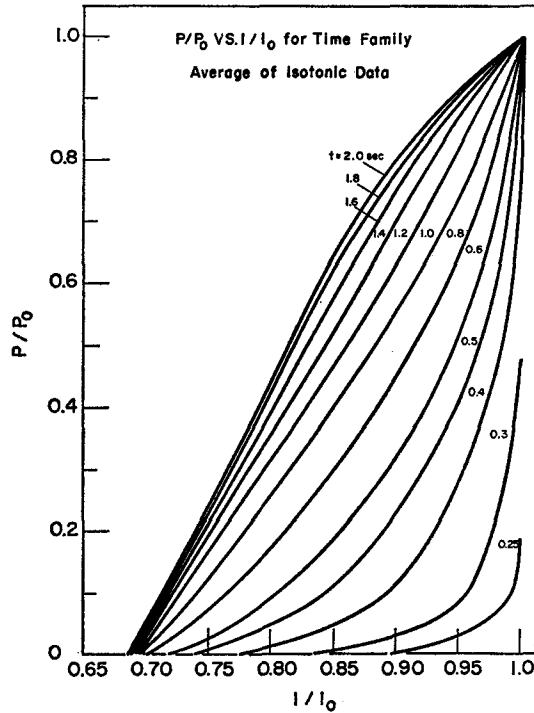


FIGURE 5. The tension (load)-length curves were obtained from the experimental isotonic contraction-time courses.

and also the reference length, l_0 , at which the P_0 is maximum. This length, l_0 , was then used as the initial length for all afterloaded contractions in the experiment. Isotonic contractions were then studied with a series of afterloads and the contractions were imposed at intervals no shorter than 10 min. Loads were varied in ascending and descending sequence. Final control isometric tension was taken at the conclusion of each experiment. Thus 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. It was then necessary to be able to compare and average all the experiments.

The first procedure was to normalize all the curves for length and load; i.e., calculating l/l_0 and P/P_0 . The normalized isotonic curves are continuous curves for length against time but are obtained for a series of loads which are not identical from

muscle to muscle, especially after the normalizing procedure. In order to obtain compatible and comparable length-time curves, an intermediate step is necessary to give us the value for a series of similar loads for all muscles. At a given time after the onset of contraction, the intersections of the family of isotonic curves describe a relation between length and tension (load) for that time. The result of this procedure is shown in Fig. 5. As an example, for time 0.50 sec after the beginning of contraction, the muscle carrying the load 0.60 normalized unit will be at a normalized length of 0.98. While under a load of 0.10 unit, the muscle will be at a length of approximately 0.84. Thus a continuous curve of muscle length vs. load at the time 0.50 sec can be drawn. This can be repeated for the selected time intervals throughout contraction.

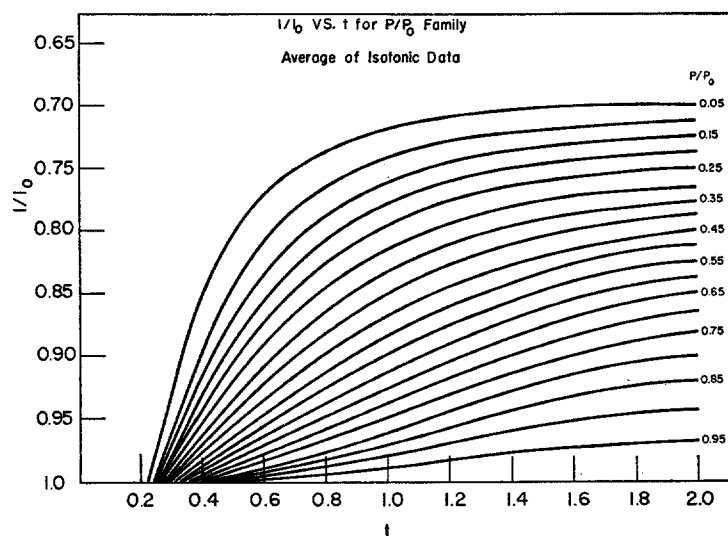


FIGURE 6. Family of isotonic shortening vs. time curves. These contraction-time courses are obtained from Fig. 5 (see text).

Each experiment gives such a family of curves and the average results are shown in Fig. 5, which is thus the tension-length profile for isotonic contraction. From these curves, the average normalized length-time curve for a series of afterloads can be reconstructed by reading off and plotting the time at which each length is reached for a given afterload (Fig. 6). The final length-tension-time relation for isotonic recordings was obtained from the average of four experiments. The standard deviations varied from $\pm 1\%$ for isotonic shortening at load $\frac{P}{P_0} = 0.95$, to about $\pm 4\%$ at load value of $\frac{P}{P_0} = 0.05$.

$$\text{Exp. 34 } P_0 = 1.85 \text{ kg/cm}^2 \quad l_0 = 43.0 \text{ mm} \quad M = 161 \text{ mg}$$

$$\text{Exp. 35 } P_0 = 2.44 \text{ kg/cm}^2 \quad l_0 = 45.0 \text{ mm} \quad M = 210 \text{ mg}$$

$$\text{Exp. 37 } P_0 = 2.38 \text{ kg/cm}^2 \quad l_0 = 45.5 \text{ mm} \quad M = 161 \text{ mg}$$

$$\text{Exp. 38 } P_0 = 2.31 \text{ kg/cm}^2 \quad l_0 = 45.5 \text{ mm} \quad M = 173 \text{ mg}$$

The load was applied to the muscle by a lever arm (type I) and displacements were transduced from movements of the lever to voltage by a photodetecting device. A vane fixed to the lever arm and between the light source and the photodiode controls the amount of light falling on the photodetector as a function of the lever displacement. The vane is made from a light Fisher board in the shape of an annulus of circles fixed to the lever with the fulcrum as the center of the annulus. As the lever moves, the edge of the vane blacks out an area linearly proportional to the distance moved by the lever, enabling a linear conversion of displacement to voltage. The position of the load is very close to the fulcrum point (load position to test point distance ratio, 1:20) in order to reduce inertia of the load applied to the muscle. The lever displacement of 18 mm range has a sensitivity of 1.14 mm/v.

RESULTS

For a given $\frac{P}{P_0}, \left(\frac{l}{l_0}, t\right)$ coordinate points can be obtained from Fig. 5 and $(l/l_0, v/l_0)$ coordinates are available from Fig. 4. Taking the same l/l_0 values from both graphs, one can obtain the v/l_0 corresponding to t so that an isotonic velocity of shortening vs. time curve can be plotted out. The resulting v/l_0 vs. t relations were thus the theoretical velocity time curves for conditions (1) and (2) and the differences are manifested in Figs. 7 and 8.

The averaged experimental shortening vs. time curves (Fig. 6) were analyzed and plotted for speed against time (v/l_0 vs. t) graphically. The resulting data points are shown in Fig. 8, superimposed on the theoretical velocity-time curves for the P/P_0 family. Comparing Figs. 7 and 8, this analysis rules out the constant maximum velocity consideration. However, in the case of condition (2), the assumption of constants a and b for any length (i.e., $l \leq l_0$), the experimental velocity-time curves show a remarkable fit with the theoretical curves. Table I compares the experimental velocity-time relation for a given load with the theoretical curve construction for constants a and b . Table II compares the velocity of shortening vs. load for a given muscle length between the experimental and theoretical curves. Tabulations for both of these tables are consistent with the idea that *Rana pipiens* sartorius muscles shorten in agreement with the force-velocity relation maintaining constants a and b for length region $l \leq l_0$.

DISCUSSION

It is well established in the literature that although no unique equation can be defined for the empirical force-velocity relation, Hill's P - v relation

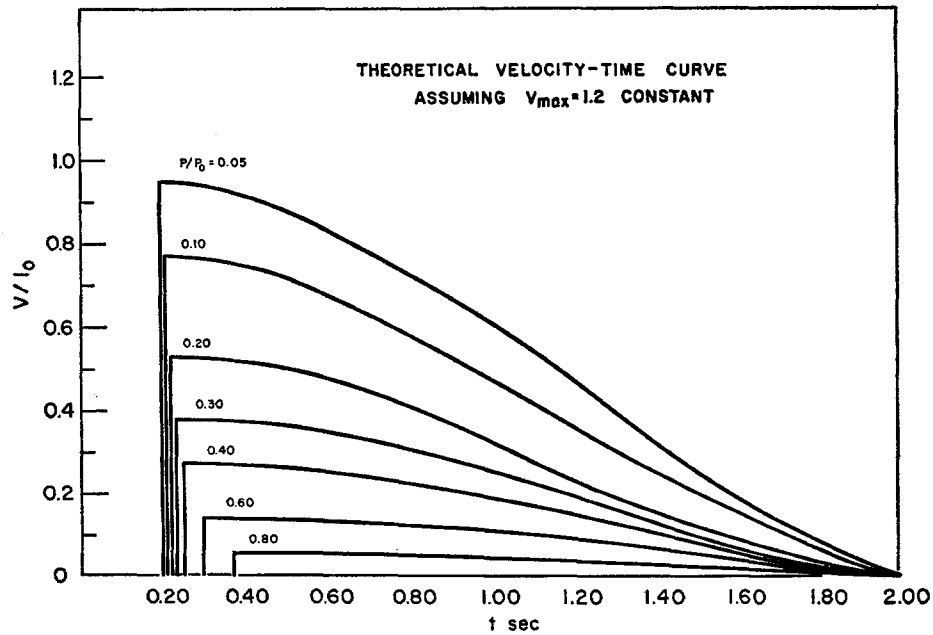


FIGURE 7. Theoretical velocity-time curves assuming v_{max}/l_0 and a/P_0 are constants. The curves are results from Figs. 4 b and 5.

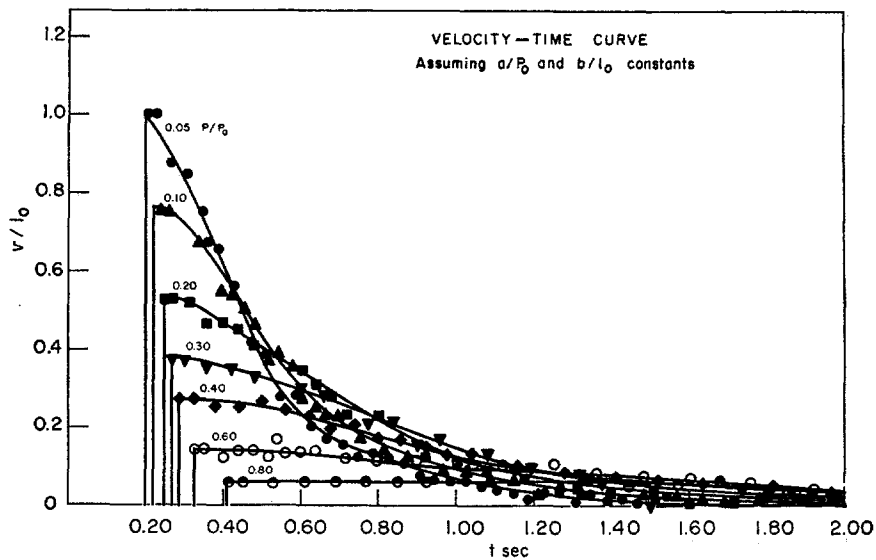


FIGURE 8. Velocity-time curves assuming a/P_0 and b/l_0 are constants. The data points were graphically analyzed from Fig. 6. The velocity-time profile is obtained from Figs. 4 a and 5 (see text).

TABLE I
SHORTENING VELOCITY v/l_0 vs. TIME

t	$\frac{v}{l_0}$													
	$\frac{P}{P_0} = 0.05$		$\frac{P}{P_0} = 0.10$		$\frac{P}{P_0} = 0.20$		$\frac{P}{P_0} = 0.30$		$\frac{P}{P_0} = 0.40$		$\frac{P}{P_0} = 0.60$		$\frac{P}{P_0} = 0.80$	
	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.
sec														
0.22	0.95	0.96												
0.24			0.77	0.75										
0.25					0.53	0.53								
0.27							0.38	0.38						
0.29							0.38	0.38	0.28	0.26				
0.30	0.82	0.83	0.72	0.72	0.52	0.52	0.38	0.38	0.28	0.26				
0.33											0.14	0.15		
0.40	0.59	0.61	0.59	0.59	0.47	0.47	0.36	0.36	0.27	0.27	0.14	0.14		
0.41													0.06	0.06
0.50	0.39	0.39	0.44	0.44	0.41	0.41	0.33	0.33	0.25	0.26	0.14	0.14	0.06	0.06
0.60	0.23	0.23	0.31	0.31	0.34	0.34	0.29	0.30	0.23	0.24	0.13	0.13	0.05	0.06
0.70	0.17	0.17	0.24	0.22	0.28	0.28	0.25	0.26	0.20	0.20	0.12	0.12	0.05	0.06
0.80	0.12	0.13	0.16	0.16	0.22	0.22	0.21	0.22	0.18	0.18	0.11	0.11	0.04	0.06
0.90	0.10	0.10	0.12	0.12	0.16	0.16	0.18	0.18	0.16	0.16	0.10	0.10	0.04	0.06
1.00	0.08	0.07	0.10	0.10	0.12	0.12	0.15	0.15	0.13	0.12	0.09	0.09	0.04	0.06

TABLE II
SHORTENING VELOCITY v/l_0 vs. LOAD P/P_0

$\frac{P}{P_0}$	$\frac{v}{l_0}$											
	$\frac{l}{l_0} = 1.00$		$\frac{l}{l_0} = 0.95$		$\frac{l}{l_0} = 0.90$		$\frac{l}{l_0} = 0.85$		$\frac{l}{l_0} = 0.80$		$\frac{l}{l_0} = 0.75$	
	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.	Theoret.	Expt.
0.05	0.95	0.96	0.87	0.90	0.75	0.77	0.59	0.60	0.39	0.38	0.20	0.17
0.10	0.77	0.75	0.70	0.71	0.60	0.60	0.46	0.46	0.29	0.28	0.13	0.12
0.20	0.53	0.53	0.48	0.50	0.40	0.44	0.29	0.35	0.16	0.24	0.03	0.02
0.30	0.38	0.38	0.34	0.36	0.27	0.31	0.18	0.23	0.08	0.12		
0.40	0.28	0.26	0.24	0.26	0.18	0.20	0.11	0.13	0.02	0.05		
0.60	0.14	0.15	0.10	0.12	0.07	0.08	0.01	0.06				
0.80	0.06	0.06	0.03	0.06								

describes quite accurately the events occurring during isotonic shortening of a wide variety of muscles. However, the hyperbolic relation was established only for initial length of contraction, l_0 . In 1953, Abbott and Wilkie studied the validity of the force-velocity relation, independent of the initial length, $l \leq l_0$, in the case of *Rana temporaria* sartorius muscles. They did find, however, that in *R. temporaria*, the final tension values at any lengths were coincident whether obtained isometrically or isotonicly. Results with *Rana pipiens*

sartorii (Matsumoto, 1965) show that the isotonic final shortening length falls short of the corresponding isometric length with the same tension and must be compared with Buchthal's results on single fibers (1951). However, analysis confirms the work of Abbott and Wilkie on the constancy of a and b . If a and b are independent of the initial length of shortening and remain constant throughout the duration of contraction, then a and b must not be functions of length or time and therefore final length of contraction.

Incidental to the result given to substantiate the constancy of a and b , analysis for the consideration of constant a , v_{\max} was done. Graphically the two assumptions, constant a , v_{\max} and constant a , b force-velocity relations, are distinguishable by observing the velocity-time curves for different loads at l_0 . For the latter case, velocity plotted against time for lighter isotonic loads decays faster to zero velocity than does the isotonic contraction at heavier loads. The family of these curves, if superimposed on the same graph paper for different loads (Fig. 8), crosses over the velocity-time course of the lighter loads on the negative slopes whereas for constant v_{\max} property, the family of velocity-time curves does not exhibit cross-over points. This analysis requires testing for uniqueness in this property for distinguishability of the two cases. If the conceptual development is correct, it may serve as a quick method for determining the constant a , v_{\max} force-velocity relation or constant a , b P - v equation.

The author wishes to thank Dr. B. C. Abbott for his help in preparing the manuscript. The work was supported by a grant from the National Institutes of Health, United States Public Health Service 5 T1 GM 720-07.

Material in this paper is taken from part of a thesis submitted to the University of California at Los Angeles in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Received for publication 20 June 1966.

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