**Energetics of the Time-Varying Elastance Model,
a Visco-Elastic Model, Matches Mommaerts'
Unifying Concept of the Fenn Effect of Muscle**

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SUMMARY

It is generally believed that the Fenn effect contradicts all visco-elastic models of muscle, including the new elastic body and the time-varying elastance models. Although it is clear that the new elastic body model can be discarded, the Fenn effect does not preclude the time-varying elastance model. Although no visco-elastic models can simulate the extra energy utilization for work above the level of the energy utilized for the maximal isometric contraction, the extra energy observed by Fenn is not generally observed, even in skeletal muscles. However, work-related extra energy utilization, above the isometric energy utilization at equivalent force (Mommaerts' unifying concept of the Fenn effect), is generally observed in both skeletal and cardiac muscles. This unifying concept of the Fenn effect in cardiac muscle can be simulated by a simple time-varying elastance model. This study demonstrates the essential difference in energetics between the new elastic body model and the time-varying elastance model.

Additional Indexing Words:

Heart Ventricle Myocardial oxygen consumption Work Heat
New elastic body Cocked spring

IT is now generally believed that a contracting muscle cannot be simulated by any visco-elastic model because the energetics of the muscle appear to be inconsistent with the energetics of this model.¹⁾⁻⁴⁾ The peculiar energetic properties of the muscle are called the "Fenn effect".^{5),6)} The Fenn effect comprises i) a load-dependent energy release, and ii) more energy release in an isotonic contraction than in an isometric contraction *at the same initial length*.^{5),6)} Although the Fenn effect^{5),6)} cannot generally be observed in either skeletal muscles^{3),7),8)} or in cardiac muscle,⁹⁾⁻¹³⁾ it is often cited as

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Partly supported by Grants-in-Aid: C63570045 from the Ministry of Education, Science and Culture, and 63A-2 and 1A-1 from the Ministry of Health and Welfare of Japan.

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Received for publication October 2, 1989.

Accepted October 12, 1989.

evidence for rejecting visco-elastic models of any muscle.^{1),2),14)}

It is true that visco-elastic models cannot simulate one major aspect of the Fenn effect, the finding that the total energy expenditure for a shortening contraction is greater than that of the maximal isometric contraction.^{1),5),6)} However, this aspect of the Fenn effect is not generally observed even in skeletal muscles.^{3),15)} Instead, muscles of different types share Mommaerts' unifying concept of the Fenn effect, that muscle work involves liberation of energy in excess of the energy of the isometric contraction *at an equivalent force*.^{3),15)}

This paper emphasizes that this unifying view of the Fenn effect does not preclude all visco-elastic models of muscles, particularly the time-varying elastance model of cardiac muscle.

BACKGROUND

The historical background of the Fenn effect is an essential basis for understanding the arguments raised in this communication. Until the discovery of the Fenn effect,^{5),6)} the generally accepted view was that a contracting muscle was merely a stretched (or cocked) spring or a damped stretched spring, i.e., a *new elastic body*, as quoted in Table I. This model can be traced back to the 1880's.^{3),16)} The primary energetic property of the new elastic body is the constancy of the sum of work and heat, regardless of the loading conditions of a contracting muscle.

Fenn^{5),6)} found in frog sartorius muscle at 0°C a peculiar but important phenomenon, which later became known as the *Fenn effect*. This phenomenon consists of an extra energy liberation for work, in excess of the energy utilization of an isometric contraction (Table II). The Fenn effect was inconsistent with the predicted energetics of the new elastic body model. Thus, the Fenn effect was recognized as a "death warrant" of the visco-elastic theory by Hill.²⁾ However, it is clear that Hill's context was the new elastic body theory, *not* all visco-elastic models.

The cardiac Fenn effect is different from the skeletal Fenn effect.^{3),9),11)–13),15),17),18)} The cardiac Fenn effect matches Mommaerts' unifying concept¹⁵⁾ of the Fenn effect that work involves a liberation of energy in excess of the equivalent isometric energy³⁾ (Table II). Despite the rejection of the visco-elastic theory (including the new elastic body theory) from skeletal muscle physiology,²⁾ the mechanoenergetics of cardiac muscle, including its Fenn effect, have been shown to be basically simulated by a *time-varying elastance model* by Gibbs' and Suga's groups.^{11)–13),19)–22)} This model differs significantly from the new elastic body model.

Table I. Origins of the New Elastic Body Model

Hill (1913)²⁸⁾

"... after the maximum tension has been developed the muscle is merely a new elastic body, whose tension energy may be used indifferently for the accomplishment of work or the production of heat."

Fenn (1923)⁹⁾

"... the view came to be accepted that on stimulation a muscle developed a given amount of heat and a given amount of elastic potential energy, both varying with the length of the fibres of the muscle. The amount of elastic potential energy which could be recovered as work depended merely upon the art of the experimenter in arranging his levers and had no relation to the total energy liberated."

Fenn (1924)⁹⁾

"Weber first regarded a stimulated muscle as a new elastic body suddenly created from the old one at the moment of stimulation and reverting to it again in relaxation. More specifically the elastic body theory in its original form states that if a muscle is able to shorten to a length, under tension T , then if stimulated at a length l it will develop a maximum tension T . In other words the maximum tension of the stimulated muscle is dependent only upon its length (compare an elastic band)."

White and Thorson (1973)¹⁰⁾

"... the idea that, following a stimulus, the muscle acts like a cocked spring along with passive elements (springs and dashpots). A common property of all such models is that the amount of energy available should be independent of the manner of contraction provided that all methods of release of energy are taken into account."

Elzinga et al (1989)¹¹⁾

"The viscoelastic model of skeletal muscle contraction was finally abandoned because Fenn (1923) showed that, for this type of muscle, the energy liberated when work was performed was higher than that measured during isometric conditions."

"... implies that the viscoelastic model, rejected for skeletal muscle contraction, appears to be valid for the intact ventricle."

Rall (1982)⁹⁾

"The viscoelastic (or new elastic body) theory of muscle contraction

"The view was held that, after a stimulus, muscle acted like a stretched spring released in a viscous medium. The stimulated muscle then would liberate, in an all-or-none fashion, an amount of energy that varied with initial length and which could appear as either heat or work. The amount of potential energy that could be converted into work depended on the skill of the experimenter in arranging levers, and thus work should bear no relation to total energy liberated. This theory predicts that the amount of energy liberated in an isotonic contraction would be independent of work or load and equivalent to energy liberated in an isometric contraction."

Gibbs and Chapman (1985)¹¹⁾

"The idea that muscle might behave as a stretched spring when activated was put forth by Weber in 1846. This idea related to the force-length relationship of an isometrically tetanized muscle that was seen to have stress-strain characteristics similar to those found for an elastic element obeying Hooke's Law. When a muscle was stimulated it was assumed to possess potential energy proportional to the area of the force-length curve to the left of its existing length."

Table II. The Fenn Effect

Fenn (1923)⁵⁾

"Whenever a muscle shortens upon stimulation and does work in lifting a weight, an extra amount of energy is mobilised which does not appear in an isometric contraction. Hence less energy is liberated in an isometric contraction than in any contraction in which the muscle is allowed to shorten."

"The energy liberated by the contraction of a single muscle fiber for a given stimulus is not dependent solely upon the initial mechanical and physiological condition of the muscle but can be modified by the nature of the load which the muscle discovers it must lift after the stimulus is over. The all-or-none law of muscular contraction must be qualified from this point of view."

Fenn (1924)⁶⁾

"It is shown that the existence of an excess heat liberation is to some extent inconsistent with the idea that a stimulated muscle is a new elastic body. It is suggested that contraction is analogous rather to the winding up of an anchor chain by a windlass than to the lifting of a weight by the energy of a stretched spring."

Gibbs et al (1967)²⁹⁾

"It is important to know that in an isotonic contraction there is additional energy liberated as heat, above that required in an equivalent isometric contraction. In some ways this result is similar to that found by Fenn (1923) in skeletal muscle at 0°C, the difference being that in cardiac muscle the isotonic energy liberated with light to medium loads never exceeds the energy liberated in a maximum isometric contraction."

Mommaerts (1969)¹⁸⁾

"Fenn showed . . . that muscles doing work mobilize additional energy, in parallel with the work performance; thus, the total amount of chemical energy is not uniquely determined at the moment of stimulation, but depends also on the mechanical conditions during the resulting contraction. A muscle doing maximal isotonic work at optimal loading mobilizes more energy than one contracting isometrically or contracting isotonically with minimal load."

"... the Fenn effect shows the muscle to be endowed with a regulatory ability; when work is done, extra metabolism is used, so that its enthalpy effect is just about equal to the work done."

"... the definition of the Fenn effect could be broadened to include all regulatory phenomena that lead to an extra mobilization of energy for work."

Hill (1970)²⁾

"It is clear that those of us who supposed that a stimulated muscle is simply a new elastic body were wrong. A muscle may possess some elastic properties but it requires more energy to do more work, a fact which is fundamentally in opposition to the elastic body theory."

"... Fenn's conclusions . . . they were obviously the death warrant of the visco-elastic theory."

"Everything that is now known makes nonsense of the visco-elastic theory and model; they had better be forgotten."

Mommaerts (1970)¹⁵⁾

"... we would give as our first definition that the Fenn-effect is a regulatory property of the muscle cell, which determines that a muscle performing work generates energy in excess of that by a muscle not performing work though excited under otherwise comparable circumstances."

Table II. Continued.

"... the main thing was that a muscle doing work mobilizes extra energy."

"I would propose a new definition... a muscle doing work mobilizes, over and above that needed for activation and the maintenance of tension, energy accounting for the work and for the dissipation of energy accompanying the work process."

Woledge (1971)³⁰⁾

"... energy liberated as heat and work in an afterloaded isotonic twitch exceeded that in an isometric twitch..."

White and Thorson (1973)¹⁶⁾

"... the total release of energy in a twitch can be regulated by mechanical changes in the muscle and is not, as had been thought, an all-or-nothing phenomenon."

"... Fenn's results demonstrate that the cocked spring models of muscles are inappropriate."

Gibbs (1978)¹⁰⁾

"... really important conclusion that the energy flux of a muscle is regulated by the mechanical constraints under which it shortens."

"Mommaerts has proposed a new definition of the Fenn effect that would encompass both cardiac and skeletal muscle experiments under all physiological conditions."

Rall (1982)³⁾

"Much of the confusion surrounding the generality of Fenn's observations seems to be attributable to the problem of determining an energetic base line for comparing isotonic and isometric contractions. Mommaerts has suggested the use of an equivalent force base line, which appears to be a useful and unifying concept."

"... work involves a liberation of heat in excess of the equivalent isometric heat."

"... the maximum isometric energy liberation is not an appropriate base line with which to compare energy liberation in working contractions. To unmask the effect of work on energy cost one must minimize effects of length per se on energy liberation or compensate for length effects by considering an equivalent isometric energy base line."

"Fenn's results were the first to demonstrate beyond doubt that muscle possesses a fundamental property that enables it to adjust its energy cost to prevailing mechanical constraints after stimulation."

Woledge et al (1985)⁴⁾

"Fenn concluded... This conclusion invalidated the visco-elastic theory of contraction which held that the amount of energy liberated in any twitch was a constant. Fenn's conclusion introduced a completely new, and still valid, idea to muscle energetics, i.e., that the driving reactions are regulated by the force and/or shortening occurring in contraction."

Gibbs and Chapman (1985)¹¹⁾

"Fenn's data were essentially incompatible with muscle behaving as a simple viscoelastic element."

Elzinga et al (1989)¹⁾

"... that most important result of Fenn's finding was not that he found that load changes after the onset of contraction affected the total energy expenditure but that the total energy output (heat + work) during loaded shortening was higher than during isometric contraction."

METHODS AND RESULTS

Figure 1 compares the new elastic body model (Panel A) and a visco-elastic model (Panel B). Both the structure of the models and the elastance (E), force (F), and length (L) curves as a function of time (t) are illustrated. We define the visco-elastic model as a type of visco-elastic model that has a gradual rise in elasticity. This definition, then, includes the time-varying elastance model, but excludes the new elastic body model. Structurally, both models consist of an active elastic element (E) (or an active spring) and a viscous element (R) in parallel. The elastance was assumed to be linear and time-varying in either model. In other words, the force generated by the elastic element is a linear function of its length at a given elastance. Any series elasticity is ignored for the sake of simplicity.

The two models differ, though, in the time course of the elastance on stimulation. The elastance increases instantly on stimulation in the new elastic body model like a cocked spring (Table I). Since there is an instantaneous rise in elastance, force also rises instantly to the level of afterloaded

Fig. 1. Comparison between the new elastic body model (A) and the visco-elastic model (B). The temporal behavior of elastance (E), force (F), and length (L) are illustrated. R is the viscosity. Curves 1, 2, and 3 correspond to isometric contraction (1), moderately afterloaded isotonic contraction (2), and totally unloaded contraction (3). t denotes time.

isotonic force (curve 1, 2, or 3 in Fig. 1A). The viscosity does not hinder the initial force development because no shortening occurs at this instant. Due to the viscosity, shortening occurs gradually after the force reaches the afterload (curve 1, 2, or 3 in Fig. 1A). Curve 1 illustrates an entirely isometric contraction, curve 2 shows a moderately afterloaded isotonic contraction, and curve 3 illustrates a totally unloaded contraction. The mathematical expressions for the curves are given in the Appendix.

By contrast, the elastance rises slowly over a finite time on stimulation in the visco-elastic model (Fig. 1B). Force and length curves are shown in the same format as Fig. 1B. Curve 1 illustrates an entirely isometric contraction, curve 2 displays a moderately afterloaded isotonic contraction, and curve 3 shows a totally unloaded contraction. The mathematical expressions for these curves are also given in the Appendix. The decisive difference in mechanics between the new elastic body and the visco-elastic model, then, is that no shortening occurs before the instant full force development in the new elastic body model whereas shortening occurs while force is being developed in the visco-elastic model (Fig. 1A and B).

This difference of the speed of the increase in elastance also causes a substantial difference in the energetics of the model. This point does not seem to have been widely recognized. In the new elastic body model, the elastic element is instantly energized and is provided with a given amount of elastic potential (or free) energy on stimulation (Fig. 2A and Table I). In the force-length diagram, this constant total energy is represented by a triangular area under the maximum force-length line (OB, Fig. 2A). This indicates that shortening occurs against a variable afterload, so that the total energy utilization ($H_T = W + H + P$) is determined at the time of the instant increase in elastic potential energy. Work (W) is only a variable fraction of H_T (Fig. 3A). What happens if the elasticity rises gradually in the visco-elastic model? It is a surprise that no one has yet attempted to consider energetics of a visco-elastic model whose elastance increases gradually with force development and shortening (Fig. 1B).

Figure 2B shows schematically that the total energy increases gradually with gradual increases in elastance in the visco-elastic model. For simplicity, viscosity in the model is first ignored, i.e., $R=0$ in Fig. 1B. Nevertheless, the elastic potential (or free) energy increases slowly with the gradual rise in elastance, even in the isometric contraction phase (Fig. 2B). External work is performed with shortening against afterloaded isotonic force, while elastance is still increasing (Fig. 2B). The total energy generated by the shortening contraction is smaller than that of the entirely isometric contraction (Fig. 2B).

Fig. 2. Comparison between the new elastic body model (A) and the visco-elastic model (B) in the time course of energy utilization and the force (F)-length (L) diagram. The trajectories of an isometric and a moderately afterloaded isotonic contraction are shown. In the new elastic body model, the time course of energy utilization is the same for both isometric and isotonic contractions. In the force-length diagram, the trajectory AB is isometric, and trajectory ACD is afterloaded isotonic. W is work. H is heat associated with W. P is residual potential energy at the end of shortening. P is reasonably assumed to be eventually dissipated as heat. The long arrow along AB means an instant shift of the force-length relation from OA to OB in the new elastic body model. The short arrows along AB mean a gradual rise of the force-length relation from OA to OB in the visco-elastic model. The dotted lines originating from origin O indicate instantaneous force-length relations.

The shortening during the gradual rise in elastance causes a decisive difference in mechanics of the visco-elastic model from the new elastic body model: The total energy expenditure ($H_T = W + P$) varies as a function of afterload (Fig. 3B). The difference in the total energy expenditure between the two models is equal to the energy H released during shortening in the new elastic body model (Fig. 2A). With a finite viscosity ($R > 0$) in Fig. 1B, some additional heat is generated during shortening. This heat must be added to H_T , but H_T of any shortening contraction cannot exceed the H_T of the maximum isometric contraction (Fig. 3B). Therefore, the dependence of the total energy expenditure on afterload is present in the visco-elastic model, regardless of the magnitude of the viscosity. This is a very important energetics consequence of a visco-elastic model with a slowly increasing elastance.

Figure 3B also shows the total energy expenditure (H_I) of isometric contractions at different preloads as a function of afterload force, according to Mommaerts' unifying concept of the Fenn effect.¹⁵⁾ H_T is always greater than H_I at any equivalent afterload force level. The difference is identical

Fig. 3. Comparison between the new elastic body model (A) and the visco-elastic model (B) in the energy-afterload relation. W is work as a function of afterload from a fixed preload. H_T is the total energy utilization in one isometric (right end of the afterload coordinate) or afterloaded isotonic contraction of the model. H_I (dotted curve) is the total energy utilization of isometric contraction with the same peak pressure as afterload. H_T minus H_I is proportional to W .

with the W of the isotonic contraction at the equivalent force. This energetics property is only a modified expression of the energetics consequence of the visco-elastic model mentioned above. Thus, the visco-elastic model is substantially different from the new elastic body in both mechanics and energetics: The visco-elastic model with a slow rise in elastance has a fundamental property of adjusting its energy expenditure to a mechanical load. The key difference in both mechanics and energetics between the new elastic body model and the visco-elastic model originates from the speed of the elastance rise. Therefore, the remaining difference between the visco-elastic model and the muscle is that, in the skeletal muscle, shortening contractions generate greater energy than the maximal isometric contraction under some limited conditions.³⁾

DISCUSSION

The present theoretical results have evidently shown the decisive difference in both mechanics and energetics between the new elastic body model and a visco-elastic model with a gradual rise in elastance. The latter model produces extra mechanical energy in proportion to work at equivalent isometric force level. This indicates that the energetic behavior of the visco-elastic model obeys Mommaerts' unifying concept of the Fenn effect¹⁵⁾ (Table II). Therefore, the Fenn effect cannot rule out all visco-elastic models; it is only inconsistent with the new elastic body model, which is equivalent to a visco-elastic model with an instant rise in elastance.²⁾

With respect to the time-varying elasticity of muscle, most recent major models of muscle contraction involve a spring in each crossbridge¹¹⁾ (quoted

Table III. Elastic Potential Energy: Important Sources

Fenn (1923)⁶⁾

"It had been shown by Heidenhain that a muscle gave off more heat in an isometric twitch than in a freely shortening twitch under varying loads, but this might mean merely that the process of shortening had prevented the development of the potential energy."

"Fick found always less heat produced when work was done on the muscle than when the muscle did work. He concluded, therefore, that it is the actual process of doing positive mechanical work, i.e. of shortening under tension, which is responsible, in muscle, for the chief expenditure of chemical energy."

Fenn (1924)⁶⁾

"My own experiments . . . suggest that a stimulated muscle, although under considerable tension, may possess very little elastic potential energy, and that the energy necessary for shortening (i.e. for work) is liberated as the shortening proceeds."

Huxley (1957)²⁵⁾

" . . . the extent of the movement being limited by an elastic connection

" . . . the tension in the elastic element is in the direction to help the muscle to shorten."

" . . . assume that the elastic element obeys Hooke's law with a stiffness

"The average value of the work done at one myosin site as one actin site is carried past it by the shortening of the muscle is . . ."

"The maximum work done in a cycle at one site is $kh^2/2$. . ."

Huxley and Simmons (1971)²⁶⁾

" . . . gives the total potential energy of the cross-bridge . . . the total potential energy of an attached cross-bridge contains also the potential energy of stretching the elastic link . . ."

Elsenberg and Greene (1980)²³⁾

"To develop a complete cross-bridge model, the concepts of cross-bridge elasticity and multiple biochemical states must be combined."

"Perhaps the biochemical concept of rapid equilibria combined with the physiological concept of cross-bridge elasticity will prove to be useful in understanding the mechanism of cross-bridge action."

Elzinga and Westerhof (1981)¹⁴⁾

" . . . arguments have been put forward that energetically, as well as mechanically, the left ventricle resembles also a time-varying compliance. This implies that the viscoelastic model, rejected for skeletal muscle contraction, appears to be valid for the intact ventricle. This difference between skeletal muscle and the heart could be due to differences in the type of muscle or related to the complex organization of the cardiac muscle fibers in the wall of the heart."

Gibbs and Chapman (1985)¹¹⁾

"However, it is interesting to note that, in the more realistic models of muscle contraction that emerged beginning with Huxley, nearly all contain an elastic energy storage element in the form of a stretched spring."

in Table III). In these models, the elastic element in the crossbridge is supposed to be energized by the free energy of ATP hydrolysis.^{4),23)–26)} The energized crossbridge can convert its free energy into mechanical work when shortening is allowed; otherwise, it dissipates the free energy as heat when the crossbridge breaks without shortening.^{4),23)–26)} The maximal work

extractable from a crossbridge is a variable fraction of the free energy of ATP hydrolysis, which depends on the loading conditions.^{4),23)-26)} However, the sum of work and heat is constant on average, equal to the enthalpy change of ATP hydrolysis.^{4),11),23)-26)} The time-varying elasticity of muscle is considered to reflect the summation of the force-generating crossbridges whose number increases and decreases with contraction in the muscle.⁴⁾

In summary, it was shown that the Fenn effect cannot rule out all visco-elastic models. The only visco-elastic model that should be discarded is the new elastic body model, which is a visco-elastic model with an instant rise in elastance. The time-varying elastance model proposed for cardiac muscle, which is a visco-elastic model with a slow rise in elastance, cannot be rejected from the viewpoint of the unifying concept of the Fenn effect.

APPENDIX

Figure 4 shows a visco-elastic model. $E(t)$, $F(t)$, and $L(t)$ represent time functions of elastance, force, and length. The elastic element is assumed to be linear, i.e., Hookean. R is viscosity or resistance. $F_1(t)$ and $F_2(t)$ represent the force components of the elastance and the resistance as functions of time. The following formulation is possible;

$$\begin{aligned} F(t) &= F_1(t) + F_2(t) \\ F_1(t) &= E(t) \cdot [L(t) - L_0] \\ F_2(t) &= R \cdot dL(t)/dt \end{aligned}$$

where L_0 is the unstressed length of the elastic element, and $dL(t)/dt$ is the time derivative of $L(t)$.

These equations yield

$$F(t) = E(t) \cdot [L(t) - L_0] + R \cdot dL(t)/dt,$$

which can be modified to

$$dL(t)/dt = \{F(t) - E(t) \cdot [L(t) - L_0]\} / R \quad (\text{Eq. 1})$$

This ordinary differential equation indicates that, in the isometric contraction phase, $L(t)$ is a constant L_1 and hence $-dL(t)/dt$ is zero. Thus, $F(t) = E(t) \cdot (L_1 - L_0)$. Therefore, force is proportional

Fig. 4. A visco-elastic model. $E(t)$ is elastance as a function of time. R is viscosity. $F(t)$ is force. $L(t)$ is length. $F_2(t)$ is force component of the elastance. $F_2(t)$ is force component of the viscosity.

to the elastance.

In the new elastic body model, $E(t)=0$ until the time of stimulation and $E(t)$ jumps stepwise to a constant E_s on stimulation (Fig. 1A). The model is isometric when $F(t)$ increases stepwise on stimulation in proportion to $E(t)$. In the afterloaded isotonic contraction phase, $F(t)$ is set to a constant F_i . The solution of Eq. 1 is

$$L(t)-L_0 = A \cdot \exp[-(E_s/R) \cdot t] + F_i/E_s \quad (\text{Eq. 2})$$

where A is a constant. A can be determined so as to make $L(t)$ equal L_i at the onset of shortening. This is an exponential function of time, as shown in Fig. 1A.

In the visco-elastic model with a slow rise in $E(t)$ (Fig. 1B), $F(t)$ rises gradually in proportion to $E(t)$ in the isometric contraction phase, where $L(t)$ is set to a constant L_i . Then, $F(t)=E(t) \cdot (L_i-L_0)$. In the afterloaded isotonic contraction phase, $F(t)$ is a constant F_i and $L(t)$ shortens with increases in $E(t)$. The solution of Eq. 1 is

$$L(t)-L_0 = \exp[-(1/R) \int E(t)dt] \{ (F_i/R) \int \exp[(1/R) \int E(t)dt]dt + B \} \quad (\text{Eq. 3})$$

where t_i is the onset of isotonic shortening, and B is an integral constant, which can be determined so as to make $L(t)$ equal to L_i at the onset of shortening. Eq. 3 predicts quasiexponential shortening, similar to the curve shown in Fig. 1B.

When $R=0$ in the visco-elastic model, the model is similar to the time-varying elastance model used for cardiac muscle²⁷⁾ and the ventricle.²⁰⁾ $F(t)=F_i(t)=E(t) \cdot [L(t)-L_0]$ is the only equation. During the isometric contraction phase, the situation is the same and is independent of R . Namely, $F(t)=E(t) \cdot (L_i-L_0)$. During the afterloaded isotonic shortening phase, the situation is simpler without R than with R . Namely, $F(t)=F_i$ and $L(t)-L_0=F_i/E(t)$, as schematically shown in Fig. 1B.

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