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GENERALIZED MODEL OF A SKELETAL MUSCLE

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A new phenomenological model of a skeletal muscle consisting of a contractile and two nonlinear viscoelastic elements is proposed. The corresponding system of differential equations of the model is obtained, which allows one to derive time-dependent relations between the axial stress and the longitudinal strain in passive and activated states of the muscle. Methods for determining the viscoelastic and functional characteristics of the muscle as input parameters of the equations mentioned above are developed. These methods are based on the joint application of known experimental relations for a single muscle fiber and the results of muscle indentation in vivo on a "Miometer UT 98-01" device.

Introduction

Skeletal muscles in many respects determine the process of vital activities of the human organism as a whole. In this connection, one of the primary goals of biomechanics, and especially biomechanics of sports activity, is the prediction of the dynamic and kinematic parameters of functioning of the muscles. This problem can be solved only if maximum complete information about the mechanical and actuator properties of muscular tissues is available. However, the use of data obtained on prepared muscles does not allow one to describe the functioning of a muscle *in vivo* with an acceptable accuracy.

One of the most widespread experimental methods for studying the properties of skeletal muscles *in vivo* implies a dynamic indentation of the surface of human body in the region of the muscle to be examined. In the process of indentation, the penetration depth and speed of indenter, as well as the resistance force acting on it, are registered. In particular, a "Miometer UT 98-01" device [1], in an automatic regime, can determine the following mechanical parameters indirectly characterizing the viscoelastic properties of a muscle: (i) vibration frequency F (Hz) of indenter, (ii) the logarithmic damping decrement D

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of vibration of indenter, and (iii) rigidity Q (N/m), equal to the ratio between the maximum reaction force of biotissue and the maximum depth of indentation.

The above-mentioned parameters depend on the organs and biological tissues surrounding the muscle examined and interacting with it. Therefore, for a biomechanical analysis of skeletal muscles, with the use of the experimental data mentioned above, various assumptions and model representations have to be used. For example, in [2, 3], based on the conditional rigidity Q registered by a myometer, the Young's modulus of a skeletal muscle is calculated. This way of determination of Young's modulus implies the neglect of rigidity of the integumentary tissues surrounding the muscle. Moreover, the use of elastic modulus for characterizing a muscle is possible only within the framework of a simple phenomenological model. An adequate model of a real muscle has to be able to describe the anisotropy of its properties [4], the nonlinearity of its deformation, changes in its mechanical characteristics upon activation of a contractile function, and the effect of these factors on the activation process.

In [5], an interpretation of the change in myometric data in the conditions of cyclic loading upon performing a corresponding physical exercise is suggested. This interpretation is based on the representation of the muscle as a composite with a variable componental structure, when the process of fatigue is characterized by an increased volume content of some conditional "rigid" phase of the muscular tissue. A method for estimating the volume fraction of this phase according to readings of the "Miometer UT 98-01" device was developed.

However, in previous studies, the possibilities of using the viscoelastic characteristics obtained by the method of dynamic indentation have not been analyzed within the framework of a phenomenological model of functioning of a muscle. There are a number of conditions complicating the direct use of these characteristics.

1. The instantaneous Young's modulus determined by the results of dynamic indentation is the characteristic of a linearly elastic material. However, experimental diagrams of elongation of a skeletal muscle in a passive state are significantly nonlinear [6, 7].

2. Indentation of a muscle is carried out in the direction transverse to the orientation of its muscular monofibers. Particular features of the internal structure of a skeletal muscle are responsible for the anisotropy of its mechanical characteristics, i.e., considerable distinctions between the elastic moduli in the longitudinal and transverse directions.

3. The functional characteristics of a skeletal muscle are mainly determined from measurements of the speed of contraction of a muscle and the force generated [8], which affect not only the parameters of the actinomyosin interaction, but also the mechanical properties of the biomaterials forming the muscle. The determination and subsequent use of the viscoelastic characteristics are to be carried out with account of experimentally found laws of mutual influence of the deformational and functional properties of skeletal muscles.

- 3.1. The longitudinal rigidity of a muscle upon realization of the contractile function considerably (by two and more orders of magnitude) exceeds its rigidity in the passive state.

- 3.2. The character of dependence of the stationary speed of isotonic contraction on the load is the same for the majority of skeletal muscles of the human body [8], but the maximum speed of contraction and the maximum force are individual.

- 3.3. The viscoelastic properties of a muscle determined in its passive state do not significantly affect the process of force generation in isometric conditions, but determines the subsequent (after the completion of activation) relaxation of this force [6].

The purpose of the present investigation is perfection of the models of skeletal muscles for an adequate description of their mechanical properties and employment of the myometric data obtained by the method of dynamic contact indentation.

1. Phenomenological Model of a Muscle

As the basic mechanical parameters of functioning of a muscle, we take the conditional axial stress σ and the conditional longitudinal strain ε :

$$\sigma = P/S, \quad \varepsilon = \Delta L/L_0. \quad (1)$$

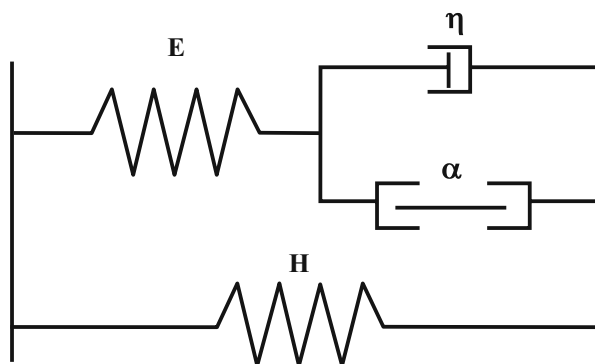


Fig. 1. Phenomenological model of muscle suggested in [9].

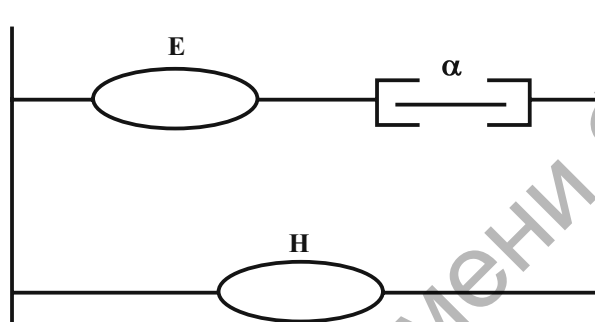


Fig. 2. Generalized viscoelastic model of muscle.

Here, P and S are the longitudinal force and the area of physiological cross section of the muscle, respectively, ΔL is the variation in muscle length, and L_0 is the length of the muscle in a stress-free state.

In [9], a phenomenological viscoelastic model of a skeletal muscle considered separately from the tendons connected to it is suggested. The model is shown in Fig. 1 and consists of two elastic (E and H), viscous (η), and contractile (α) elements. We have to agree that the model in view does not allow one to interpret some experimentally stated facts. For example, it is known that the rigidity of a “series” (relative to the contractile element) elastic element E greatly exceeds the rigidity of the muscle in a passive state [8]; a muscle in isometric conditions needs less time for generation of a maximum force than for the subsequent relaxation of this force [10].

In this connection, for describing the deformation of a skeletal muscle in a passive state and upon realization of its contractile function, it is reasonable to employ the “classical” [11] arrangement of elements in the model (Fig. 2). To widen the possibilities of the model, the “series” and “parallel” elastic elements are replaced by generalized nonlinearly viscoelastic ones.

Within the framework of the present study, for describing the functioning of the contractile element, we will use the “sliding-filament” hypothesis [8], according to which the axial stress σ_α in a single muscular fiber is determined by the relation $\sigma_\alpha = f(n - m + 2p)/S_l$. Here, n , m , and p are the numbers of “pulling,” “braking,” and “superpulling” actinomyosin transverse bridges, respectively, f is the force generated by one transverse bridge, and S_l is the cross-sectional area of an individual fiber. The quantities n , m , and p satisfy the following differential equations [12]:

at $v \leq 0$,

$$\begin{aligned} \dot{s} &= k_1 (\alpha - s - n - m - p) - k_4 s, \\ \dot{n} &= k_4 s - n \frac{|v|}{\delta}, \quad \dot{m} = -k_2 m + n \frac{|v|}{\delta}, \quad \dot{p} = -k_3 p; \end{aligned} \quad (2a)$$

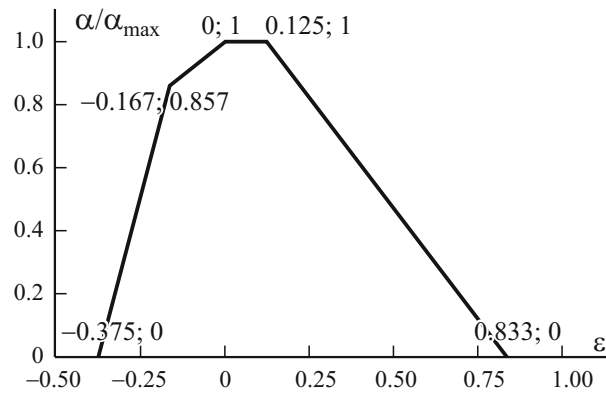


Fig. 3. Relative number of actinomyosin bridges on the half-length of sarcomere vs the longitudinal strain of muscle.

at $v > 0$,

$$\begin{aligned} \dot{s} &= k_1(\alpha - s - n - m - p) - k_4s, \\ \dot{n} &= k_4s - d_\delta n \frac{|v|}{\delta}, \quad \dot{m} = -k_2m, \quad \dot{p} = -k_3p + n \frac{|v|}{\delta}. \end{aligned} \quad (2b)$$

Here, s is the number of bridges in a passive state; v is the speed of relative sliding of actin and myosin filaments; α is the general number of bridges on the half-length of sarcomere; δ is the distance between the equilibrium locations of the pulling and braking bridges ($\delta = 8 \cdot 10^{-3} \mu\text{m}$); k_1 , k_2 , k_3 , and k_4 are the time constants of formation and break of the bridges. The quantity α depends on the current length of sarcomere [6] and, hence, on the strain ε . This relation depends on the inner structure of sarcomere and is described by a piecewise linear function (Fig. 3). Upon transition from an individual monofiber to the muscle as a whole, it is convenient to normalize the number of bridges to the quantity α_{\max} . In this case, $\alpha_{\max} = \alpha(0)$ is the maximum number of bridges corresponding to the stress-free state of the muscle. In what follows, without introduction of additional designations, the symbols s , n , m , and p will stand for the ratio between the number of corresponding actinomyosin bridges and the quantity α_{\max} . Then, the longitudinal stress in the contractile element can be calculated from the formula

$$\sigma_a = \frac{f\alpha_{\max}}{S_l}(n - m + 2p) = \frac{P_0}{S}(n - m + 2p) = \sigma_a(n - m + 2p), \quad (3)$$

where P_0 is the force generated by the muscle in isometric conditions at a zero initial strain and σ_a is the axial stress corresponding to this force.

The quantity σ_a is an analogue of the “absolute muscular force” [13] F_a (kgf/cm²) — $\sigma_a = 9.81 \cdot 10^4 F_a$, whose values for some muscles, borrowed from [14], are presented in Table 1. In addition, in the system of equations (2), the speed of relative sliding of filaments is replaced by the speed of longitudinal elongation of the contractile element

$$\dot{\varepsilon}_a = v \frac{2}{d} = \dot{\varepsilon} - \dot{\varepsilon}_E, \quad (4)$$

where d is the length of sarcomere ($d = 2.2 \mu\text{m}$); $\dot{\varepsilon}$ and $\dot{\varepsilon}_E$ are the strain rates of the muscle and the “series” viscoelastic element, respectively.

For describing the deformation of the nonlinearly viscoelastic elements **H** and **E** in the generalized model of muscle (see Fig. 2), we use the physical equations suggested in [15, 16], based on which the relation between the axial stress and time in the uniaxial stress state of the element can be written as

TABLE 1. Values of the Absolute Force of Skeletal Muscles [14]

Muscle	F_a , kgf/cm ²	σ_a , MPa
Gastrocnemius	5.9	0.58
Shoulder flexor	8.1	0.80
Neck extensor	9.0	0.88
Chewing muscle	10.0	0.98
Biceps muscle of arm	11.4	1.12
Brachial	12.1	1.19
Triceps muscle of arm	16.8	1.65

$$\sigma(t) = \frac{F}{S} = (1 + \varepsilon(t)) \left[T_1^y(t) - \frac{\gamma}{\tau} \int_0^t T_1^y(x) \exp\left(-\frac{t-x}{\tau}\right) dx \right]. \quad (5)$$

Here, σ is the engineering axial stress (the ratio between the longitudinal force and the initial cross-sectional area); ε is the longitudinal strain of the element; T_1^y is the nonzero component of the Piola–Kirchhoff tensor in the uniaxial stress state, which is determined neglecting viscosity of the element; γ and τ are viscoelastic parameters (the parameter τ corresponds to the relaxation time of the element).

Let us supplement Eq. (5) with the function of longitudinal strain $s(\varepsilon) = (1 + \varepsilon)T_1^y(\varepsilon)$. Then,

$$\sigma(t) = s(\varepsilon(t)) - \frac{\gamma}{\tau} \int_0^t s(\varepsilon(x)) \exp\left[-\frac{t-x}{\tau}\right] dx. \quad (6)$$

For the linearly viscoelastic element, the function $s(\varepsilon)$ is determined as $s(\varepsilon) = E\varepsilon$, where E is Young's modulus.

Differentiating equality (6) with respect to time, after subsequent mathematical transformations, we can write the equation for the viscoelastic element in the form

$$\dot{\sigma} + \frac{1}{\tau} \sigma = s'(\varepsilon) \dot{\varepsilon} + \frac{1-\gamma}{\tau} s(\varepsilon), \quad (7)$$

where $s'(\varepsilon) = \frac{ds}{d\varepsilon}$.

Combining the differential equations obtained for elements of the generalized model into a system, we come to relations between the axial stress σ and the longitudinal strain ε of the muscle modeled:

$$\begin{aligned} \dot{s} &= k_1 (z(\varepsilon - \varepsilon_E) - s - n - m - p) - k_4 s, \\ \dot{n} &= k_4 s - d_\delta n |\dot{\varepsilon} - \dot{\varepsilon}_E|, \quad \dot{m} = -k_2 m + d_\delta n |\dot{\varepsilon} - \dot{\varepsilon}_E|, \quad \dot{p} = -k_3 p, \\ \dot{\sigma} + \frac{\sigma}{\tau_H} - \sigma_a (\dot{n} - \dot{m} + 2\dot{p}) - \sigma_a \frac{n - m + 2p}{\tau_H} &= s'_H(\varepsilon) \dot{\varepsilon} + \frac{1-\gamma_H}{\tau_H} s_H(\varepsilon), \\ \sigma_a (\dot{n} - \dot{m} + 2\dot{p}) + \sigma_a \frac{n - m + 2p}{\tau_E} &= s'_E(\varepsilon) \dot{\varepsilon} + \frac{1-\gamma_E}{\tau_E} s_E(\varepsilon); \end{aligned} \quad (8a)$$

at $\dot{\varepsilon} \leq \dot{\varepsilon}_E$ and

$$\begin{aligned} \dot{s} &= k_1 (z(\varepsilon - \varepsilon_E) - s - n - m - p) - k_4 s, \\ \dot{n} &= k_4 s - d_\delta n |\dot{\varepsilon} - \dot{\varepsilon}_E|, \quad \dot{m} = -k_2 m, \quad \dot{p} = -k_3 p + d_\delta n |\dot{\varepsilon} - \dot{\varepsilon}_E|, \end{aligned}$$

$$\begin{aligned} \dot{\sigma} + \frac{\sigma}{\tau_H} - \sigma_a (\dot{n} - \dot{m} + 2\dot{p}) - \sigma_a \frac{n - m + 2p}{\tau_H} &= s'_H(\varepsilon) \dot{\varepsilon} + \frac{1 - \gamma_H}{\tau_H} s_H(\varepsilon), \\ \sigma_a (\dot{n} - \dot{m} + 2\dot{p}) + \sigma_a \frac{n - m + 2p}{\tau_E} &= s'_E(\varepsilon_E) \dot{\varepsilon}_E + \frac{1 - \gamma_E}{\tau_E} s_E(\varepsilon_E); \end{aligned} \quad (8b)$$

at $\dot{\varepsilon} > \dot{\varepsilon}_E$. Here, $z(\varepsilon) = \frac{\alpha(\varepsilon)}{\alpha_{\max}}$ is the relative number of actinomyosin bridges on the half-length of sarcomere (see Fig. 3); $s_E(\varepsilon_E)$, γ_E , and $\tau_E(s_H(\varepsilon_H), \gamma_H, \tau_H)$ are a function of longitudinal strain, a dimensionless parameter of the relaxation kernel, and the relaxation time of the elements **E** and **H**, respectively. In the system of equations (8), for brevity, the constant $d_\delta = \frac{d}{2\delta} = 137.5$ is introduced. For a given time function $\varepsilon(t)$, this system allows one to determine six functions of time — $\sigma(t)$, $\varepsilon_E(t)$, $s(t)$, $n(t)$, $m(t)$, and $p(t)$. At a given function $\sigma(t)$, the functions $\varepsilon(t)$, $\varepsilon_E(t)$, $s(t)$, $n(t)$, $m(t)$, and $p(t)$ can be found.

2. Determination of Viscoelastic Parameters of the Model

Element E. Experimental determination of parameters of the series (relative to the contractile one) viscoelastic element **E** is a rather complicated task [17]. Therefore, without reducing the generality of the model developed, we can assume that $\gamma_E = 0$ and $\tau_E \rightarrow \infty$. Then, for characterizing the element **E** in the model, it suffices to know the function $s_E(\varepsilon_E)$. In [8, 17], the following relation between the longitudinal force P acting on the elastic “series” element and the relative elongation ε of this element is given:

$$\frac{P}{P_0} = f_E(\varepsilon) = \begin{cases} 89,700\varepsilon^3 + 348\varepsilon^2 + 20\varepsilon, & \varepsilon \leq 0.0115, \\ 63.6\varepsilon - 0.319, & \varepsilon > 0.0115. \end{cases} \quad (9)$$

Normalization of the longitudinal force to the value of P_0 allows us to employ the function $f_E(\varepsilon)$ from (9), derived in [17] for the tailor’s muscle of frog, to model any skeletal muscle by using the relation

$$s_E(\varepsilon_E) = \sigma_a f_E(\varepsilon_E). \quad (10)$$

Element H. To determine the viscoelastic characteristics of the parallel element **H**, we use experimental data on the dynamic contact diagnostics of muscles, obtained on the “Miometer UT 98-01” device [1], and the identification technique described in [2, 5]. In [5], it is shown that the long-term elastic modulus E_1 of a muscle in transverse loading is negligibly small. The long-term E_1 and instantaneous E_0 elastic moduli are connected by the relation

$$E_1 = E_0(1 - \gamma). \quad (11)$$

Assuming that $\gamma = 1$, it is possible to obtain [2] rather simple relations connecting the relaxation time τ and the instantaneous elastic modulus of a muscle to the myometric parameters registered by the Miometer UT 98-01:

$$\tau = \frac{1}{2FD}, \quad E_0 = \frac{mF^2}{0.851\pi R} (4\pi^2 + D^2). \quad (12)$$

Here, $R = 1.5$ mm is the radius of the circular plane contact site of indenter and $m = 20$ g is its weight.

Relations (12) were used to analyze the results of myometric investigations performed at a scientific laboratory of physical training and sports of the Skorina Gomel State University on the above-mentioned “Miometer UT 98-01” device. Results of the measurements are presented in Table 2. An analysis of the data obtained makes it possible to conclude the following.

TABLE 2. Results of Myometric Investigations of Skeletal Muscles

Muscle	Passive state			Stressed state		
	F , Hz	D	Q , N/m	F , Hz	D	Q , N/m
Biceps muscle of arm	12.9	1.01	201	14.0	1.01	232
Long radial wrist extensor	14.7	0.88	200	17.4	1.25	340
Gastrocnemius	20.1	1.18	250	25.9	1.04	428
Tibial	18.3	0.82	292	22.9	0.80	449
Intermediate vastus muscle	13.2	1.05	206	16.6	1.01	344
Lateral vastus muscle	15.8	1.39	227	19.2	0.96	466

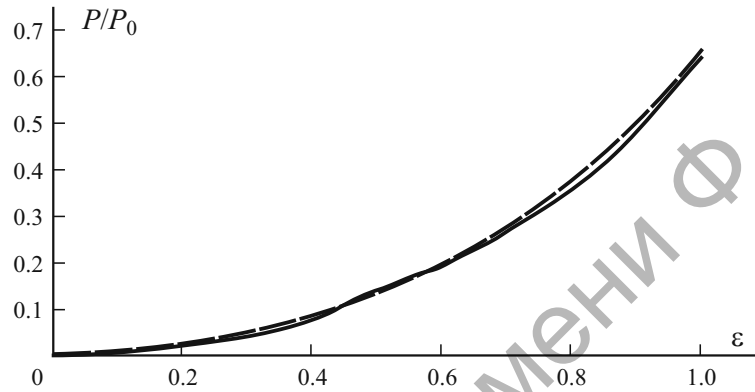


Fig. 4. Normalized longitudinal force P/P_0 in a muscle vs the longitudinal strain ε upon static deformation in a passive state. (—) — experimental diagram [6] and (---) — cubic approximation.

1. The values of viscoelastic characteristics of each muscle are individual.

2. At the greatest possible activation of the contractile function of a muscle in isometric conditions (transition to an active state), the instantaneous elastic modulus E_0 grows considerably, while the parameter τ changes less noticeably.

There are publications (see, for example, [6, 7, 15]) that contain experimental tension diagrams of isolated skeletal muscles and separate muscular fibers in a passive state. Figure 4 shows an experimental relation (borrowed from [6]) between the normalized longitudinal force P/P_0 and the longitudinal strain ε of an individual muscular monofiber, which can be approximated by the exponential function

$$\frac{P}{P_0} = f_H(\varepsilon) = 0.05[\exp(2.4\varepsilon) - 1]. \quad (13)$$

In approximation by the method of least squares, the average relative deviation of calculated values of the normalized longitudinal force from the corresponding experimental data in the range of deformations from 0 to 1 was 7.9%. We should note that, in the case of approximation of the function $f_H(\varepsilon)$ by a third-degree polynomial, the error was 10%.

The character of nonlinear deformation of a skeletal muscle, in many respects, is determined by its plumosity [18]. Further, we will consider only muscles formed by rectilinear monofibers of identical length (zero angle of plumosity). To characterize the element **H** of the generalized viscoelastic model of such muscles, function (13) can be used directly. The relation in Fig. 3 was obtained in static loading when the relative elongation under a load applied was measured after completion of the creep process. Therefore, the presence of the nonzero function $f_H(\varepsilon)$ does not allow one to use the assumption $\gamma_H = 1$ (neglect of the long-term elastic modulus) in the longitudinal direction, which was adopted in analyzing the results of transverse dynamic indentation [Eqs. (12)]. In addition, according to function (13), the initial ($\varepsilon = 0$) value of the long-term elastic modulus of muscle is determined by the relation

TABLE 3. Viscoelastic Characteristics of Skeletal Muscles

Muscle	Passive state		Active state	
	E_0 , kPa	τ , ms	E_0 , kPa	τ , ms
Biceps muscle of arm	33.61	38	39.59	35
Long radial wrist extensor	43.38	39	61.97	23
Gastrocnemius	82.35	21	135.69	19
Tibial	67.06	33	104.92	27
Intermediate vastus muscle	35.26	36	55.66	30
Lateral vastus muscle	51.56	23	74.28	27

$$E_{IL} = \sigma_a \left. \frac{df_H}{d\varepsilon} \right|_{\varepsilon=0} = 0.05 \cdot 2.4 \sigma_a = 0.12 \sigma_a. \quad (14)$$

Then, for the biceps muscle of arm, $E_{IL} = 134$ kPa, which is twofold greater than the instantaneous elastic modulus E_0 determined by the results of dynamic contact indentation (see Table 2). The impossibility of direct use of the quantity E_0 is caused both by the anisotropy of structure and properties of skeletal muscles and by the influence of deformability of the biotissues surrounding the muscles on the myometric parameters. To increase the informativeness of results of the calculation technique (12), a simplified structural model of a skeletal muscle is suggested, according to which the muscle is regarded as a circular cylinder weakened by continuous longitudinal holes. The material of the cylinder (further, matrix material) is nonlinearly viscoelastic. For the given material, we assume that the long-term elastic modulus is equal to zero ($\gamma_m = 1$). On the axis of each is hole located a continuous fiber whose diameter is smaller than that of the hole. Thus, upon transverse deformation, such a fiber does not contribute to the rigidity of the muscle. The material of the fiber is nonlinearly elastic ($\gamma_f = 0$, $\tau_f \rightarrow \infty$).

Using the known relations of composite mechanics for the effective initial instantaneous elastic modulus E_{0T} of the composite cylinder examined [19], it is possible to obtain the following equation

$$E_{0T} = E_{0m} \frac{2(1-c)}{2+3c}. \quad (15)$$

Here, E_{0m} is the initial instantaneous elastic modulus of matrix material and $c = S_0/S$ is the ratio of the total cross-sectional area of holes to the total cross-sectional area of the cylinder (physiological cross section). The effective longitudinal instantaneous E_{0L} and long-term E_{IL} elastic moduli are determined by the relations

$$E_{4;L} = E_f c_f, \quad E_{0L} = E_f c_f + E_{0m}(1-c). \quad (16)$$

Here, E_f is the initial elastic modulus of material of the fibers and $c_f = S_f/S$ is the ratio between the total cross-sectional area of fibers and the physiological cross section. To simplify further calculations, it is assumed that the modulus E_{0T} corresponds to the modulus E_0 determined by the method of dynamic contact indentation [relations (12)], $E_{0T} = E_0$. The long-term longitudinal elastic modulus is determined by Eq. (14). The instantaneous and long-term longitudinal moduli are connected by the relation

$$E_{0L} = \frac{E_{IL}}{1-\gamma_H}. \quad (17)$$

It is known [8] that, when a muscle is subjected to the action of a force $P = P_0$, activation of the contractile function does not lead to muscular contraction. Hence,

$$\sigma_a = s_H(\varepsilon_{\max}), \quad (18)$$

where ε_{\max} is the maximum relative elongation of a muscle at which the contractile function is realized. According to the data of Fig. 3, $\varepsilon_{\max} = 0.833$. Condition (18), with account of Eq. (17), makes it possible to find the parameter γ_H :

$$\gamma_H = 1 - f_H(\varepsilon_{\max}) = 0.681. \quad (19)$$

Using relations (14)-(16), we find that

$$c = \frac{2}{3} \left(\frac{0.12\sigma_a}{E_0} \frac{\gamma_H}{1-\gamma_H} - 1 \right). \quad (20)$$

Let us pass now from relations for the initial elastic moduli to a physical equation of form (6) for the element H:

$$\sigma_H(t) = \sigma_f(\varepsilon)c_f + (1-c)\sigma_m(t) = \sigma_a f_H(\varepsilon) + (1-c) \left[s_m(\varepsilon(t)) - \frac{1}{\tau_H} \int_0^t s_m(\varepsilon(x)) \exp\left(-\frac{t-x}{\tau_H}\right) dx \right]. \quad (21)$$

In this equation, it is assumed that, at static elongation, the stress in the composite cylinder depends only on fibers. The quantity τ_H in Eq. (21) coincides with the relaxation time τ determined by Eqs. (12). We assume that the nonlinear function $s_m(\varepsilon)$ for the matrix material in the model suggested is similar to the function $f_H(\varepsilon)$ and differs from it by a coefficient k , namely $s_m(\varepsilon) = k\sigma_a f_H(\varepsilon)$. The value of k is found from the condition

$$(1-c)k = \frac{\gamma_H}{1-\gamma_H}. \quad (22)$$

With account of Eq. (22), relation (21) takes the form

$$\sigma_H(t) = \frac{\sigma_a f_H(\varepsilon(t))}{1-\gamma_H} - \frac{\gamma_H}{\tau_H} \int_0^t \frac{\sigma_a f_H(\varepsilon(x))}{1-\gamma_H} \exp\left(-\frac{t-x}{\tau_H}\right) dx. \quad (23)$$

Here, the function $f_H(\varepsilon)$ results from approximation of experimental data and, for an individual muscular fiber, is described by Eq. (13). The parameter γ_H is specified by Eq. (19). The relaxation time τ_H is calculated by using myometric data [relations (12)].

The simplified mechanical model suggested here does not pretend to description of the real structure of muscular tissue, but serves for substantiation of relation (23).

3. Determination of the Functional Characteristics of a Muscle

The parameters k_1, k_2, k_3 , and k_4 , characterizing the rate of formation and break of actinomyosin bridges, are traditionally determined by approximating the experimental relationship between the stationary speed of isotonic contraction of the muscle v_s and the load P_s [8]. Within the framework of the generalized model suggested (see Fig. 2), the stationary isotonic contraction of the muscle is realized at the following conditions:

$$\begin{aligned} \dot{s} = \dot{n} = \dot{m} = \dot{p} = \dot{\sigma} = 0, \quad z(\varepsilon) = z(0) = 1, \quad s_E(\varepsilon_E) = s_E(0) = 0, \\ s_H(\varepsilon) = s_H(0) = 0, \quad \sigma = \text{const} = \sigma_s. \end{aligned} \quad (24)$$

In this case, the system of equations (8a) allows us to derive an expression for the relative load on the muscle:

$$\frac{P_s}{P_0} = \frac{b - v_s a_2}{b + v_s (1 + a_1)}. \quad (25)$$

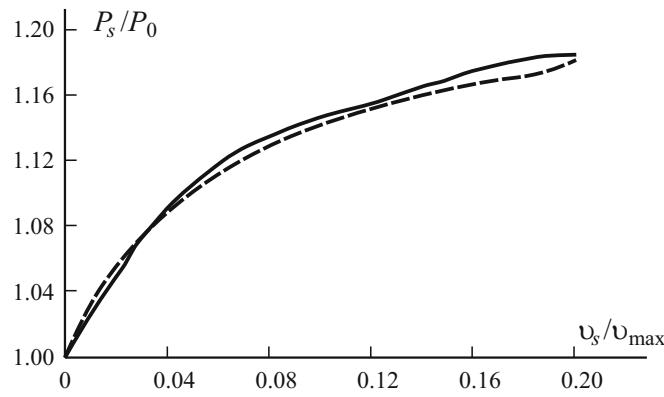


Fig. 5. Load on the muscle as a function of the stationary speed of eccentric isotonic contraction. (—) — experiment [21] and (---) — approximation (29) at $k_3 = 32 \text{ s}^{-1}$.

Here, the following designations are introduced:

$$b = \frac{k_1 k_2 L}{d_\delta (k_1 + k_2 + k_4)}, \quad a_1 = \frac{k_1 k_2 - k_4^2}{k_4 (k_1 + k_2 + k_4)}, \quad a_2 = \frac{k_1}{k_1 + k_2 + k_4}. \quad (26)$$

Representation of the function $P_s(v_s)$ in form (25) makes it possible to compare it with the refined Hill equation [12]:

$$(P_s + 0.16P_0 + 0.18P_s)v_s = b(P_0 - P_s) \Rightarrow \frac{P_s}{P_0} = \frac{b - v_s \cdot 0.16}{b + v_s(1 + 0.18)}. \quad (27)$$

Consequently, $a_1 = 0.18$ and $a_2 = 0.16$. The constant b in Eqs. (27) can be expressed in terms of the maximum speed of isotonic contraction v_{\max} , corresponding to $P_s = 0 - b = v_{\max} a_2$. Solving the system of equations (26), we have for the parameters k_1 , k_2 , and k_4

$$k_4 = \frac{v_{\max} a_2 d_\delta}{2L(1 + a_1 - a_2)} \left[1 - \frac{a_1}{a_2} + \sqrt{\left(1 + \frac{a_1}{a_2}\right)^2 + 4\left(\frac{1}{a_2} - 1\right)} \right] = 53.127 \frac{v_{\max}}{L}, \quad (28)$$

$$k_1 = \frac{a_2 L k_4^2}{v_{\max} a_2 d_\delta - a_1} = 36.31 \frac{v_{\max}}{L}, \quad k_2 = \frac{v_{\max} d_\delta}{L} = 137.5 \frac{v_{\max}}{L}.$$

As shown in [20], for an individual muscular fiber, at the maximum level of activity of the ATPase, the ratio v_{\max}/L is equal to 2.3 s^{-1} . Then, $k_1 = 83.513 \text{ s}^{-1}$, $k_2 = 316.25 \text{ s}^{-1}$, and $k_4 = 122.192 \text{ s}^{-1}$.

To determine the parameter k_3 , we have to consider the state of stationary elongation of the muscle in an active state under the action of a constant load exceeding P_0 (eccentric contraction [12]). Taking into account conditions (24) in system (8b), we can write for a relative load on the muscle

$$\frac{P_s}{P_0} = \frac{k_1 k_4 \left(k_3 + 2d_\delta \left(\frac{v_s}{v_{\max}} \right) \left(\frac{v_{\max}}{L} \right) \right)}{k_1 k_3 k_4 + d_\delta \left(\frac{v_s}{v_{\max}} \right) \left(\frac{v_{\max}}{L} \right) [(k_1 + k_4)k_3 + k_1 k_4]} + \left(\frac{v_s}{v_{\max}} \right) \left(\frac{v_{\max}}{L} \right) \frac{s'_H(0)\tau_H}{\sigma_\alpha} \quad (29)$$

In [21], an experimental relationship between the relative load on the muscle and the relative stationary speed of elongation of an individual muscular fiber is given (Fig. 5). Let us compare this experimental relation with function (29) at $k_1 = 83.513 \text{ s}^{-1}$, $k_4 = 122.192 \text{ s}^{-1}$, and $v_{\max}/L = 2.3 \text{ s}^{-1}$; $s'_H(0)/\sigma_\alpha = 0.12/(1 - \gamma_H) = 0.376$ and $\tau_H = 38 \text{ ms}$ (biceps). As a

result of approximation by the method of least squares, it is found that $k_3 = 32 \text{ s}^{-1}$, and the average relative deviation of values of the approximating function (29) from experimental values in the range v_s/v_{\max} from 0 to 0.2 is 0.4%.

Thus, in the generalized viscoelastic model of skeletal muscle suggested (see Fig. 2) and the corresponding mathematical model (8), the initial parameters are determined as follows. Deformation of the element **E** is described by relations (9) and (10) at $\gamma_E = 0$ and $\tau_E \rightarrow \infty$. The nonlinear viscoelastic behavior of the element **H** is defined by physical equation (23), where the function $f_H(\varepsilon)$ is found by approximation of the experimental diagram of static elongation of the muscle in a passive state. For a muscle formed by rectilinear fibers, the given function is described by expression (13). The parameter γ_H in Eq. (23) is found from condition (19).

The relaxation time τ_H can be determined using the data of dynamic contact indentation of the muscle *in vivo*, obtained by the Miometer UT 98-01 and Eq. (12). The deformation function $z(\varepsilon)$, describing the relation between the number of actinomyosin bridges involved and the length of sarcomere, is given in Fig. 3. The parameters k_1 , k_2 , and k_4 are related to the maximum speed of isotonic contraction of the muscle by formulas (28). After calculation of the values of k_1 , k_2 , and k_4 to determine the parameter k_3 , the relationship between the speed of stationary isotonic elongation and the load have to be approximated by function (29). The above-mentioned values of the parameters k_1 , k_2 , k_3 , and k_4 refer to a muscle formed by rectilinear fibers at the maximum level of activity of the ATPase.

Conclusions

It is shown that, within the frameworks of the generalized phenomenological and simplified structural models of skeletal muscles suggested, it is possible to interpret some experimentally established laws.

1. The mechanical characteristics of a muscle in passive and activated states differ considerably.
2. The force–elongation relation in longitudinal deformation of a muscle in a passive state is nonlinear.
3. Realization of the contractile function of a muscle under the action of a longitudinal load whose magnitude exceeds the force P_0 generated in isometric conditions at the natural length of the muscle is impossible.
4. The mechanical characteristics of muscles at which the longitudinal rigidity in tension significantly exceeds the rigidity in transverse compression are anisotropic.

Within the framework of the investigation performed here, results of the mathematical model (8) developed were not compared with data on the deformation of skeletal muscles in an organism. Such a comparison is complicated by the limited volume of experimental data and the necessity for an additional account of deformation of tendons in deriving calculated estimates. The employment and experimental approbation of the models suggested will be the subject of further investigations.

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