Medical Hypotheses 83 (2014) 6–10

Contents lists available at ScienceDirect

Medical Hypotheses

journal homepage: www.elsevier.com/locate/mehy

Muscle as a molecular machine for protecting joints and bones by absorbing mechanical impacts

Armen Sarvazyan [a], Oleg Rudenko [b], Salavat Aglyamov [c,*], Stanislav Emelianov [c]

[a] ARTANN Laboratories, Lambertville, NJ 08530, USA
[b] Department of Physics, Moscow State University, Vorob'evy Gory, Moscow 119992, Russia
[c] Department of Biomedical Engineering, University of Texas at Austin, Austin, TX 78712, USA

ARTICLE INFO

Article history:
Received 22 November 2013
Accepted 12 April 2014

ABSTRACT

We hypothesize that dissipation of mechanical energy of external impact to absorb mechanical shock is a fundamental function of skeletal muscle in addition to its primary function to convert chemical energy into mechanical energy. In physical systems, the common mechanism for absorbing mechanical shock is achieved with the use of both elastic and viscous elements and we hypothesize that the viscosity of the skeletal muscle is a variable parameter which can be voluntarily controlled by changing the tension of the contracting muscle. We further hypothesize that an ability of muscle to absorb shock has been an important factor in biological evolution, allowing the life to move from the ocean to land, from hydrodynamic to aerodynamic environment with dramatically different loading conditions for musculoskeletal system. The ability of muscle to redistribute the energy of mechanical shock in time and space and unload skeletal joints is of key importance in physical activities. We developed a mathematical model explaining the absorption of mechanical shock energy due to the increased viscosity of contracting skeletal muscles. The developed model, based on the classical theory of sliding filaments, demonstrates that the increased muscle viscosity is a result of the time delay (or phase shift) between the mechanical impact and the attachment/detachment of myosin heads to binding sites on the actin filaments. The increase in the contracted muscle's viscosity is time dependent. Since the forward and backward rate constants for binding the myosin heads to the actin filaments are on the order of 100 s^{-1}, the viscosity of the contracted muscle starts to significantly increase with an impact time greater than 0.01 s. The impact time is one of the key parameters in generating destructive stress in the colliding objects. In order to successfully dampen a short high power impact, muscles must first slow it down to engage the molecular mechanism of muscle viscosity. Muscle carries out two functions, acting first as a nonlinear spring to slow down impact and second as a viscous damper to absorb the impact. Exploring the ability of muscle to absorb mechanical shock may shed light to many problems of medical biomechanics and sports medicine. Currently there are no clinical devices for real-time quantitative assessment of viscoelastic properties of contracting muscles *in vivo*. Such assessment may be important for diagnosis and monitoring of treatment of various muscle disorders such as muscle dystrophy, motor neuron diseases, inflammatory and metabolic myopathies and many more.

Introduction

Any textbook on physiology states that the primary function of skeletal muscle is converting chemical energy into mechanical energy to generate motion and force. The second physiological function is generation of heat by shivering in cold conditions to contribute to the homeostasis of body temperature. We hypothesize that there is another important fundamental function of skeletal muscle, which to the best of our knowledge, missed the attention of physiologists and biomechanics researchers: dissipation of mechanical energy of external impacts to absorb mechanical shock. Ability of muscle to redistribute the energy of impact in time and space and unload skeletal joints is of key importance in physical activities, such as running, playing basketball and soccer, jumping and wrestling. The ability of skeletal muscles to eliminate harmful effects of mechanical shocks has been created by biological evolution to allow the living specious to move from the ocean to the earth, to enable the appearance of animals capable of running, jumping, hunting and fighting.

In physical systems, the common mechanism for absorbing mechanical shock is achieved with the use of viscous elements.

* Corresponding author. Tel.: +1 512 232 2892; fax: +1 512 471 0616.
E-mail address: aglyamov@utexas.edu (S. Aglyamov).

http://dx.doi.org/10.1016/j.mehy.2014.04.020
0306-9877/

Biological evolution created and implemented in the muscle an extremely efficient molecular mechanism of controlled viscosity for absorbing and dissipating mechanical impact. Quantitative assessment of muscle elasticity and viscosity will shed light to many problems of medical biomechanics and sports medicine.

Viscoelastic properties of skeletal muscle

Generation of motion and force is a major part of activities of animals and skeletal muscle comprises the largest single organ of the body (about 40% of the body mass in humans). Studies of muscle mechanical properties have played a pivotal role in the development of our understanding of muscle physiology [1,2], but surprisingly, unlike all technical materials used in man-made systems, there are little quantitative data on the viscoelastic parameters of passive and contracted muscle [3]. The available data are often contradictory. The published values of Young's modulus, E, of skeletal muscle vary in the range from 1 kPa to tens and even hundreds of kPa [4–19]. Much less is known about dynamic viscosity of the muscle. Studies on viscoelasticity of muscle have primarily focused on characterizing the elastic behavior, largely neglecting the viscous component.

Current techniques assessing mechanical function of muscles, such as myotonometry, dynamometry and ergometry are not designed for evaluation of tissue intrinsic elasticity and viscosity. Myotonometry evaluates muscle tonic parameters from mechanical impedance measurements and vibration tests of surface tissues. The data are semi-quantitative, not localized, and are subject to artifacts due to skin impedance. Dynamometry and ergometry measure muscle strength achievable by a subject under a test load. The data are not directly related to mechanical parameters. In the last couple of decades, after the technique of Elasticity Imaging has emerged [20], non-invasive *in vivo* evaluation of muscle mechanical properties became possible. The technique is based on externally or internally inducing vibration in the tissue and measuring resulting tissue motion using ultrasound or MRI. Elasticity imaging methods provided a possibility for evaluation of the elastic and viscous properties of a specified muscle site located at a certain depth within the body and assessment of dynamic changes of the viscoelastic properties during loading or other physiological tests. In the publication of Levinson et al. [21] muscle elasticity and viscosity in situ were evaluated by measuring propagation parameters of shear waves. Shear wave propagation in the biceps of a subject during sustained contractions has been investigated in both the transverse and axial (longitudinal fiber orientation) directions. It was shown that transverse viscosity of muscle is significantly greater than axial viscosity and that transverse viscosity increases dramatically with load to the point that propagation of shear waves in transverse direction is suppressed entirely at the loads over 0.8 kg. The authors do not provide quantitative data on the muscle viscosity but a rough estimate that can be made from the experimental data shows that the viscosity change accompanying muscle contraction is far greater than one order of magnitude. The quantitative assessment of the contracting muscle viscosity changes has been made in the work Kanai on imaging of the sound wavefront propagation along the heart wall [22]. It was estimated that during the cardiac cycle the viscosity of the myocardium changes from 0.1 kPa s to about 2.1 kPa s. Various aspects of muscle viscosity were discussed in the recent publications [10–19].

Muscle viscosity as a property necessary for absorbing mechanical shock

The impact time is one of the key parameters in generating destructive stress in the colliding objects. Viscosity is a property which helps to extend the impact time and absorb mechanical shock.The force F produced by an object with mass M moving with the velocity V is inversely proportional to the duration of the impact T: $F = MV/T$. Let us consider a few examples of impacts on the human body to estimate the scale of generated forces. When a soccer player redirects a ball's path using his head, the impact produces enormous forces. The duration of an impact can be estimated based on the equation for two colliding spheres [23]. For instance, the duration of impact of the ball moving with the speed of 30 m/s is of the order of 1 ms and the generated force is about $2{\cdot}10^4$ N which is equivalent to the static load of about 2 tons.

Obviously, the soccer player may slightly increase the impact time by pulling back his head in the beginning of the impact, but it will not be a significant reduction of forces affecting cervical vertebral bones. Without neck muscles to absorb the impact, the mechanical strength of atlas, the upper-most vertebra supporting and balancing the head, is far from sufficient to allow the soccer player to use his head for redirecting the ball.

A trained athlete may easily jump down a height of over 3 m without damaging his knee joints. Suppose that the mass of that athlete who jumps down a 3 m height is 80 kg and the distance that his center of gravity travels from the moment he touches the ground till complete stop is 20 cm (due to bending of his knee joints). It is easy to estimate that the resulting force affecting his menisci, the cartilage pads between the weight bearing joint surfaces of the femur and the tibia, will be over 1000 kg. The menisci may function as shock absorbers at moderate impacts such as those occurring during walking and running. But without major contributions of leg skeletal muscles to the shock absorption, the jumping down from 2 to 3 m height will hardly be possible. The knees of downhill skiers competing in slalom skiing receive repetitive impacts of hundreds of kg without any damage to the menisci because, as we hypothesize, they are protected by the unique viscosity characteristics of contracted skeletal muscles. Experts of oriental martial arts can break bricks and pieces of wood in two with their bare palms, without causing themselves any damage because of the ability of the contracted hand muscles to dissipate impact.

Skeletal muscle biomechanics; linear and nonlinear viscosity

The role of the viscoelastic parameters in the process of muscle contraction has been extensively studied although the studies have primarily focused on characterizing the elastic properties, mostly neglecting the viscosity. Typically, the viscosity is considered as a damping factor preventing the muscle to generate maximum possible contracting force [24–26]. Several theoretical estimations suggested that the role of viscous forces in muscle contraction is insignificant [1,27–29]. However, other evidences indicate that the viscous force for active muscle is an order of magnitude higher the calculated hydrodynamic force [24,30,31]. Moreover, it is shown that activated muscles display a significant viscosity [32–36] and a hydrodynamic viscous drag is comparable with the magnitude of the isometric contraction force [30].

The results of the relaxation experiments on frog skeletal muscle fibers showed that the increase of internal viscosity is present in fully activated muscle fibers [32,34,35]. It was shown also that viscosity increases nonlinearly during activation. Based on comparison between relaxed and activated fibers, Cecchi et al. suggested that active and passive viscosities in the fiber have different mechanisms, in particular, the viscosity of the active fiber is due to the cross-bridge mechanism of the muscle contraction [32,34]. Estimation of the viscoelastic parameters of the human forearm *in vivo* based on the impedance measurements demonstrated significant viscosity increase in the low frequency range (less than 20 Hz) [33]. On the other hand, the measurements of the shear wave propagation in human skeletal muscles *in vivo* showed that shear viscosity weakly increased for contracted muscles in comparison with relaxed ones [10,15,16,19]. It is likely that the difference in fast and slow viscoelastic responses may be explained by different biomechanical processes in the contracted muscle.

Fast muscle response to external mechanical load is defined by elastic and inertial reactions, when energy applied to muscle is stored and redistributed in time and space using the mechanism of shear wave propagation [37]. While for high frequency excitation damping is a result of fast molecular transitions, for low frequency it is defined by the temporal relationship between the mechanical impact and the attachment/detachment of myosin heads to binding sites on the actin filaments [38]. Therefore, the viscoelastic response of muscle to external load cannot be fully characterized using only one strain rate, and is required a multi-scaled approach.

Standard tests to measure material viscosity are relaxation and creep tests, when material is characterized through its response to abruptly applied stress or loading state [39]. Relaxation and creep tests provide information about low frequency muscle response, while the measurement of shear wave propagation permits to assess the viscous properties of muscle for high frequencies.

Classical mechanical model of muscle introduced by Hill includes a contractile component in series with an elastic component both in parallel with an elastic component [40]. To describe multiple decay rates in relaxation tests, the Hill model has been adapted to include additional viscous and elastic components, where muscle viscosity is usually modeled as linear [41–43]. Even when hyperelastic models are used to model skeletal muscle mechanics the contribution of viscosity is usually neglected or considered as linear [44]. In nonlinear viscoelastic models the viscosity is considered as a function of strain and strain rate to represent highly nonlinear viscous behavior of the muscle [24,45]. Meyer et al. described pseudoplastic model of passive muscle viscosity and demonstrated that this model is better able to represent stress relaxation in the mouse muscle fiber than the 3rd order Hill and quasi-linear viscoelastic models [45].

In opposite to quasi-static case, where muscle demonstrates complicated behavior with time, in the case of shear wave propagation, usually standard viscoelastic model of a Voigt body is considered. In addition, the measurement of the shear wave propagation along and orthogonal to muscle fibers gives opportunity to assess the muscle anisotropy both for elastic and viscous processes [10,15,16,19]. For example, anisotropic mechanical properties were characterized for the brachialis muscle *in vivo* using a supersonic shear imaging technique [16]. While significant increase in elastic modulus was demonstrated along fibers, orthogonally, both viscous and elastic modulus showed no significant changes.

Earlier we developed a mathematical model [38] explaining the absorption of mechanical shock energy due to the increased viscosity of contracting skeletal muscle. Possible mechanism of dependence of the muscle hydrodynamic "transversal viscosity" on the contraction level can be qualitatively explained by a model of parallel strings submerged into a viscous medium and subjected to variable tension. The strings of this model may be interpreted as myofibrils or actin and myosin filaments of striated muscle. When such system is subjected to a transversal impact in the absence of tension of the strings, the strings move together with surrounding medium. With increasing tension the mobility of strings decreases and the impact displaces the medium relative to the strings. The raise of the viscosity is the result of the friction caused by the relative motion of strings and the medium.

Molecular mechanism of "axial viscosity"

The frequency spectrum of the external load could be wide and include both high (up to tens of kHz) and low frequencies (tens and hundreds of Hz). The mechanism of the damping of the high frequencies is defined by elastic conformational transformations of macromolecules and spatial redistribution of the energy through shear wave propagation. Transformation of macromolecules under shock wave absorbs the energy and then returns it to the system with delay damping the shock wave. Molecular viscosity increases the duration of the shock front and, as a result, its traumatic effect decreases.

Low frequency components of the external load are attenuated due to actin–myosin bridges association/dissociation dynamics in the contracted muscle [38]. The actomyosin complex is an efficient chemical-to-mechanical ATP energy converter [46]. Pairs of actin and myosin filaments are parallel. They are only capable of interacting through cross-bridges which reside in a regular manner on myosin filaments.

According to the "sliding filament model" introduced by Huxley on the basis of electron microscopy studies, each cross-bridge can be in one of two states: an attached state in which cross-bridge is attached to actin and a detached state [1]. The bridge works cyclically: in attached state it develops force in a certain interval of the relative filament motion, and then detaches. In the contracting muscle, the attached bridges produce a pulling force.

Descherevski proposed a model of muscle dynamics based on the following assumptions [47]. Formation of the actin–myosin bond results in developing a force which causes the point of connection between the bridge and actin to slide along the myosin filament. As the sliding continues, the force developed by the cross-bridge passes through zero and, becomes negative, because the pulling cross-bridge turns into a braking one. The braking bridge opens and immediately returns to the initial state.

We considered a generalization of the model of Descherevski that describes the controlled shock dissipation mechanisms [38]. Consider the oscillatory stress applied at some frequency to the muscle under isometric tension. Time delay between the external load and the attachment/detachment of myosin heads to binding sites on the actin filaments results in wave attenuation, and dynamic viscosity in this case can be expressed as a function of the rates at which the cross-bridges attach and detach, and the frequency of oscillations [38].

For low frequencies (below 10 Hz) the viscosity increases with the static muscle tension, while for high frequencies (above 100 Hz) viscosity is inversely proportional to the square of frequency.

At high frequencies, cross-bridges are no longer capable of following the rapidly oscillating load and the damping mechanism described above disappears. Viscosity is a result of the finite times at which the cross-bridges attach and detach. If the cross-bridges attach and detach instantly, viscosity related to the cross-bridges dynamics becomes zero.

Functional aspects of the muscle viscosity and medical significance of the studies aiming at understanding its mechanisms

Since muscle contraction can cause a pulling action but not a pushing action, even the simplest movement, therefore, requires two muscles: agonist and antagonist (flexor and extensor, one muscle to bend a joint and a separate one to straighten it out again). It is believed that when an agonist contracts, in order to cause the desired motion, the antagonists should relax. However, the situation could be not as simple. To effectively implement the function of the muscle related to the absorbing mechanical impact, it would be natural to use simultaneously both agonist and antagonists muscle in that process. Moreover, possibility to redistribute the mechanical impact in space will improve the effectiveness of absorbing the impact, therefore this couple of muscle which was called "agonist" and "antagonist" should work together and are no more "antagonistic".

Another important issue to mention is on the possible role of nervous system in controlling the contraction of agonists and antagonists to optimize the process of transforming mechanical energy into heat.

Quantitative assessment of muscle elasticity and viscosity will shed light to many problems of medical biomechanics and sports medicine.

Exploring these proposed concepts may open new areas of investigation of muscle physiology and pathology. The list of muscle disorders that can be assessed by devices for quantitative assessment of muscle viscosity and elasticity includes muscle dystrophy, motor neuron diseases, inflammatory and metabolic myopathies and many more. The fields of potential applications of such devices include:

(1) General clinical applications: diagnosis and monitoring of muscle condition in different types of pathology associated with muscle atrophy and dystrophy in neuralgic diseases, myopathies, immobilization, etc.;
(2) Rehabilitation and occupational medicine;
(3) Sports medicine: assessment of muscle condition and performance in athletes;
(4) Gerontology: assessment of muscle changes in aging, particularly following total weakening of musculoskeletal system during osteoporosis and osteoarthritis, estimation of the prophylactics efficacy.

Numerous questions arise regarding the role of controlled muscle viscosity in the development of various diseases. Is the development of osteoporosis the only reason for the increased probability of bone fracture in elderly people? In addition to reduction of bone density, could a decrease in the effectiveness of the muscular impact defense system be responsible for broken bones? If so, are the age related changes in the viscosity characteristics of muscle and simply decreased muscle mass contributing significantly to the probability of bone fracture? Is a slowing brain, less able to direct muscular viscosity, also to blame? Could the improper use of muscles be one cause of joint diseases, such as tendonitis, bursitis and osteoarthritis, and could a joint problem be anticipated by monitoring muscle viscosity?

Investigation of the mechanisms of voluntary controlled viscosity of skeletal muscle could also be important for non-medical fields such as robotics. In creating anthropomorphic robots it is necessary to carefully study the lessons of biological evolution. To protect the skeletal system of robots from shocks and the resulting damage, it might be necessary to mimic the means implemented in living systems.

Conflict of interest statement

None.

Acknowledgment

This work was supported by NIH – United States Grant R21AR065024.

References

[1] Huxley AF. The activation of striated muscle and its mechanical response. Proc R Soc Lond Biol 1971;178(50):1–27 [Review].
[2] Schoenberg M, Wells JB, Podolsky RJ. Muscle compliance and the longitudinal transmission of mechanical impulses. J Gen Physiol 1974;64(6):623–42.
[3] Sarvazyan A. Elastic properties of soft tissues [Review]. In: Levy, Bass, Stern, editors. Handbook of elastic properties of solids, liquids and gases, vol. 3. Academic Press; 2001. p. 107–27 [Chapter 5].
[4] Madsen EL, Sathoff HJ, Zagzebski JA. Ultrasonic shear wave properties of soft tissues and tissue like materials. J Acoust Soc Am 1983;74:1346–55.
[5] Krouskop TA, Dougherty DR, Vinson FS. A pulsed Doppler ultrasonic system for making noninvasive measurements of the mechanical properties of soft tissue. J Rehabil Res Dev 1987;24(2):1–8.
[6] Levinson SF, Shinagawa M, Sato T. Sonoelastic determination of human skeletal muscle elasticity. J Biomech 1995;28:1145–54.
[7] Chen EJ, Novakofski J, Jenkins WK, O'Brien WD. Young's modulus measurements of soft tissues and application to elasticity imaging. IEEE Trans Ultrason Ferroelectr Freq Control 1996;42:191–4.
[8] Basford JR, Jenkyn TR, Kai-Nan A, Ehman RL, Heers G, Kaufman KR. Evaluation of healthy and diseased muscle with magnetic resonance elastography. Arch Phys Med Rehabil 2002;83(11):1530–6.
[9] Ringleb SI, Bensamoun SF, Chen Q, Manduca A, An KN, Ehman RL. Applications of magnetic resonance elastography to healthy and pathologic skeletal muscle. J Magn Reson Imaging 2007;25(2):301–9.
[10] Hoyt K, Kneezel T, Castaneda B, Parker KJ. Quantitative sonoelastography for the in vivo assessment of skeletal muscle viscoelasticity. Phys Med Biol 2008;53(15):4063–80.
[11] Chen S, Urban MW, Pislaru C, Kinnick R, Zheng Y, Yao A, et al. Shearwave dispersion ultrasound vibrometry (SDUV) for measuring tissue elasticity and viscosity. IEEE Trans Ultrason Ferroelectr Freq Control 2009;56:55–62.
[12] Urban MW, Greenleaf JF. A Kramers–Kronig-based quality factor for shear wave propagation in soft tissue. Phys Med Biol 2009;54:5919–33.
[13] Urban MW, Chen S, Greenleaf JF. Error in estimates of tissue material properties from shear wave dispersion ultrasound vibrometry. IEEE Trans Ultrason Ferroelectr Freq Control 2009;56:748–58.
[14] Deffieux T, Montaldo G, Tanter M, Fink M. Shear wave spectroscopy for in vivo quantification of human soft tissues visco-elasticity. IEEE Trans Med Imaging 2009;28:313–22.
[15] Klatt D, Papazoglou S, Braun J, Sack I. Viscoelasticity-based MR elastography of skeletal muscle. Phys Med Biol 2010;55(21):6445–59.
[16] Gennisson J-L, Deffieux T, Macé E, Montaldo G, Fink M, Tanter M. Viscoelastic and anisotropic mechanical properties of in vivo muscle tissue assessed by supersonic shear imaging. Ultrasound Med Biol 2010;36:789–801.
[17] Scola MR, Baggesen LM, Gallippi CM. Multi-push (MP) acoustic radiation force (ARF) ultrasound for assessing tissue viscoelasticity, in vivo. Conf Proc IEEE Eng Med Biol Soc 2012:2323–6.
[18] Song P, Chen S, Chen Q, Greenleaf JF, An KN. Validation of shear wave elastography in skeletal muscle. J Biomech 2013;46(14):2381–7.
[19] Debernard L, Leclerc GE, Robert L, Bensamoun SF. In vivo characterization of the muscle viscoelasticity in passive and active conditions using multifrequency MR elastography. J Musculoskelet Res 2013;16(2):1350008.
[20] Sarvazyan A, Hall TJ, Urban MW, Fatemi M, Aglyamov SR, Garra BS. An overview of elastography – an emerging branch of medical Imaging. Curr Med Imaging Rev 2011;7(4):255–82.
[21] Levinson S, Catheline S, Fink M. Anisotropic elasticity & viscosity deduced from supersonic shear imaging in muscle. Annual report, Rochester Center for Biomedical Ultrasound; 2004. p. 17.
[22] Kanai H. Viscoelasticity measurement of heart wall in in vivo. Conf Proc IEEE Ultrason Symposium 2003;1:482–5.
[23] Landau LD, Lifshitz EM. Theory of elasticity. New York: Pergamon; 1986.
[24] Martin A, Martin L, Morion B. Theoretical and experimental behaviour of the muscle viscosity coefficient during maximal concentric actions. Eur J Appl Physiol Occup Physiol 1994;69:539–44.
[25] Chase PB, Denkinger TM, Kushmerick MJ. Effect of viscosity on mechanics of single, skinned fibers from rabbit psoas muscle. Biophys J 1998;74:1428–38.
[26] Grazi E, Bona CD. Viscosity as an inseparable partner of muscle contraction. J Theor Biol 2006;242:853–61.
[27] Rieser P. The protoplasmic viscosity of muscle. Protoplasma 1949;39(1):95–8.
[28] Schoenberg M. Equilibrium muscle cross-bridge behaviour. Theoretical considerations. Biophys J 1985;48:467–75.
[29] Tawada K, Sekimoto K. A physical model of ATP-induced actin–myosin movement in vitro. Biophys J 1991;59(2):343–56.
[30] Elliott GF, Worthington CR. Muscle contraction: viscous-like frictional forces and the impulsive model. Int J Biol Macromol 2001;29:213–8.
[31] Grazi E. Experimental basis of the hypotheses on the mechanism of skeletal muscle contraction. Muscles Ligaments Tendons J 2011;1:77–84.
[32] Cecchi G, Bagni MA, Cecchini E, Colombini B, Colomo F. Crossbridge viscosity in activated frog muscle fibres. Biophys Chem 1997;68:1–8.
[33] Skovoroda AR, Aglyamov SR. Determination of mechanical properties of multilayer viscoelastic media based on impedance measurements. Biophysics (Pergamon) 1998;43:327–32.
[34] Bagni MA, Cecchi G, Cecchi E, Colombini B, Colomo F. Force responses to fast ramp stretches in stimulated frog skeletal muscle fibres. J Muscle Res Cell Motil 1998;19:33–42.

[35] Bagni MA, Cecchi E, Colombini B, Colomo F. Mechanical properties of frog muscle fibres at rest and during twitch contraction. J Electromyogr Kinesiol 1999;9:77–86.
[36] Sabra KG, Konti S, Roux P, Kuperman WA. Passive in vivo elastography from skeletal muscle noise. Appl Phys Lett 2007;90:194101.
[37] Sarvazyan AP, Rudenko OV, Swanson SD, Fowlkes JB, Emelianov SY. Shear wave elasticity imaging: a new ultrasonic technology of medical diagnostics. Ultrasound Med Biol 1998;24(9):1419–35.
[38] Rudenko OV, Sarvazyan AP. Wave biomechanics of the skeletal muscle. Acoust Phys 2006;52:720–32.
[39] Christensen RM. Theory of viscoelasticity. An introduction. New York and London: Academic Press; 1971.
[40] Hill AV. The heat of shortening and the dynamic constants of muscle. Proc R Soc B 1938;126:612–745.
[41] Taylor DC, Dalton JD, Seaber AV, Garrett WE. Viscoelastic properties of muscle-tendon units. Am J Sports Med 1990;18(3):300–9.
[42] Anderson J, Lib Z, Goubel F. Models of skeletal muscle to explain the increase in passive stiffness in desmin knockout muscle. J Biomech 2002;35:1315–24.
[43] Tamura Y, Ito A, Cresswell AG. A systematic muscle model covering regions from the fast ramp stretches in the muscle fibres to the relatively slow stretches in the human triceps surae. Comput Methods Biomech Biomed Eng 2013;790016:1–10. http://dx.doi.org/10.1080/10255842.2013.
[44] Lu YT, Zhu HX, Richmond S, Middleton J. A visco-hyperelastic model for skeletal muscle tissue under high strain rates. J Biomech 2010;43:2629–32.
[45] Meyer GA, McCulloch AD, Lieber RL. A nonlinear model of passive muscle viscosity. J Biomech Eng 2011;133:09100.
[46] Volkenshtein MV. Biophysics. Moscow: Nauka; 1988.
[47] Descherevski VI. Mathematical models of muscle contraction. Moscow: Nauka; 1977 [in Russian].