Proc. Estonian Acad. Sci. Eng., 1999, 5, 4, 312–321
https://doi.org/10.3176/eng.1999.4.06

ESTIMATION OF SKELETAL MUSCLE ELASTICITY ON SUBTONIC TENSION LEVEL

Arved VAIN

Institute of Experimental Physics and Technology, University of Tartu, Tähe 4, 51010 Tartu, Estonia; vain@physic.ut.ee

Received 14 December 1998, in revised form 5 February 1999

Abstract. On the elasticity of the skeletal muscle depend the prevention of muscle traumas as well as the economy of energy consumption in the process of active movements and posture maintenance by the muscular tone. The aim of this study is to establish the elastic properties of skeletal muscles in the state of subtonic tension. The experiments were carried out on specimens of *m.triceps surae* of rabbits. The load was steadily increased from the initial load for 10 N in 20 s and after that steadily decreased to the initial load in 20 s. During the loading cycle the oscillation frequency and logarithmic decrement were recorded at one-second intervals using a myometer. The loading cycle with steady increase and decrease of the load was repeated for several initial loads. In the two first stages of our experiment, 10 and 20% of the strength of the specimens was used. In these two cases the restoration of the initial frequency and logarithmic decrement of the natural oscillation of the specimen were the fullest in comparison with the other cases (initial loads 32 and 42 N). We can conclude that the passive elasticity of the skeletal muscles is apparent in the process of loading the muscles up to 20% of their tensile strength.

Key words: skeletal muscle, muscle elasticity, muscle tone, myometry.

1. INTRODUCTION

Basic functions of skeletal muscles are the realization of body movements, posture maintenance via muscular tone, and the production of thermal energy necessary to maintain the inner temperature of the body. These functions are performed via functional properties of muscles: excitability, contractility, extensibility and elasticity [1]. Of these properties in recent years less attention has been paid to elasticity, although it had already evoked the interest of the 19th century scientists [2–4]. The ability of the skeletal muscle to restore its initial shape after termination of the influence of external or contractile forces is determined by elasticity of the skeletal muscle. So the conditions for metabolic processes in the muscle depend on the muscle initial shape restoration velocity, i.e., muscle elasticity. Today the object of scientific discussion is: which morphological structures of muscles are used to realize its elasticity [5,6].

According to the muscle model by Hill, tendons of contracted muscles play an important part in the process of the mechanical elastic energy recuperation. But the data published by Tillmann and Töndury [7] show that the elastic compliance of a tendon cannot be more than about 2% of its length. This fact shows that tendons can not perform a very significant part in the mechanical elastic energy recuperation process of the muscle. The elastic deformation of the parallel elastic elements takes place only if the stiffness of endo-, peri-, and epimyseum is small. When the force created by the muscle increases, these structures loose their compliance [8].

In the muscle model by Hill we do not find the third filament of the sarcomere – the titin. Investigations of recent years concerning the position of titin filaments [9] and their elastic properties in skeletal muscles [10,11] make it possible to conclude that titin filaments can play a significant part in the elastic properties of skeletal muscles. In case of the muscle model by Hill the elastic morphological structure of an active muscle includes only the myosin cross-bridges and in case of the same muscle in the state of tonic tension only the helica of collagen fibres situated in endo-, peri-, and epimyseum of the muscle.

A new approach to understanding of the essence of the elasticity of skeletal muscles is made possible by a new biomechanical model of the skeletal muscle [12,13]. In accordance with this model, the mechanical tension in muscles is evoked by the radial pressure of myosin cross-bridges in the collagen network of endo-, peri-, and epimyseum of the muscle, which passes directly over into tendons. As the collagen fibres in above-mentioned structures are crimped, elastic deformations of the crimps occur on a large scale and also the stiffness can change for several times. In case the muscular tone is abnormally high, elements of the muscle collagen network are less crimped and the ability of the muscle to accumulate the energy of elasticity is decreased. In accordance with the new model of the skeletal muscle the titin filaments are situated in sarcomere in such a way that one end of the filament is fixed in a Z-disc and it can be assumed that its head lies behind the M-line, so that in the process of the radial pressure of myosin cross-bridges or preceding stretching out the muscle, the heads of titin filaments are fixed in sarcomere. As a result of this, in the process of stretching the muscle the mechanical energy of elasticity, stored by the elastic part of titin filaments, is added to the energy of elasticity of collagen fibres [14]. The aim of this study is to establish the elastic properties of skeletal muscles on subtonic tension level.

2. MATERIALS AND THE METHOD

The experiments were carried out on ten specimens of *m.triceps surae* of rabbits. Before stepwise loading, the specimens were submitted to an electro-stimulation procedure under an initial load of 2 N, consisting of repeated 1 s long contractions with interval of 1 s. The procedure was applied up to the moment, when the specimen ceased to react with contraction to the electrostimulation. In this way the elasticity of myosin cross-bridges was eliminated. Now the load was steadily increased for 9.8 N in 20 s and after that decreased to the initial load in 20 s (Fig. 1). During the loading cycle, using the displacement probe, changes in the length of the specimen were recorded. Changes in the perimeter of the specimen were recorded with the perimeter probe. Analogue signals of the displacement and perimeter probe were transmitted synchronously to PC via DAQ Card^{TM}-700 using digitization at 10 Hz. The frequency and logarithmic decrement of the natural oscillation of the muscle were recorded using a myometer at one-second intervals. Myometer is an original device designed and constructed at the University of Tartu [15]. The principle of its functioning lies in giving the muscle under investigation a dosed mechanical impact via special myometric pickup and recording the mechanical response of the muscle by an acceleration transducer (Fig. 2). The frequency of the natural oscillation of the muscle characterizes the stiffness (tone) of the muscular tissue. The logarithmic decrement of the oscillation Θ characterizes the ability of the muscle to dissipate mechanical energy:

$$\Theta = \ln\left(\frac{a_1}{a_3}\right).$$

The more elastic the muscle, the less the value of the logarithmic decrement Θ.

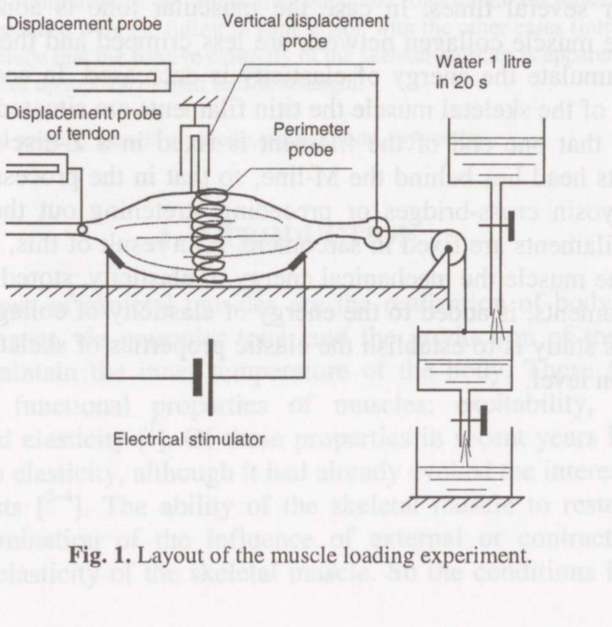

Fig. 1. Layout of the muscle loading experiment.

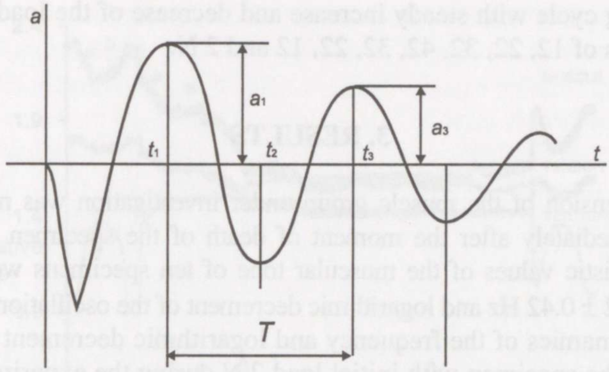

Fig. 2. Dependence of the myometric pickup acceleration *a* on time.

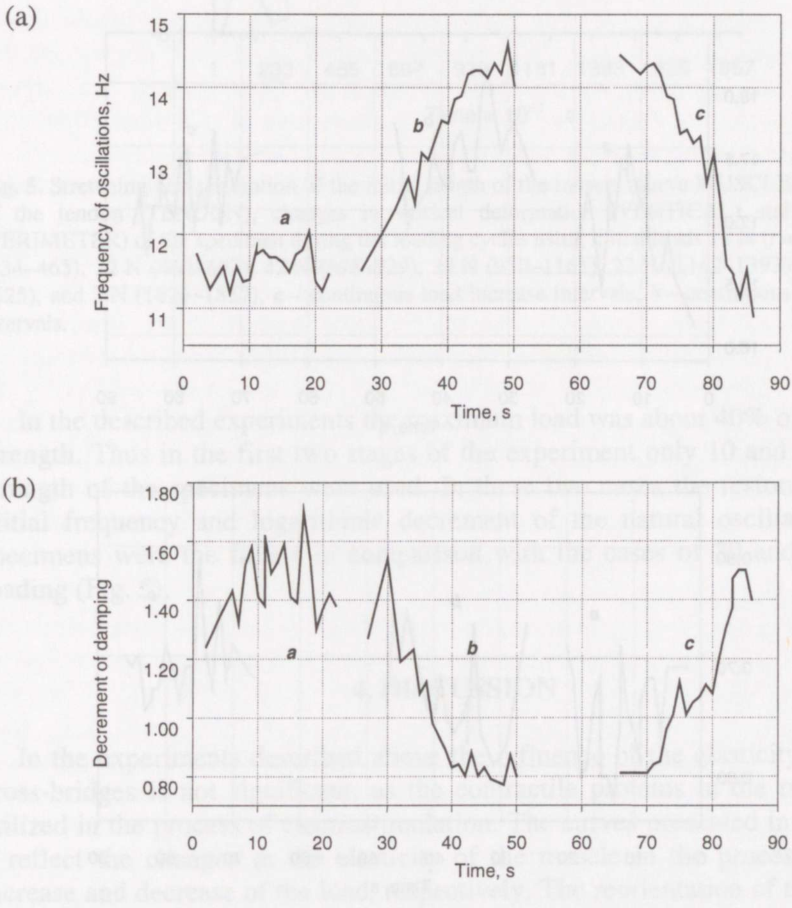

Fig. 3. Frequency (a) and logarithmic decrement of damping (b) of the natural oscillations of the sample in case of the initial load of 2 N: ***a*** – constant initial load 2 N; ***b*** – steady load increase up to 12 N; ***c*** – steady load decrease to the initial load 2 N.

The loading cycle with steady increase and decrease of the load was repeated for initial loads of 12, 22, 32, 42, 32, 22, 12 and 2 N.

3. RESULTS

The tonic tension of the muscle group under investigation was measured using myometer immediately after the moment of death of the specimen. The averaged mean characteristic values of the muscular tone of ten specimens were: oscillation frequency 15.92 ± 0.42 Hz and logarithmic decrement of the oscillation 1.13 ± 0.11.

In Fig. 3 dynamics of the frequency and logarithmic decrement of the natural oscillation of the specimen with initial load 2 N during the experiment is shown. In Fig. 4 is presented the case when the initial load of the muscle under investigation was 32 N.

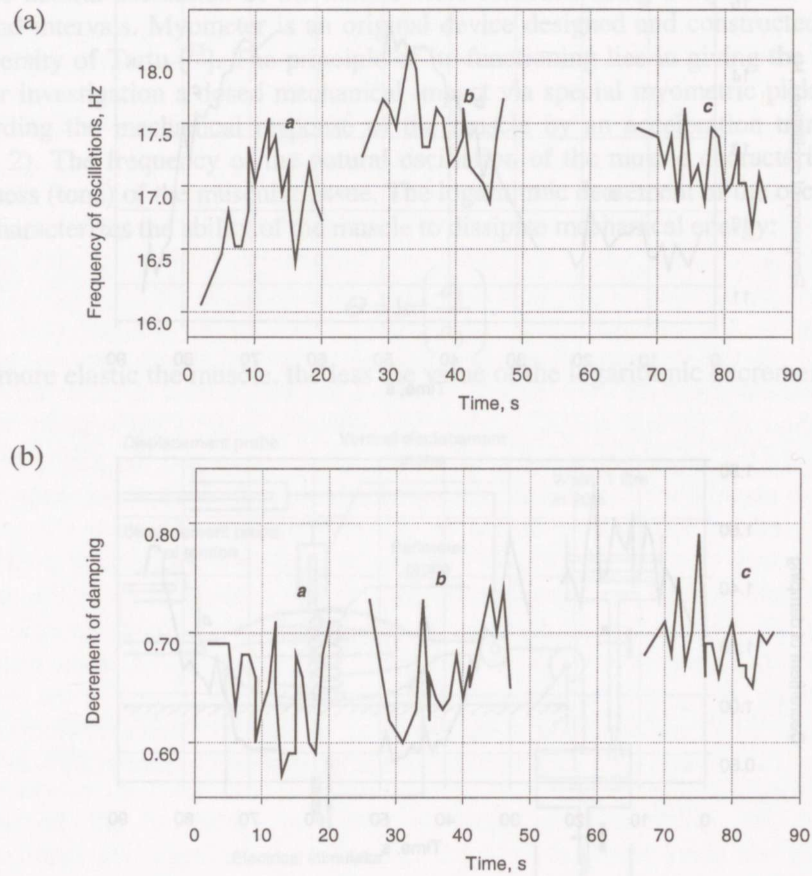

Fig. 4. Frequency (a) and logarithmic decrement of damping (b) of the natural oscillations of the sample in case of initial load 32 N: ***a*** – constant initial load 32 N; ***b*** – steady load increase up to 42 N; ***c*** – steady load decrease to the initial load 32 N.

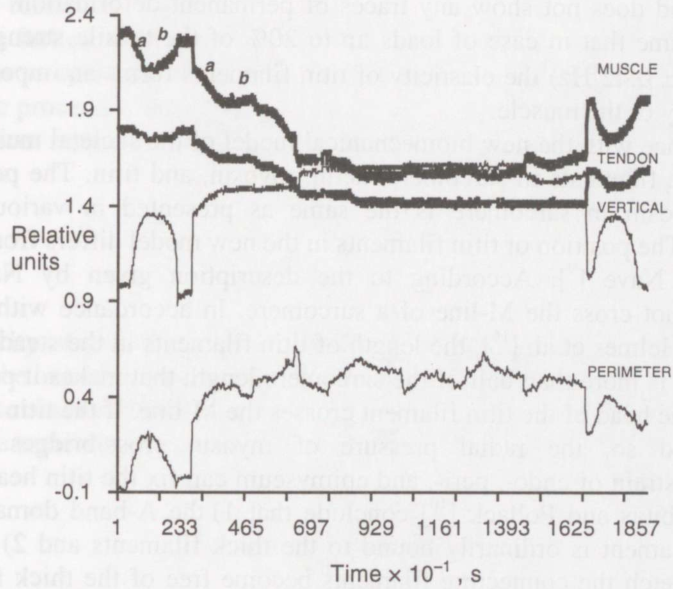

Fig. 5. Stretching and restoration of the initial length of the muscle (curve MUSCLE), deformation of the tendon (TENDON), changes in vertical deformation (VERTICAL) and in perimeter (PERIMETER) of the specimen during the loading cycles using initial loads 12 N (t = 1–233), 22 N (234–465), 32 N (466–697), 42 N (698–929), 32 N (930–1161), 22 N (1162–1393), 12 N (1394–1625), and 2 N (1626–1857); ***a*** – continuous load increase intervals; ***b*** – continuous load decrease intervals.

In the described experiments the maximum load was about 40% of the tensile strength. Thus in the first two stages of the experiment only 10 and 20% of the strength of the specimens were used. In these two cases the restoration of the initial frequency and logarithmic decrement of the natural oscillation of the specimens were the fullest in comparison with the cases of 30 and 40% level loading (Fig. 5).

4. DISCUSSION

In the experiments described above the influence of the elasticity of myosin cross-bridges is not significant, as the contractile proteins in the muscle were utilized in the process of electrostimulation. The curves presented in Figs. 3 and 4 reflect the changes in the elasticity of the muscle in the process of steady increase and decrease of the load, respectively. The reorientation of the helica of collagen fibres in endo-, peri-, and epimyseum of the muscle in the process of change of the muscle length causes a permanent deformation of the specimen in the interval $t = 23.0$–162.5 s (Fig. 5). Our experiments show that it takes place only in case of higher loads (22 and 32 N). The graph of the decrement in case of

2 N initial load does not show any traces of permanent deformation. This fact allows to assume that in case of loads up to 20% of the tensile strength (tonic tension 15.92 ± 0.42 Hz) the elasticity of titin filaments forms an important part of the elasticity of the muscle.

In accordance with the new biomechanical model of the skeletal muscle [12,13] there are three filaments in sarcomere: actin, myosin, and titin. The position of actin and myosin in sarcomere is the same as presented in various earlier publications. The position of titin filaments in the new model differs from the one described by Nave [9]. According to the description given by Nave, titin filaments do not cross the M-line of a sarcomere. In accordance with the data presented by Helmes et al. [16], the length of titin filaments in the steady state of the sarcomere is more than half of the sarcomere length that makes it possible to assume that the head of the titin filament crosses the M-line. If the titin filaments are positioned so, the radial pressure of myosin cross-bridges and the simultaneous strain of endo-, peri-, and epimyseum can fix the titin heads on the M-line. Trombitás and Pollack [10] conclude that 1) the A-band domain of the connecting filament is ordinarily bound to the thick filaments and 2) at higher degrees of stretch the connecting filaments become free of the thick filaments, and the freed segments are intrinsically elastic.

On the tonic strain (the strain, necessary to maintain the body posture) level the muscle works only to maintain the intramuscular pressure. The straining force which maintains the position of body parts relative to one another originates from the force of elasticity of titin filaments. That explains why the muscle work is very economical in the muscular tone maintenance process. If our conclusions describe the real situation adequately, the elasticity of stretched muscles must be better than that of the relaxed ones. When the muscle is stretched out by an external force, the increase of intramuscular pressure takes place [17–20] and the stiffness of endo-, peri-, and epimyseum increases [8]. In result the heads of titin filaments become fixed. This means that under the influence of the external force the elastic part of titin filament is also stretched out. Under the 2 N load the mechanical tension (tone) of the muscle specimen is lower than its normal tone level (15.92 Hz). Evidently in result of this the sarcomere length is also less than 2.0 μm. In this state the forces of elasticity of the titin filaments of the muscle do not take part in balancing the external load. There are reasons to assume that in the process of the first continuous load increase (Figs. 3 and 5, interval ***a***), the straightening of the crimps of the collagen helica situated in endo-, peri-, and epimyseum of the muscle fibres takes place. Evidently the process ends at the tonic tension level, i.e., when the average frequency of the natural oscillations of the muscle reaches 15.92 Hz. This state is established in the process of the second continuous loading cycle (22 N). Figure 5 shows that in the process of the second continuous loading cycle (interval ***b***) the decreasing of the load does not cause the restoration of the initial length and perimeter of the specimen. This fact allows to conclude that the elasticity resources of the collagen helica have been used up. In the process of further loading of the specimen (32 N, Fig. 4) the elasticity resources of titin come also to their end and further load increase does not cause further decrement decrease. On the mechanical tension level of 17 to 18 Hz the non-elastic behaviour of the muscle is apparent. Due to that the metabolic processes in the muscle are disturbed. We can conclude that the elastic deformation range of the titin is used up and the stiffness of titin filaments increases.

5. CONCLUSIONS

Elasticity of titin filaments of skeletal muscles is apparent in the process of loading the muscles up to 20% of their ultimate tensile load. That makes it possible to assume that the elastic properties of titin filaments play a significant part in the tonic tension maintenance process of the skeletal muscle.

ACKNOWLEDGEMENT

This study has been carried out at the Department of Forensic Medicine of the University of Helsinki and has been supported by Prof. A. Penttilä and E. Vuori.

REFERENCES

1. Marieb, E. N. *Human Anatomy and Physiology*. Benjamin Cummings, Redwood, 1989.
2. Volkmann, A. W. Über die Elastizität der organischen Gewebe. *Arch. Anatomie, Physiologie und Wissenschaftliche Med.*, 1859, 22, 293–313.
3. Volkmann, A. W. Von den Beziehungen der Elastizität zur Muskelthätigkeit. In *Arch. Gesamte Physiologie der Menschen und der Thiere, B. VII*. Verlag von Max Cohen & Sohn, Bonn, 1873.
4. Westermann, H. *Ein Beitrag zur Physik des Muskels*. W. Glasers Verlag, Dorpat, 1868.
5. Huijing, P. A. and Woittiez, R. The effect of architecture on skeletal muscle performance: A simple planimetric model. *Neth. J. Zool.*, 1984, **34**, 21–32.
6. Huijing, P. A., Robbert, M. F., and van Ingen Schnau, G. J. Analysis of muscle performance: Combining functional morphology of isolated muscle with biomechanics of complex human movement. In *Biomechanics in Medicine and Surgery, Vol. I*. Riga, 1986, 457–462.
7. Tillmann, B. and Töndury, G. Bewegungsapparat. In *Anatomie des Menschen: Lehrbuch und Atlas, B. 1*. (Rauber, A. and Kopsch, F., eds.). Georg Thieme Verlag, Stuttgart, 1987.
8. Purslow, P. P. Strain-induced reorientation of an intramuscular connective tissue network: Implications for passive muscle elasticity. *J. Biomech.*, 1989, **22**, 1, 21–32.
9. Nave, R. *Titin – die elastische Komponente des quergestreiften Muskels: Korrelation zwischen dem isolierten Molekül und seiner Lokalisation im Sarkomer*. Dissertation, Universität Hannover, Hannover, 1990.
10. Trombitás, K. and Pollack, G. H. Elastic properties of connecting filaments along the sarcomere. In *Mechanism of Myofilament Sliding in Muscle Contraction* (Sugi, H. and Pollack, G. H., eds.). Plenum Press, New York, 1993, 71–79.
11. Granzier, H., Helmes, M., and Trombitás, K. Nonuniform elasticity of titin in cardiac myocytes: A study using immunoelectron microscopy and cellular mechanics. *Biophys. J.*, 1996, **70**, 1, 430–442.

12. Vain, A. *On the Phenomenon of Mechanical Stress Transmission in Skeletal Muscles*. Tartu University, Tartu, 1990.
13. Vain, A. A new biomechanical model of the skeletal muscle. In *Abstracts of the Second World Congress of Biomechanics*. Amsterdam, 1994, 1, 87.
14. Vain, A. On mechanical energy recuperation mechanism of skeletal muscle according to the new biomechanical model of the muscle. In *Book of Abstracts, XVth Congress of the International Society of Biomechanics*. Jyväskylä, 1995, 954–955.
15. Vain, A. Estimation of the functional state of skeletal muscle. In *Control of Ambulation Using Functional Neuromuscular Stimulation* (Veltink, P. H. and Boom, H. B. K., eds.). University of Twente, Enschede, The Netherlands, 1995, 51–55.
16. Helmes, M., Trombitás, K., and Granzier, H. Titin develops restoring force in rat cardiac myocytes. *Circulation Res.*, 1996, **79**, 3, 619–626.
17. Körner, L., Parker, P., Almstrom, C., and Andersson, G. Intramuscular pressure and mechanical function of skeletal muscle. In *Proceedings of the World Congress on Medical Physics and Biomedical Engineering* (Bleifield, W. D., Harder, W., Leetz, H.-K., and Schaldach, M., eds.). MPBE, Hamburg, 1982.
18. Petrofsky, J. S. and Hendershot, D. M. The interrelationship between blood pressure, intramuscular pressure and isometric endurance in fast and slow twitch skeletal muscle in the cat. *Eur. J. Appl. Physiol.*, 1984, **53**, 2, 106–111.
19. Kirby, R. L., Marlow, R. W., MacLeod, D. A., and Marble, A. E. The effect of locomotion speed on the anterior tibial intramuscular pressure of normal humans. *J. Biomech.*, 1988, **21**, 5, 357–360.
20. Järvholm, U., Palmerud, G., Herberts, P., Högfors, C., and Kadefors, R. Intramuscular pressure and electromyography in the supraspinatus muscle at shoulder abduction. *Clin. Orthop.*, 1989, 245, 102–109.

SKELETILIHASE ELASTSUSE HINDAMINE TOONILISE PINGE LÄHEDASTEL PINGETEL

Arved VAIN

Töö põhiülesandeks oli uurida skeletilihase elastsusomadusi toonilise pinge lähedastes seisundites. Eksperimentaalsed uuringud tehti kümnel jänese *m.triceps surae* preparaadil. Enne preparaadi järkjärgulist koormamist allutati see elektrostimulatsioonile algkoormusel 2 N. Elektrostimulatsiooni rakendati seni, kuni preparaat lakkas sellele reageerimast kontraktsiooniga. Sel moel elimineeriti müosiini ristsildade elastsuse toime. Seejärel suurendati koormust 20 s jooksul 10 N ning vähendati uuesti sujuvalt 20 s jooksul algkoormuseni. Koormustsükli vältel registreeriti preparaadi pikkuse muutused kasutades nihkeandurit ning preparaadi perimeetri muutused perimeetrianduri abil. Preparaadi omavõnkesagedus ja võnkumiste sumbumise dekrement registreeriti müomeetri abil ühesekundilise intervalliga. Koormustsüklit koormuse sujuva suurendamise ja vähendamisega korrati algkoormustel 12, 22, 32, 42, 32, 22, 12 ja 2 N. Ülalkirjeldatud katse puhul moodustas maksimaalne koormus ligikaudu 40% katkemiskoormusest. Seega kasutati katse kahel esimesel etapil vastavalt 10 ja 20% preparaadi tugevusvarust. Nendel kahel juhul oli esialgse võnkesageduse ja sumbuvuse dekremendi taastumine täielikum võrreldes juhtudega, kus koormust suurendati sujuvalt väärtusteni 30 ja 40% katkemiskoormusest.

Koormusel 2 N on lihaspreparaadi mehaaniline pingus (toonus) väiksem normaaltoonusest (15,92 Hz). Sellest tingituna on ilmselt ka sarkomeeri pikkus väiksem kui 2,0 µm. Selles seisundis ei osale lihase titiinifilamentide elastsusjõud välise koormuse tasakaalustamisel. On põhjust arvata, et esimesel sujuval koormamisel (joon. 3 ja 5, vahemik *a*) toimub endo-, peri- ja epimüüseumis paiknevate kollageeniheeliksite lainelisuse vähenemine, mis ilmselt lõpeb toonilisel pingel, kui lihase omavõnkesagedus on keskmiselt 15,92 Hz. Selline seisund saabub teisel sujuval koormamisel (22 N). Jooniselt 5 on näha, et teise koormustsükli korral ei kutsu koormuse vähendamine (vahemik *b*) esile ei pikkuse ega läbimõõdu taastumist. See lubab väita, et kollageeniheeliksite elastsus on ammendatud. Preparaadi edasisel koormamisel (32 N, joon. 4) on ka titiini elastsus ammendatud (koormuse suurenemisega ei kaasne dekremendi vähenemist). Lihase sellise pinguse korral (17–18 Hz) on ilmne lihase mitteelastne käitumine ja sellest tulenevalt metaboolsete protsesside häirumine.

Sellest, et endo-, peri- ja epimüüseumi kollageeniheeliksite elastsus ammendatakse tõmbekoormustel kuni toonilise pingeni, võib järeldada, et skeletilihase titiinifilamendid käituvad elastselt lihase koormamise protsessis koormustel kuni 20% katkemiskoormusest.