Journal of Biomechanics 49 (2016) 1156–1161

Contents lists available at ScienceDirect

Journal of Biomechanics

journal homepage: www.elsevier.com/locate/jbiomech
www.JBiomech.com

Force reduction induced by unidirectional transversal muscle loading is independent of local pressure

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ARTICLE INFO

Article history:
Accepted 29 February 2016

Keywords:
Muscle compression
Viscoelastic material properties
Impact load
Isometric contraction
Rattus norvegicus

ABSTRACT

Transversal unidirectional compression applied to muscles via external loading affects muscle contraction dynamics in the longitudinal direction. A recent study reported decreasing longitudinal muscle forces with increasing transversal load applied with a constant contact area (i.e., leading to a simultaneous increase in local pressure). To shed light on these results, we examine whether the decrease in longitudinal force depends on the load, the local pressure, or both. To this end, we perform isometric experiments on rat *M. gastrocnemius medialis* without and with transversal loading (i) changing the local pressure from 1.1–3.2 N cm^{-2} ($n=9$) at a constant transversal load (1.62 N) and (ii) increasing the transversal load (1.15–3.45 N) at a constant local pressure of 2.3 N cm^{-2} ($n=7$). While we did not note changes in the decrease in longitudinal muscle force in the first experiment, the second experiment resulted in an almost-linear reduction of longitudinal force between 7.5 ± 0.6% and 14.1 ± 1.7%. We conclude that the observed longitudinal force reduction is not induced by local effects such as malfunction of single muscle compartments, but that similar internal stress conditions and myofilament configurations occur when the local pressure changes given a constant load. The decreased longitudinal force may be explained by increased internal pressure and a deformed myofilament lattice that is likely associated with the decomposition of cross-bridge forces on the one hand and the inhibition of cross-bridges on the other hand.

1. Introduction

The vast majority of muscle research examining muscle contraction and its influencing factors has been performed on isolated muscle preparations (e.g., research on the force–length (Gordon et al., 1966) and force–velocity relationships (Hill, 1938)). In real life, skeletal muscles are embedded within other muscles, connective tissue, and bones that possibly modify the muscle's force production along its line of action. This fact is important because changes in longitudinal muscle force alter joint torques and therefore potentially influence movement and control of the segment chain. External tensile forces can be transmitted via extramuscular connective tissue that has continuity with the muscle belly (Maas et al., 2001; Yucesoy et al., 2003). These external forces can deform the muscle, affecting, for example, sarcomere lengths and hence modifying the force-producing mechanism of the muscle (Yucesoy, 2010). The physiological relevance of these effects is disputed. Several studies have reported that such forces seem to be irrelevant within physiological boundaries at least for several muscles (Maas and Sandercock, 2008; Tijs et al., 2015). In contrast, other studies have reported substantial mechanical interaction between muscles in situ (Bernabei et al., 2015) and in vivo (Carvalhais et al., 2013; Huijing et al., 2011; Yaman et al., 2013). Furthermore, kinesio taping can influence passive muscle shape and architecture (Pamuk and Yucesoy, 2015) and change at least the initial conditions of a contraction. On the other hand, transversal compressive forces that do not necessarily require structural continuity with the muscle belly to be transmitted can lead to a decrease in longitudinal muscle force, and this decrease is of the same order of magnitude as the transversal load (Siebert et al., 2014b).

It seems plausible that muscles are compressed mainly in a transversal direction via interactions with their environment and by the action of neighboring muscles and bones. This loading condition deviates significantly from increased external steady pressure in all directions that has been shown to have almost no influence on longitudinal muscle force; the maximal isometric tension was depressed by ~1% per 100 N cm^{-2} (Geeves and Ranatunga, 1987). This finding is likely due to the fact that muscles

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http://dx.doi.org/10.1016/j.jbiomech.2016.02.053
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are water-filled structures characterized by the property of volume constancy (Swammerdam, 1737). External transversal compression in largely one direction may occur rather locally, e.g., in the back and abdominal muscles when wearing lifting belts, in limb muscles when wearing ortheses, in the deltoideus when carrying a backpack, in the gluteus when cycling, or in shank muscles when wearing ski boots; on the other hand, external transversal compression may act on rather large fractions of the muscle surface, e.g., when stemming from neighboring muscles and bones during walking or running (e.g. in the quadriceps).

In a recent study, Siebert et al. (2014b) examined the influence of increasing unidirectional transversal muscle loading on longitudinal contraction dynamics using rat *M. gastrocnemius medialis* (GM). The muscle was loaded by a plunger in a transversal direction. During contraction, the muscle deformed and lifted the load. Compared with the unloaded contraction, increasing the transversal loads from 0.64 to 2.60 N resulted in a reduction of the rate of longitudinal force development (20–36%) as well as in an almost linear decrease of the longitudinal steady-state muscle force (5–13%) and the lifting height of the plunger (1.7–0.6 mm). Due to the chosen experimental design with a constant plunger contact area, increasing transversal loads corresponded to increasing the local transversal pressure from 1.3 to 5.3 N cm^{-2}. These transversal pressures are of the same order of magnitude as those found in the human gluteus muscle during sitting (Linder-Ganz et al., 2007). However, these results prevent one from drawing conclusions as to whether local pressure effects are involved in generating the observed decrease in longitudinal muscle force.

High, local, unidirectional transversal pressures may lead to large local stresses and large deformations of the myofilament structure within adjacent muscle compartments that could hamper their effectiveness at longitudinal force production. In this case, one would expect a dependency of the decrease in longitudinal force on the local pressure associated with a constant external load. On the other hand, if the active muscle structure is stiff enough in the longitudinal direction and local deformations remain rather small, similar internal stresses may result regardless of the local pressure at a constant transversal load. Then, the decrease in longitudinal force would depend more on the transversal load than on the local transversal pressure. Determining these dependencies is important for further development and validation of simple, computationally inexpensive muscle models that can account for effects of two- or three-dimensional loading conditions of muscles (Siebert et al., 2012, 2014a).

To examine whether longitudinal muscle force depends on load, local pressure, or both, we performed in situ experiments (i) varying the local transversal pressure at constant transversal load and (ii) increasing the transversal load while keeping the local pressure constant.

2. Methods

2.1. Experimental setup

The experiments were approved according to Section 8 of the German animal protection law (Tierschutzgesetz, BGBl I 1972, 1277). We performed the experiments on rat (*Rattus norvegicus*, Wistar) *M. gastrocnemius medialis* (GM; $n=9$, $m_{GM}=821\pm100$ mg, mean ± standard deviation (SD), Table 1). The experimental setup was described in detail previously in the literature, and we refer the interested reader to Siebert et al. (2014b) and Till et al. (2008).

Briefly, the rats were anaesthetized with sodium pentobarbital (100 mg per kg of body mass). Their body temperature was maintained at 33–36 °C using a heating pad (Föhr Medical Instruments, Seeheim-Ober Beerbach, Germany). The muscle was freed from its surrounding tissues and fixed in a horizontal position. The distal tendon was attached to a muscle lever system (Aurora Scientific 305B-LR, Aurora, Canada). The sciatic nerve was stimulated (Aurora Scientific 701C) with 100 μs square wave, 3–8 mA pulses (three times the twitch threshold) at 100 Hz (maximal tetanical muscle stimulation).

Table 1
Muscle and animal mass, as well as the experiments conducted for each rat *M. gastrocnemius medialis* (GM) muscle. Loaded experiments were performed with increasing plunger contact areas (50, 75, 100, 125, and 150 mm^2).

	GM1	GM2	GM3	GM4	GM5	GM6	GM7	GM8	GM9
Rat mass [g]	290	305	280	312	338	332	330	264	320
GM mass [mg]	792	862	913	987	905	728	736	685	785
Constant load: 1.62 N	x	x	x	x	x	x	x	x	x
Constant pressure: 2.3 N cm^{-2}			x	x	x	x	x	x	x

Table 2
Contact area sizes of the rectangular plunger. Its longer side was orientated in the direction of the muscles' line of action.

Plunger contact area [mm^2]	50	75	100	125	150
Contact area side lengths [mm]	7.1 × 7.0	10.7 × 7.0	14.3 × 7.0	12.5 × 10.0	15 × 10.0

2.2. Loaded isometric experiments

The experimental procedure was very similar to that of our previous study (Siebert et al., 2014b). The unidirectional transversal load was applied in the middle of the muscle belly by one of five custom-made plungers with different contact areas (Table 2). To ensure that the muscle could withstand the induced transversal forces, it was supported from below by a horizontal plate. The plunger was able to move freely in the vertical direction, and its vertical movement was recorded using a high-speed camera (Vosskühler, Osnabrueck, Germany; 462 frames s^{-1}). To minimize friction on the contact areas, the muscle was coated with paraffin oil.

All of the experiments were performed in alternating sequences of contractions with transversal loading and unloaded reference contractions. In the first sequence, we performed loaded experiments at a fixed transversal load of 1.62 N and changing pressure. Here, increasing the plunger contact area (50, 75, 100, 125, and 150 mm^2) leads to decreasing local transversal pressure (3.2, 2.2, 1.6, 1.3, and 1.1 N cm^{-2}; $n=9$, Table 1). In the second sequence, we conducted experiments at a fixed pressure of 2.3 N cm^{-2} ($n=7$, Table 1) and changing transversal load. Constant pressure was achieved by compensating the increasing transversal load (1.15, 1.73, 2.30, 2.88, and 3.45 N) by a proportional increase in the contact areas (50, 75, 100, 125, and 150 mm^2). The plunger covered 6.5–19.5% of the 7.7 cm^2 GM surface area. In each experiment, the muscle was stimulated for 300 ms at optimal muscle length. The resting phase between the experiments was 3 min to minimize muscle fatigue. The isometric force of the unloaded reference contractions declined by approximately 3.7 ± 3.1% over the course of each sequence of experiments. This decline was compensated for by taking the mean of forces of the two neighboring reference contractions as the unloaded reference force for each loaded contraction.

We determined the maximal steady-state isometric longitudinal force F_{im} as well as the rate of force development (*RFD*) from each experiment. We calculated *RFD* as the fraction of force difference between $0.1F_{im}$ and $0.9F_{im}$ divided by the corresponding required time. The percentage difference in F_{im} between the unloaded (suffix 'unlo') and loaded (suffix 'lo') experiments was:

$$\Delta F_{im}=\frac{F_{im\_lo}}{F_{im\_unlo}}\cdot 100-100. \tag{1}$$

We likewise calculated the percentage difference in the rate of force development ΔRFD. The lift height Δh of the plunger was calculated as the difference between its maximal height during contraction and its initial height in the passive state.

2.3. Statistical analysis

We assumed a linear model for the dependence of longitudinal force, rate of force development, and lifting height, respectively, on the transversal pressure in the experiments varying the local transversal pressure at a constant load. We calculated the slopes of the dependence for each muscle by linear regression using the Matlab® (The Mathworks, Inc., Nattick, MA, USA) function "regress.m." To obtain confidence intervals at a confidence level of 0.99 for the slopes, we performed linear regressions over the combined experimental values of all nine muscles. Likewise, a linear model was assumed for the dependence of the longitudinal force, rate of force development, and lifting height, respectively, on the load in the experiments varying the load at constant local transversal pressure (seven muscles). We performed the calculations of the slopes and the confidence intervals in the same way as described above.