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INFLUENCE OF MUSCLE COMPRESSION ON DYNAMIC MUSCLE PERFORMANCE

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Abstract. *During daily activities such as sitting, carrying loads or wearing orthoses, skeletal muscles are compressed. Surrounding muscles and bones can also induce force leading to compression of the muscle. The aim of the present study was to examine the influence of varying unidirectional transversal muscle loading on contraction dynamics. We performed isometric experiments on isolated rat M. gastrocnemius medialis* (n = 10) *without and with five different transversal loads (0.64, 1.13, 1.62, 2.11, 2.60 N). The muscles were loaded by a custom-made plunger in transversal direction. The muscle force was measured at the distal tendon and the vertical movement of the plunger was captured with a high-speed camera during supramaximal muscle stimulation. Increasing transversal muscle force resulted in an almost linear decrease in maximum isometric muscle force* (F_{im}) *from 5.0 ± 1.5 %* F_{im} *to 13.1 ± 2.1 %* F_{im}. *Compared with an unloaded isometric contraction, the rate of force development (RFD) decreased from 20.7 ± 4.1 % RFD to 35.2 ± 5.8 % RFD. The lifting height of the plunger decreased from 1.7 ± 0.2 mm at the lowest transversal load to 0.6 ± 0.2 mm at the maximum load applied. Unidirectional transversal compression depresses longitudinal force development in skeletal muscles and, thus, should be considered in musculo-skeletal models simulating the interaction of muscles with their mechanical environment, e.g. in impact biomechanics. The interactions between the muscle and one unidirectional transversal load could be explained reasonably well with a simple model including a hill-type muscle model, a geometric model transferring transversal forces into a longitudinal direction and a viscoelastic model representing the characteristics of passive muscle tissue. Data presented in this study may be important to develop and validate muscle models which enable simulation of muscle contractions under compression and reveal the mechanisms behind.*

INTRODUCTION

It is well known that active muscle force depends on different parameters such as muscle length [1,2] or contraction velocity [3]. Traditionally these dependencies were determined on isolated muscle preparations. However, *in vivo* skeletal muscles are embedded in an environment of other muscles, connective tissue and bones. These surrounding structures are supposed to exert external forces to the muscle belly, thereby influencing active muscle force. External tensile forces can be transmitted via extramuscular connective tissue to the muscle [4]. These forces act mainly in longitudinal direction (in the line between muscle origin and insertion: line of action). In addition, forces may act in transversal direction (perpendicular to the line of action) thereby compressing the muscle [5]. Transversal muscle loading may be induced during sports exercises, e.g. by lifting belts, bench shirts and compressing swimsuits or occurs during daily activities, such as carrying loads, wearing orthoses, or sitting.

In a recent study [5] the influence of increasing transversal muscle loading on contraction dynamics was examined using rat *M. gastrocnemius medialis* (GM). The muscle was loaded unidirectional by a plunger which was able to move in transversal direction (Fig. 1). During muscle contraction the muscle deforms, and work was performed to lift the load. Compared with the unloaded contraction, transversal muscle loading with 0.64 N resulted in a decrease in maximal isometric muscle force (F_{im}) and rate of force development (RFD) by 5% and 25%, respectively. Due to given contact area of the plunger (0.5 cm^2) the applied pressure was 1.3 N/cm^2, which corresponds to about the mean pressure at the body-seat interface during human sitting [6,7]. Comparatively higher muscle compressions are, however, expected for e.g. car drivers during accidents or athletes involved in contact sports (e.g. boxing and wrestling). Thus, the aim of the present study was to examine the influence of varying unidirectional transversal muscle loading on contraction dynamics of isolated rat *M. gastrocnemius medialis*. Parts of this study are published in [8].

METHODS

Experimental procedure was similar to [5]. Experiments were approved according to Section 8 of the German animal protection law (Tierschutzgesetz, BGBl I 1972, 1277). Experiments were performed on rat (*Rattus norvegicus*, Wistar) GM (n = 10, mass GM = 894 ± 88 mg). Muscle preparation, anaesthesia and setup have been described in detail earlier [9]. Briefly, the rats were anaesthetized with sodium pentobarbital (100mg/kg body mass). Body temperature was maintained at 33-36°C using a heating pad (Föhr Medical Instruments). 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). The sciatic nerve was stimulated (Aurora Scientific 701C) with 100 µs square wave pulses of 3–8 mA (threefold the twitch threshold) at100 Hz (maximal tetanical muscle stimulation).

The transversal load was applied in the middle of the muscle belly by a custom made plunger with 0.5 cm^2 contact area (Fig. 1). To withstand the induced transversal forces, the muscle was supported from below by a horizontal plate. The plunger was able to move freely in vertical direction and its movement was measured with a high-speed camera (Vosskühler, 462 frames/sec). To minimize friction between the plunger and the muscle surface, the attachment area was coated with paraffin oil. Variable suffixes ‘lo’ and ‘unlo’ distinguish loaded and unloaded experiments, respectively.

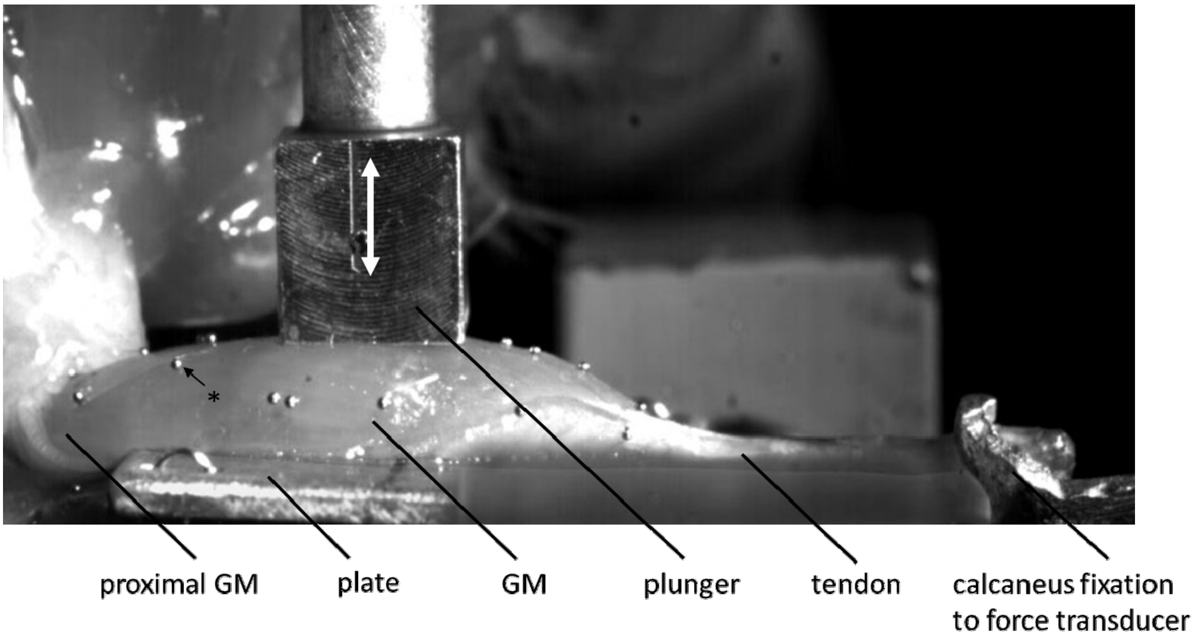

Figure 1: Experimental setup. Transversal load is induced on rat *M. gastrocnemius medialis* (GM) by a plunger which is able to move freely in vertical direction. The small markers on the muscle surface (*) were used for analyses in another study.

An alternating sequence of experiments without a transversal load and with a transversal load was conducted. The muscle was stimulated for 300 ms at optimum muscle length. The resting phase between the experiments was 3 min to minimize muscle fatigue. Five loaded experiments were performed with increasing transversal loads (0.64, 1.13, 1.62, 2.11, and 2.60 N) corresponding to increasing pressures (1.3, 2.3, 3.3, 4.3, and 5.3 N/cm^2). The plunger covered about 20 % of the muscle's surface area visible from the top. After each loaded experiment the muscle was able to reproduce F_{im} in the unloaded reference contraction.

We determined F_{im} as well as *RFD* from each experiment. *RFD* was calculated as force difference between 10–90% F_{im} divided by the corresponding difference in time. ΔF_{im} and ΔRFD indicate percentage changes of F_{im} and *RFD*, respectively, from unloaded to loaded experiments. In the loaded experiments, the lifting height $\Delta h= h\text{-}h_0$ was measured, where h_0 is the initial height of the load in the passive condition. The maximum value of Δh over contraction time is the maximum lifting height h_{max}.

For statistical analyses we used a linear model for the dependencies of ΔF_{im}, ΔRFD, and Δh, respectively, on transversal force. The slopes of the dependencies were calculated 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, linear regressions were performed over the combined experimental values of all ten muscles.

RESULTS

Unidirectional transversal muscle loading with different loads impacts longitudinal muscle force, rate of force development and lifting height of the load (Fig. 2).

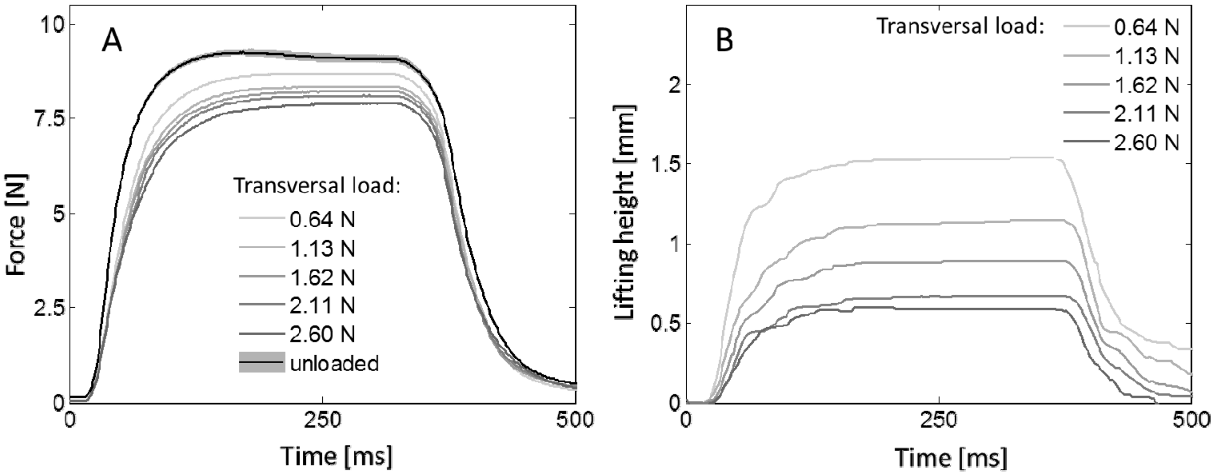

Figure 2: Force-time (A) and lifting height - time traces depending on different transversal loads exemplarily shown for GM9. Mean (black line) and standard deviation (grey) are given for the force-time traces of the unloaded reference contractions. Stimulation started at $t = 0$ and ended at $t = 300$ ms.

Increasing the transversal load from 0.64 N to 2.60 N resulted in consistent and almost linear changes of ΔF_{im} from 5.0 ± 1.5 % F_{im} to 13.1 ± 2.1 % F_{im} ($R^2 > 0.95$; Fig. 3A), of ΔRFD from 20.7 ± 4.1 % RFD to 35.2 ± 5.8 % RFD ($R^2 > 0.84$; Fig. 4), and of Δh from 1.7 ± 0.2 mm to 0.6 ± 0.2 mm ($R^2 > 0.97$; Fig. 3B), respectively. Linear regression analyses indicated a strong influence of load on ΔF_{im}, ΔRFD, and Δh (Fig. 3, Table 1). The upper as well as the lower bounds of the .99 confidence intervals of the slopes were all negative, indicating a strong effect of load on the considered variables (Table 1). The calculated confidence interval for the slope of ΔF_{im} implicates a decrease of longitudinal muscle force by at least 5.9% over the range of examined load values.

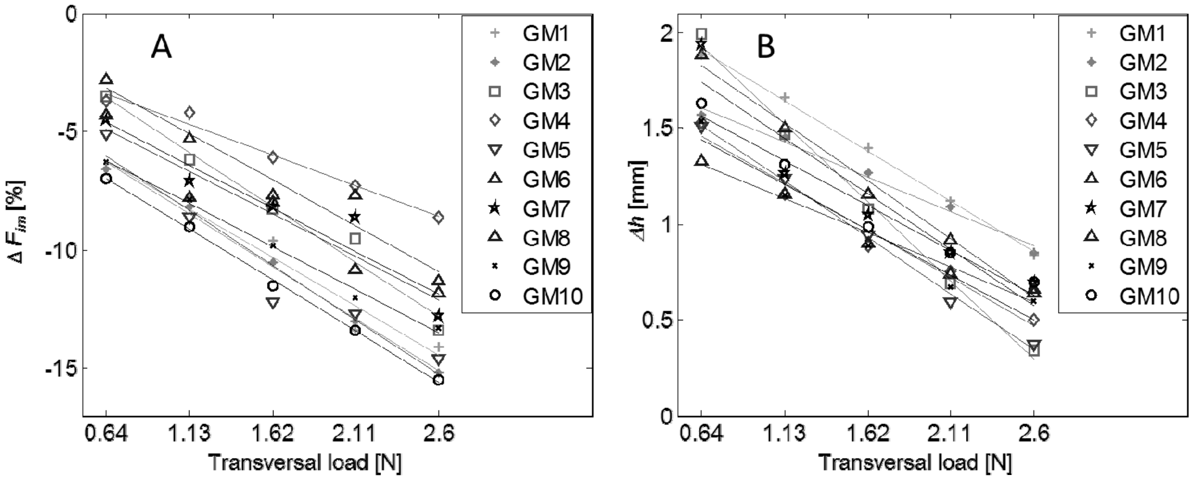

Figure 3: Influence of transversal loading with different loads (0.64, 1.13, 1.62, 2.11, 2.60 N) on isometric muscle force (A) and lifting height (B). Data and individual regression lines are shown for all ten muscles.

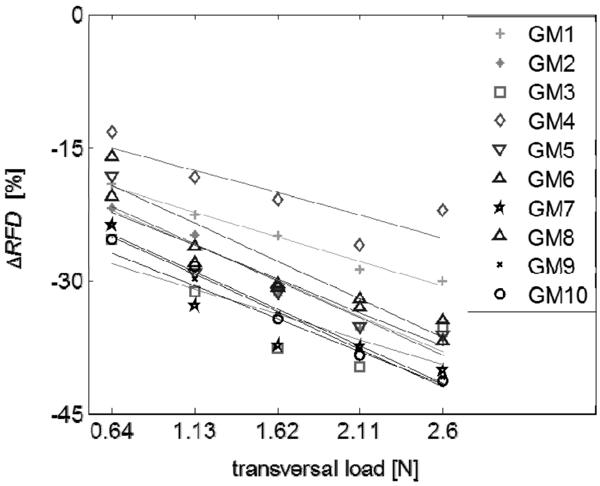

Figure 4: Influence of transversal loading with different loads (0.64, 1.13, 1.62, 2.11, 2.60 N) on rate of force development (*ΔRFD*). Data and individual regression lines are shown for all ten muscles.

independent variable	dependent variable	range of calculated slopes	.99 confidence interval of slope	
			lower bound	upper bound
load [N]	ΔF_{im} [%]	-4.714 to -2.633	-5.026	-3.000
	ΔRFD [%]	-8.735 to -5.143	-10.089	-4.764
	Δh [mm]	-0.833 to -0.367	-0.638	-0.437

Table 1: Slopes of linear regressions and the corresponding 99 % confidence intervals for the dependencies of change in isometric longitudinal muscle force ΔF_{im}, change of rate of force development ΔRFD, and change of lifting height Δh on transversal load. Confidence intervals were calculated over the combined experimental values of all muscles.

DISKUSSION

Varying unidirectional transversal force influences longitudinal contraction dynamics (Fig. 2). Increasing transversal load resulted in an almost linear decrease in maximum isometric force and rate of force development. In our experiments, muscles produce work to strain the series elastic component, to lift the load, and to deform the muscle itself during an end-held isometric contraction. After performing this work, the muscle has to balance the transversal load in the static case. These interactions between the muscle and its mechanical environment could be explained reasonably well with a simple phenomenological model [5] including a hill-type muscle model, a viscoelastic model representing the characteristics of passive muscle tissue and a geometric model transferring transversal forces into a longitudinal direction. The gearing ratio of the geometric model can be explained by a simple ellipsoid muscle model [10].

Various factors may contribute to the observed reduction in muscle force induced by transversal muscle loading. For example, considering a spatial arrangement of muscle fibers transversal muscle loading may induce changes in muscle thickness and fiber pennation angle influencing muscle force generation [11]. Moreover, muscle fibers are connected to the extracellular matrix [12]. Local deformations induced by the plunger may induce local length changes along muscle fiber and thus decrease muscle force.

As most muscles are packed in ‘muscle packages’ [13] transversal forces induced by surrounding tissues may impact on large parts of the muscle surface. This may be especially true for inner muscles like rat soleus and plantaris which are almost completely surrounded by other calf muscles. If surrounding muscles contract, they will deform [14,15] and thus may transfer transversal forces over the complete surface to these inner muscles. Thus, the given plunger contact area used in this study may represent rather a local loading compared with the physiological loading situation in muscle packages. Thus, it seems of great importance to examine the intermuscular pressure (between neighboring muscles) in muscle packages during contractions. Based on these insights, basic questions about evolution of muscle architecture can be addressed and it may be speculated whether muscle architectures are designed to minimize mutual transversal loading in between neighboring muscles. Maybe muscle architectures are adjusted such that muscles exert only small intermuscular pressures during contraction generating. This might be one explanation for complex muscle architectures, exhibiting e.g. distributions of varying fiber lengths and pennation angles or inner tendon sheets [16,17,18,19]. If, however, minimization of intermuscular pressure is no design criteria, transversal forces induced by contracting muscles may have a function. For example, they could contribute to stabilization of muscle packages in impact situations (e.g. foot contact during cyclic locomotion). Moreover, transversally compressed muscles can act under dynamically favourable conditions, e.g. transversal loading can result in increased work production of the contractile component [5]. Furthermore, work performed transversally on adjacent muscles may be saved and released subsequently in addition to energy savings in series [20,21] and parallel elastic structures [22] which might enhance efficiency of cyclical locomotion. However, these questions have to be addressed in future studies.

Summing up, experimental observation of the impact of transversal muscle loading on contraction dynamics may help to better understand muscle tissue properties and to describe more precisely compression of the human body e.g. in rehabilitation studies. Moreover, applying transversal loads to muscles opens a window to analyze three-dimensional muscle force generation. The data presented in this study can be used to advance and validate muscle models which enable simulation of muscle contractions under compression and possibly reveal the mechanisms behind.

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