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Impact of transversal calf muscle loading on plantarflexion

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ABSTRACT

Muscle compression commonly occurs in daily life (for instance wearing backpacks or compression garments, and during sitting). However, the effects of the compression on contraction dynamics in humans are not well examined. The aim of the study was to quantify the alterations of contraction dynamics and muscle architecture in human muscle with external transverse loads.

The posterior tibialis nerve of 29 subjects was stimulated to obtain the maximal double-twitch force of the gastrocnemius muscle with and without transverse compression that was generated using an indentor. The muscle architecture was determined by a sonographic probe that was embedded within the indentor. Five stimulations each were conducted at 5 conditions: (1) pretest (unloaded), (2) indentor loading with 2 kg, (3) 4.5 kg, (4) 10 kg, and (5) posttest (unloaded).

Compared to the pretest maximal force decreased by 9%, 13% and 16% for 2 kg, 4.5 kg and 10 kg, respectively. The half-relaxation time increased with increased transverse load whereas the rate of force development decreased from pretest to 2 kg and from 4.5 kg to 10 kg. The lifting height of the indentor increased with transverse load from 2 kg to 4.5 kg but decreased from 4.5 kg to 10 kg. Increases in pennation during the twitches were reduced at the highest transverse load.

The results demonstrate changes of the contraction dynamics due to transversal muscle loading. Those alterations are associated with the applied pressure, changes in muscle architecture and partitioning of muscle force in transversal and longitudinal direction.

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1. Introduction

The compression of muscles has been examined in view of mechanical, neuromuscular, and metabolic effects on muscular performance and recovery (Bottaro et al., 2011; Duffield et al., 2008; Trenell et al., 2006). Compression garments seem to have a beneficial effect on recovery (Marqués-Jiménez et al., 2016). The results regarding muscle performance are contradictory (Beliard et al., 2015) in man, although, in animal studies compression experiments on single isolated muscles indicate a decrease of muscle performance (Siebert et al., 2016). However, the effect of transversal loading on dynamic contraction is still unknown for human muscles.

Transversal compression of muscle tissue influences muscle properties: repeated muscle compression causes decreases to the muscular viscoelasticity and increases to the muscle stiffness (van Loocke et al., 2008; van Loocke et al., 2009). The effect of compression on longitudinal force production was also examined on the muscle fiber level (Maughan and Godt, 1981). To measure this skinned muscle fibers were compressed by including long-chain polymers (e.g. Dextran, T-500) in a bathing solution. It was observed that force starts to decrease when the fiber was compressed to 58% of the baseline and further compression lead to a sharp decrease of force production (Godt and Maughan, 1981; Gulati and Babu, 1985). Gulati and Babu (1985) assumed that a critical filament interspace exists below which the cross-bridge cannot function. Changes to the muscular contraction dynamics on muscle level have also been reported when the whole muscle was constrained by bandages (Wakeling et al., 2013), rigid tubes (Azizi et al., 2017) or indentors (Siebert et al., 2014b; Siebert et al., 2014a).

Siebert et al. (2014a) demonstrated a decrease of maximal contraction force and rate of force development for the rat medial gastrocnemius when the muscle was loaded by an indentor in the transversal direction (i.e. perpendicular to the line of action). These reduced contractile characteristics depend on the applied transverse force but not on the contact area of the loading (Siebert et al., 2016). However, those changes of the contraction dynamics were observed in single muscle experiments only. It has not been examined yet if the contraction dynamics change in living human

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muscle, too. The muscle skeletal system in living humans is more complex (e.g., muscles are packed in muscle packages, several muscles act on a joint, muscle force cannot be measured directly) and thus, differences regarding the contraction dynamics during muscle compression are expected.

Muscle architecture is an important determinant of muscle force (Gans and Gaunt, 1991; Lieber and Ward, 2011; Stark and Schilling, 2010). We suspect that muscle architecture changes with transversal load and thus, contributing to the decreased contraction dynamics. So far alterations of muscle architecture (in particular changes of the pennation angle) during transversal muscle loading using an indentor in association with contraction dynamics have not been examined yet.

The aim of the study was to quantify the alterations of contraction dynamics and muscle architecture in regard to the transversal muscle load in living human muscles. It was hypothesized that the maximal muscle force, the rate of the force development (RFD) and the pennation angle would decrease with increasing transverse load applied by an indentor.

2. Methods

2.1. Subjects

Twenty nine normal active subjects (male: 26; female: 3; height: 181.2 ± 7.0 cm; mass: 77.6 ± 9.3 kg; BMI: 23.6 ± 1.9; age: 25.1 ± 4.7 years) participated in this study. All subjects were informed about the risks of the experiments and gave their written consent. The study was approved by the ethical committee of the university hospital of Tuebingen (ID: 596/2015BO2) and conducted according to the latest declaration of Helsinki.

2.2. Double-twitch force and indentor kinematics

The double-twitch force is a commonly used parameter to examine contraction dynamics in human experiments (Stutzig and Siebert, 2015a,b) and is highly reproducible (Stutzig and Siebert, 2016) and thus, was used as force parameter in this study. To assess the double-twitch force the posterior tibialis nerve was stimulated. The anode (5 × 10 cm) was fixed on the thigh approximately 2 cm proximal to the patella and the cathode was fixed in the popliteal fossa as close as possible to the tibialis nerve. Electrical paired stimuli (pulse interval 10 ms) were generated using a high current stimulator (DS7AH Digitimer, Herfordshire, UK). The maximal stimulation intensity was assessed using a ramp protocol: starting at 10 mA, and increasing by 10 mA every 10 s until the double-twitch force did not further increase. The double-twitch force during stimulation was recorded (sample rate: 1000 Hz) using a 3D force plate (Type 9260 AA3, Kistler Instrumente AG, Winterthur, Switzerland). The vertical displacement of the indentor, lift height, was recorded (sample rate: 1000 Hz) using a draw wire sensor (SX50, WayCon, Taufkirchen, Germany).

2.3. Sonography

Pennation angles were measured from videos (604 × 515 pixels; 80 Hz) obtained using an ultrasound system (Echoblaster 128, Telemed, Lithuania). The ultrasound probe had a 65 mm field of view, and scanning depth was set to 50 mm.

2.4. Experimental protocol

The experiments started with a standardized warm-up consisting of 5 min running on a treadmill, 3 × 10 calf raises and 10 repetitive calf jumps. Then, the subjects were asked to lie prone in a calf press apparatus with one foot attached to a 3D force plate (Fig. 1). The second foot was placed and secured beside the force plate. The stimulation electrodes were attached on the skin and the subject was immobilized in this position (full extended knee, ankle angle at 90°) with shoulder barriers and with a hip belt. Subjects then performed a further warm-up consisting of 10 submaximal isometric plantarflexions.

The main experiments started with 5 paired stimuli, applied to the posterior tibialis nerve every 10 s at rest for the pre-test baseline. Then, the loaded indentor was placed on the gastrocnemius muscle belly and 5 doublets were repeated for each of three different loads (2 kg, 4.5 kg and 10 kg). The loads corresponded to the pressures (indentor size: 100 × 34 mm; area of the contact face: 3.4 cm^2, indentor weight: 920 g) applied in our previous work (Siebert et al., 2014b; Siebert et al., 2014a; Siebert et al., 2016). The experimental order of the indentor loads was randomised. Finally, the posterior tibialis nerve was stimulated with 5 doublets every 10 s at rest for the post-test condition to assess possible conditional changes during the experiment.

In a separate experiment we tested if the internal muscle moment arm between the tendon and ankle joint centre considered to coincide externally with the malleolus alters due to transversal muscle loading. If the moment arm were to decrease with transversal load, then this would contribute to decreased joint torque and muscle force given a measured external net force and moment. However, results from five subjects showed no significant change in muscle moment arm occurred between the unloaded and loaded conditions.

2.5. Data analysis

The force data and kinematic data were smoothed using a moving average filter (window length: 11 samples, respectively). The net force was then calculated for each double-twitch and used to quantify the maximal double-twitch force (F_{mt}), rate of force development (RFD), half relaxation time (HRT), sink and lift height of the indentor using custom-made Matlab scripts (MATLAB R2013a, The MathWorks, Inc., Natick, MA, USA). RFD was calculated as the fraction of force difference between 0.1 F_{mt} and 0.9 F_{mt} divided by the corresponding duration between these points. HRT was determined as the time delay starting at F_{mt} until 50% of F_{mt}. The lift height of the indentor was calculated as the difference between its maximal height during contraction and its initial (sink) height when the passive muscle was compressed. The mean and standard deviation of a stimulation series (e.g., 5 doublets at rest, at 2 kg) was assessed and used for further statistical analyses.

Traces were made on each of the superficial and deep aponeuroses, and fit with 2nd order polynomials to define the region of interest (ROI) of the muscle belly. Each ultrasound image was filtered using a multi-scale vessel enhancement filter (Frangi et al.,

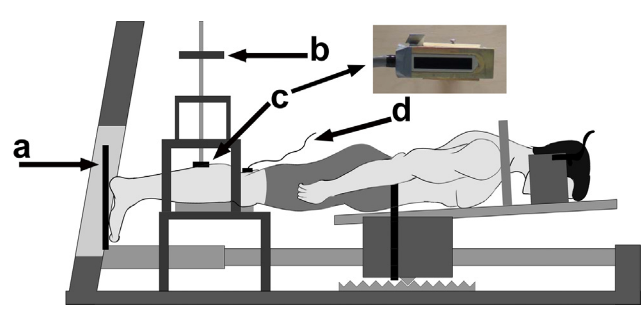

Fig. 1. Experimental setup. (a) Force plate; (b) weights; (c) indentor with integrated sonographic probe; (d) cathode.

1998) to emphasize vessel-like structures within the muscle, and the ROI segmented from the aponeurosis (with the superficial and deep boundaries reduced by 10 pixels to ensure no parts of aponeurosis featured within this ROI). A Hough transformation was applied to the ROI to parameterize straight segments aligning with the fascicles within the muscle belly: the mean orientation of these lines were considered to be the fascicle orientation. The pennation was the angle between this fascicle orientation and the midline calculated between the digitized aponeuroses (Fig. 2). Image processing was performed using custom-software (Mathematica; Wolfram Research, Champaign, USA).

2.6. Statistical analyses

All data are presented as means and standard error when not otherwise described. The data were normally distributed, as confirmed using a Kolmogorov-Smirnov Test. One-way rANOVAs for repeated measures were conducted for the force parameters, the pennation angle and the lifting parameters to test for differences between conditions (rest (pretest), 2.0 kg load, 4.5 kg load, 10 kg load and rest (posttest)). Note that pre- and post-measurements for the pennation angle and the lifting parameters were not possible due to the experimental approach. The level of significance was set at $p < 0.05$. Significant main effects or interactions of the ANOVA were probed using Bonferroni post-hoc tests. Effect size was determined using partial eta squared (η_P^2) and classified as follows: low $\eta_P^2 = 0.01$, medium $\eta_P^2 = 0.06$, and large $\eta_P^2 = 0.14$ (Cohen, 1988). All statistical analyses were performed using IBM SPSS Statistics for Windows (Version 22.0, IBM Corp., Armonk, NY).

3. Results

3.1. Pennation angle

Transversal muscle loading influenced the intra-muscular architecture. A representative example for changes of the pennation angle are shown for a single subject in Fig. 2. Pictures A) and B) illustrate that the gastrocnemius muscle is more compressed with a 10 kg transverse load compared to 2 kg. During muscle activation the thickness between the upper and lower aponeurosis at 2 kg load is greater and the pennation angle is higher compared to the 10 kg load.

The statistical analysis shows significant effects (of muscle loading) for initial passive ($F_{2,\ 56} = 5.4,\ p = 0.007,\ \eta_P^2 = 0.16$) and active ($F_{2,\ 56} = 78.8,\ p < 0.001,\ \eta_P^2 = 0.74$) pennation angles as well as their changes ($F_{2,\ 56} = 12.8,\ p < 0.001,\ \eta_P^2 = 0.31$) during contraction. The post hoc tests revealed significant differences for changes of the pennation angle during stimulation between 2 kg and 10 kg as well as 4.5 kg and 10 kg but not for 2 kg and 4.5 kg (Table 1).

3.2. Double-twitch force and lifting height

Fig. 3 shows representative force-time and lifting-time curves of 5 stimulations under 3 loading conditions. The force-time curves indicate decreasing maximal force when loading increases. Lift height increased in 4.5 kg loading and decreased with 10 kg load compared to 2 kg (Fig. 3B).

The rAnova revealed significant differences for F_{mt} between the loading conditions ($F_{4,\ 112} = 79.3,\ p < 0.001,\ \eta_P^2 = 0.74$). Furthermore, the post-hoc tests indicate significant differences between all loading conditions but not between pre- and posttest (Fig. 4). F_{mt} decreased for the 2 kg, 4.5 kg, and 10 kg loading by 9%, 13%, and 16%, respectively.

The rate of force development decreased when transversal load increased ($F_{4,\ 112} = 42.4,\ p < 0.001,\ \eta_P^2 = 0.60$). Significant differences were observed between all loading conditions except for 2 kg and 4.5 kg (Fig. 5). The pre- and posttest did not change throughout the experiments.

The half relaxation time increased almost linearly with increased loading. The rAnova revealed significant differences ($F_{4,\ 112} = 21.4,\ p < 0.001,\ \eta_P^2 = 0.43$) between all loading conditions but not between pre- and posttest (Fig. 6). The pre- and posttest did not change throughout the experiments.

The reference point of the indentors height was determined when it just touched the skin. At transversal loads of 2 kg, 4.5 kg, and 10 kg the indentor sank into the passive muscle by 8.7 ± 0.3 mm, 14.4 ± 0.3 and 21.4 ± 0.5 mm, respectively. The post-hoc test revealed significant differences in sink height between all loadings (Fig. 7A). During contraction the maximal lift height of the indentor, starting from the compressed passive muscle, was 15.2 ± 0.7 mm, 16.3 ± 0.7 mm, and 14.1 ± 0.8 mm for the transversal loads of 2 kg, 4.5 kg, and 10 kg, respectively. A significant difference in lift height was observed between the transversal loads of 2 kg and 4.5 kg ($p < 0.001$) as well as for 4.5 kg and 10 kg ($p < 0.001$) but not for 2 kg and 10 kg ($p = 0.119$) (Fig. 7B).

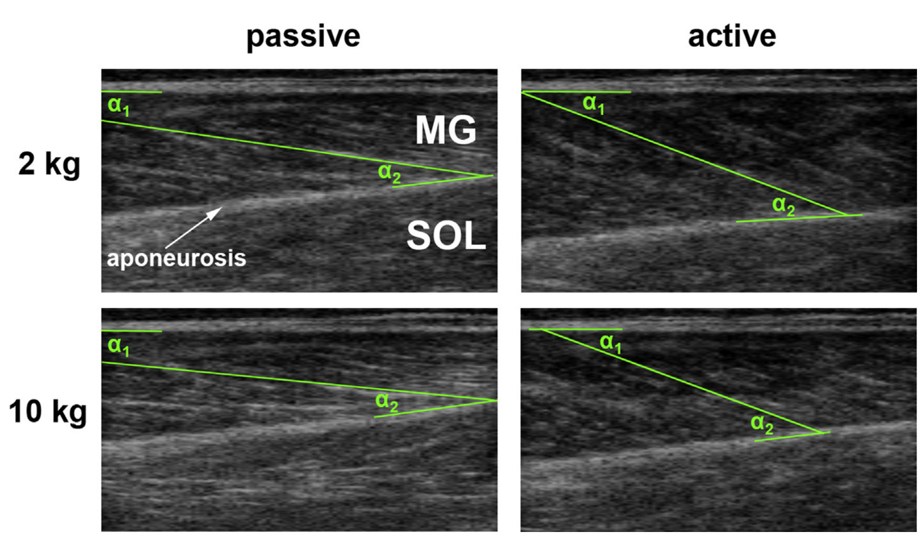

Fig. 2. Typical ultrasound images of the gastrocnemius muscle (MG) and the soleus muscle (SOL) with 2 kg and 10 kg load in active and passive state. The mean of the angles (α_1 and α_2) represent the pennation angle.

Table 1
Mean and standard error (SE) for the pennation angle in passive and active state at three different loading conditions (2 kg, 4.5 kg and 10 kg).

Pennation angle	Load 2 kg		Load 4.5 kg		Load 10 kg		Significance
	Mean	SE	Mean	SE	Mean	SE	
Passive [°]	12.1	±0.5	10.9	±0.6	10.5	±0.6	‡, †
Active [°]	18.1	±0.6	16.7	±0.7	14.3	±0.6	‡, +, †
Change [°]	6.0	±0.4	5.8	±0.4	3.7	±0.4	+, †

Symbols for significant differences between loads: ‡ – 2 kg and 4.5 kg; + – 4.5 kg and 10 kg; † – 2 kg and 10 kg.

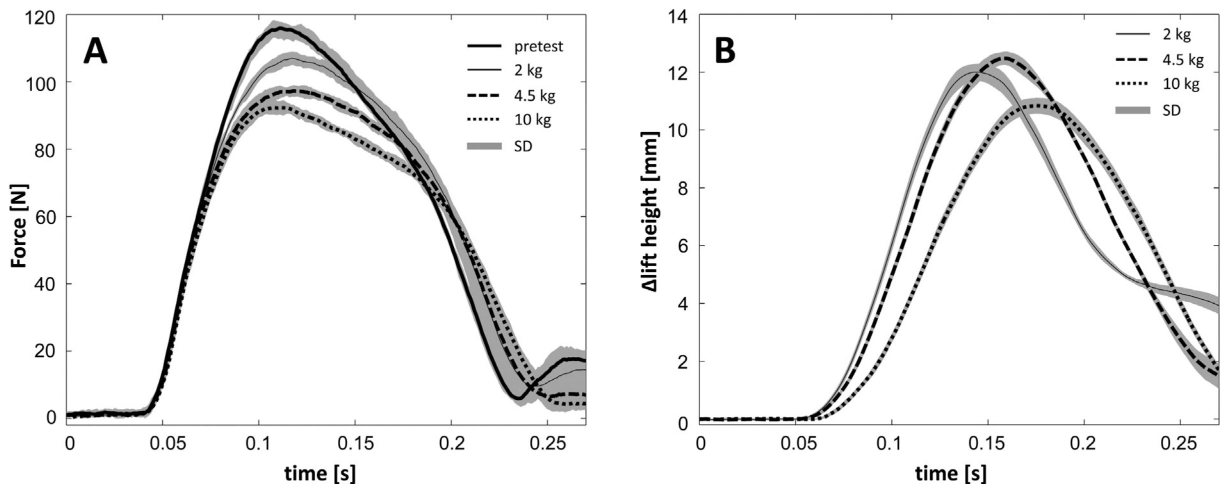

Fig. 3. Mean and standard deviation (SD) of 5 stimulations of a single subject. (A) Shows the force-time curves of the pretest and 3 loading conditions (2 kg, 4.5 kg, and 10 kg) whereas (B) illustrates the lift height of the indentor in three different loading conditions.

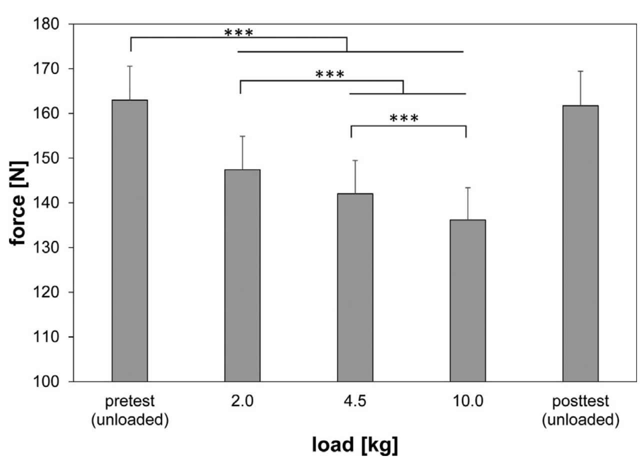

Fig. 4. Mean and standard error of maximal double-twitch force for pretest, loading conditions (2 kg, 4.5 kg and 10 kg), and posttest. Significance: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

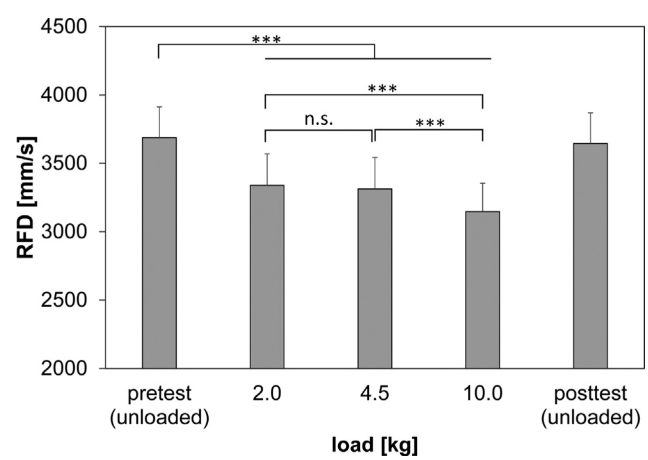

Fig. 5. Mean and standard error of rate of force development (RFD) for pretest, loading conditions (2 kg, 4.5 kg and 10 kg) and posttest. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

4. Discussion

The results of the present study reveal that transversal muscle loading changes the muscular contraction dynamics. The maximal muscle force during double-twitch stimulation decreased with increasing loading. Furthermore, the increases in the pennation angle during contraction were reduced and the half relaxation time increased when contracting with greater transverse loads.

Siebert et al. (2014b) performed a similar study on the rat medial gastrocnemius. They used pressures of 1.3 and 3.3 N/cm^2 which is comparable to our muscle loading of 4.5 kg (1.6 N/cm^2) and 10 kg (3.2 N/cm^2). In their study the isometric force decreased by 5 and 9%, respectively which was slightly less than in the present study (force decrease of 13%, and 17%, respectively; Fig. 4). The decrease in RFD reported by Siebert et al. (2014b) (20% and 30%) was almost twice as high as in the present study (11% and 14%). For isolated rat muscles an almost linear decrease in lifting height (up to 63%) with increasing load was reported (Siebert et al. 2014b), which differs from our observation of an maximum lifting height at a medium load of 4.5 kg (Fig. 7B). This might be due to differences in the object of investigation (single isolated muscle vs. muscle package). In this current study, the lifting height of the indentor would result from deformations in both the soleus and medial gastrocnemius muscles, however, the impact of the

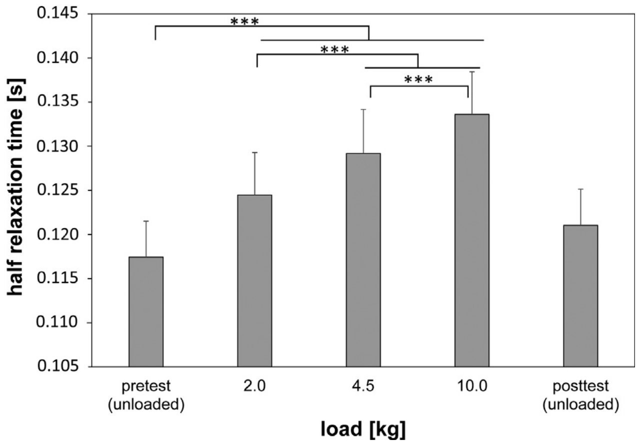

Fig. 6. Mean and standard error of half relaxation time for pretest, loading conditions (2 kg, 4.5 kg and 10 kg) and posttest. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

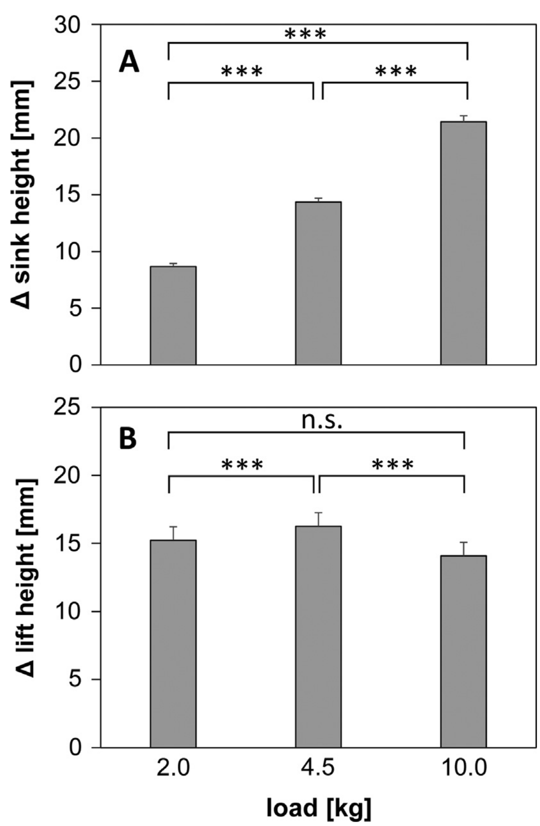

Fig. 7. Mean and standard error of the indentors passive sink height under transversal loading of 2 kg, 4.5 kg, and 10 kg (A) and the indentors active lifting height (B) during muscle contraction.

transversal loading on the soleus muscle as well its deformation is currently unclear. Furthermore, the different muscle architectures of soleus and gastrocnemius as well as potential load transfer in between synergistic muscles (Reinhardt et al., 2016) may lead to more complex muscle package deformations and thus, differences in the lifting-height to load relation compared to experiments obtained on isolated muscles. Nonetheless, we observed qualitatively the same phenomena (force decrease, RFD decrease, changing lift height) in human muscle as was reported for the isolated medial gastrocnemius from the rat (Siebert et al., 2014b).

Compression-induced decreases in muscle force have previously been reported by Wakeling et al. (2013) using elasticated bandages around the calf muscle: these findings were discussed in association with changes in muscle fascicle length, velocity and orientation. In the present study, the transversal compression by the indentor on the passive muscle caused a reduction in muscle thickness (Fig. 2) and pennation angle (Table 1) that would likely result in an increase in fascicle length (Wakeling et al., 2013). This increase in fascicle length that would occur with transverse compression would shift the working point of the fascicle on its force-length curve. Assuming that the uncompressed muscle worked in the ascending limb of its force-length relation during contraction (Kawakami and Fukunaga, 2006), a shift to longer fascicle lengths would move the fascicle towards the plateau of its force-length curve leading to greater contractile force. However, this would contradict the observed decrease in muscle force (Fig. 4). Thus, fascicle lengthening may be excluded as the cause for the decrease in muscle force induced by transversal muscle loading. Moreover, potential fascicle lengthening during transversal muscle loading would oppose the reduction in muscle force and thus, the effect of muscle compression on muscle force might be underestimated.

Siebert et al. (2014a) and Siebert et al. (2018) presented a simple model approach describing the interaction of the transversal load with the muscle. Based on a Hill-type muscle model using a lever to convert transverse force and length change into longitudinal force and length change, this approach was able to reproduce the reduction in muscle force. However, the model neglected 3D muscle deformation and changes in muscle architecture during contraction that might further influence dynamic force generation during muscle compression. When the muscle belly deforms in 3D, the base material stiffness in the transverse direction requires internal work to allow transverse deformation and this can result in a decrease in the net longitudinal contractile force. This effect increases when additional work must be done to displace the external transverse load (Siebert et al. 2014a; Siebert et al., 2018).

Changes in the muscle architecture may alter the gearing through which muscle fibers operate (Azizi et al., 2008), where the gearing is defined as the ratio of the shortening velocity of the muscle belly and the shortening velocity of the muscle fascicles. Azizi et al. (2008) predicted that situations where the transverse expansion was reduced would result in lower gearing, faster fascicle velocity and thus lower muscle force. Whilst the ankle was held at a fixed angle during the twitches in this study, the muscle belly and fascicles would still shorten due to elastic compliance within the tissues, and thus this gearing effect may contribute to the reduced forces with the higher transverse loads where the increases in muscle thickness were constrained (Wakeling et al., 2013).

Interestingly, Azizi et al. (2017) limited the radial expansion of the muscle during dynamic muscle contraction using a rigid pipe around the muscle. They observed a reduced muscle shortening as well as decreased work output at 50% MVC but the maximal force production in the longitudinal direction reduced from 1.66 ± 0.36 N to 1.58 ± 0.30 N for the constrained muscle. Whilst this reduction was statistically indistinguishable (Azizi et al., 2017) it was of a similar magnitude (5%) to a force decrease of 5% that was statistically confirmed in recent studies (Siebert et al., 2014b; Siebert et al., 2014a) with low transversal loads. It is possible that the difference in statistical significance between these studies reflect the differences in statistical power and sample size (4 muscles in Azizi et al. 2017 but 9 muscles in Siebert et al. (2014b), rather than a difference in the actually effect.

The muscle fibre is surrounded by collagen fibers in a helical-like way and this network contributes to muscle stiffness in two ways (1) as longitudinal force directly opposing tension and (2) as pressure force on the muscle fibers resulting in an indirect longitudinal force (Gindre et al., 2013). The orientation of the collagen fibers depends e.g. on the specific muscle or age, and alters if the muscle shape is changing (e.g., during contraction, relaxation). The muscle itself is like a liquid filled bladder and is constraint by the collagen network. Sleboda and Roberts (2017) observed that the interaction between collagen network and the incompressible fluid within the muscle influences the mechanical behavior of the muscle, i.e. during contraction the intra-muscle pressure increases and might reduce the force in longitudinal direction (Siebert et al., 2016).

In experiments with transversal compression of passive cubic muscle tissue it was observed that the elastic properties depend on muscle fiber orientation (Böl et al., 2012; Takaza et al., 2013; van Loocke et al., 2006). They found that stiffness increases, when the muscle was loaded more perpendicular in relation to muscle fibre orientation. We observed that the increased transverse force squeezed and thus lengthened the fascicles. As the fascicles reduce in thickness then they must rotate to lower pennation angle to maintain their spatial packing within the muscle. The greater the transverse force, the less the fascicles will increase in thickness, and thus the less they will rotate to higher pennation which might be associated with increasing passive muscle stiffness. Increasing muscle stiffness might hamper muscle deformation and thus contribute to the observed changes in muscle performance.

In contrast to the reduction in maximal longitudinal muscle force, we found enhanced forces in the last part of the contraction (Fig. 3A, $t = 0.18–0.23$ s) and an increased half relaxation time (Fig. 5). Part of the work done to lift the indentor or to deform the muscle might return during muscle deactivation when the load falls down and the muscle relaxes, thereby increasing the muscle force in this phase. Work performed transversally on the indentor, adjacent muscles or elastic tissue sheets may be conserved and released subsequently. This may represent an additional way of recovering energy during cyclical locomotion in addition to energy savings in series elastic structures (Alexander, 2002) and parallel elastic structures (Rode et al., 2009). The physiological relevance of effects related to transversal compression like changing muscle performance, energy flow or efficiency of muscle contraction during stretch shortening cycles should be examined in future studies.

5. Conclusions

The experiments of this study demonstrate that transversal muscle loading alters the contraction dynamics in the longitudinal direction in living humans. The results are confirmed by experiments on single dissected animal studies that observed the same phenomena like decreased maximal force, decreased rate of force development, and decreased half relaxation time in a load dependent manner. In light of wearing compression garments to increase sportive performance further studies addressing influence of muscle compression on muscle force and energy flow are required. It should be considered that transversally compressed muscles might act under dynamically more favorable conditions and that energy stored in elastic compression garments might be recovered.

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Conflict of interest statement

The authors have no conflicts of interest that are directly relevant to the content of this study.

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