

Acknowledgement:

To finish my study rehabilitation science and physiotherapy with specialization sports I chose a master thesis involving muscle contraction and the phenomenon of force enhancement. The learning process during this study resulted in knowledge applicable in practice. The author gives special thanks to following for the help during this research project. The author gives special thanks to Dr. Pieter van Noten for being my promoter. He made everything possible. As well fellow students who took part in the testing, my family and fellow students who participated in the tests and checked the spelling and the grammar of this thesis. Also the author gives thanks to the institution of REVAL. This research center focuses on rehabilitation and is part of the University of Hasselt, Belgium, where it was made possible to complete the protocol with the needed instruments.

Research context:

This pilot study focuses on the phenomenon of force enhancement because it still remains unexplained within the framework of the cross-bridge theory. Force enhancement is defined as the difference between an isometric force after an active stretch and a pure isometric contraction at the same length (Herzog 1998). There are three hypotheses based on muscular fibers that could all coexist (Fábio Carderelli Minozzo et al. 2013). The involvement of tendons on force enhancement has not been studied before. Tendons are a serial elastic component of muscle filaments, and could thus influence the force enhancement. The stretch of the tendon at high force effects the fiber length to avoid lengthening. Because force enhancement can only be achieved by an active stretch, the impact of eccentric training on this phenomenon is a very interesting item to study as well.

This subject interested me because several implications of the involvement of tendons and training effect on force enhancement in terms of being beneficial for natural human movement are possible. Firstly, the relevance to physiotherapy, to enhance force production in situations requiring high amounts of force like landings, walking downstairs and fall prevention after stumbling (Wolfgang Seiberl et al. 2015). Secondly, the relevance in the specialization sport, improving neuromuscular economy and saving of metabolic energy during every day human locomotion or sport performances (Joumaa et al. 2008).

The test protocol, which was set up in consultation with promoter and five other colleague students, resulted in a test battery that was usable for all students. Two weeks of testing were organized before and two after the four week eccentric training. The search for subjects to include in our study was done in team. In this study an eccentric training was designed in collaboration with the other colleague students. The testing and supervised training was divided equally. Each student accompanied three to four subjects in making appointments for the testing, guiding their home based exercises using social media or mobile phone and control the supervised training once a week. We received the data from our promoter after the test period. The data analysis and writing was done individually with the support of my promoter.

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The effect of eccentric training and tendon length on force enhancement

Abstract:

Introduction: When an isometric phase is preceded by an eccentric phase within the same contraction, an increased force output is observed compared to a continuous isometric contraction. This increased force output is referred to as force enhancement (FE) and its origin remains unclear until this day. The role of tendons, as a serial elastic component of muscles will be examined, as well as the impact of a four-week eccentric training program on FE.

Participants: 17 healthy males between 18 and 30 years old without injuries of the non-dominant lower extremity.

Measurements: FE was determined as the difference between an eccentric-isometric contraction and a referential isometric contraction, using an isokinetic dynamometer. The speed of the eccentric phase was set at 30- and 60 degrees per second ($^{\circ}/s$). To distinguish between tendon/fiber length ratio, m. triceps surae (TS) and m. quadriceps femoris (QF) were tested, with the TS having a 2.6 larger average tendon/fiber length ratio than QF.

Results: Participants were not fatigued during the protocol. TS shows 19 to 99 percent more FE than QF. A training effect of the eccentric-isometric contraction was shown at QF 30 $^{\circ}/s$ and TS 60 $^{\circ}/s$, whereas FE improved in the TS at 60 $^{\circ}/s$.

Discussion/conclusion: Existence of FE at the TS in this study could be explained by the suppressed inhibition and co-contraction due to the beneficial effect of tendon. because the TS was relatively more in stretched position than the QF could also explain the appearance of FE at the TS. Possible explanations of improved FE of TS at 60 $^{\circ}/s$ are a beneficial influence of tendons. Larger movement speeds could affect the FE after eccentric training as a result of decreasing tendon stiffness. The TS can withstand a higher amount of force after an active stretch of 60 $^{\circ}/s$ as a result of a four week eccentric training program.

Keywords: Force enhancement, Passive force enhancement, Eccentric training, Tendons.

Introduction

The first publications describing the analysis of muscle contraction are 60 years old. Observing two sets of interacting filaments, actin and myosin, that slide past one another and form a cross-bridges cycle during muscle shortening (sliding filament theory; Figure 1)

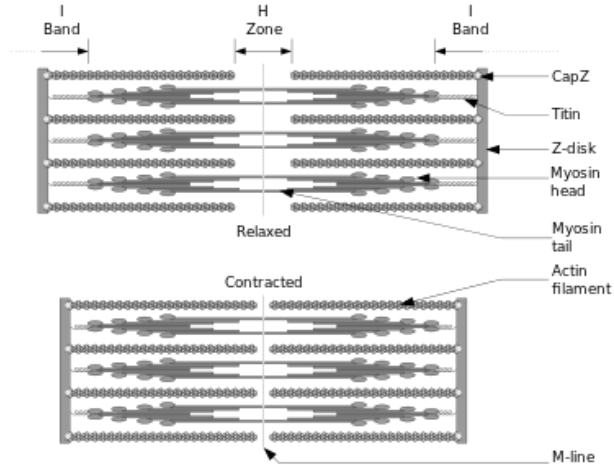


Figure 1: Sliding filament model: When a sarcomere contracts, the Z-disks moves closer together and the I-band gets smaller. At full contraction, the thin filaments overlap. Titin is a connective protein that connects the Z- and the M-line in the sarcomere (Boundless 2015).

(Huxley and Niedergerke, 1954). When a cross-bridge is formed after binding of calcium ion (Ca^{2+}) with troponin, myosin heads rotate towards the center of the sarcomere (power stroke) hydrolyzing adenosine triphosphate (ATP) into adenosine diphosphate (ADP) and a free phosphate group (P_i). As myosin heads bind ATP, it detaches from actin. If Ca^{2+} is still present, the entire cycle is repeated (Cross-bridge theory; Huxley 1969) (Figure 2).

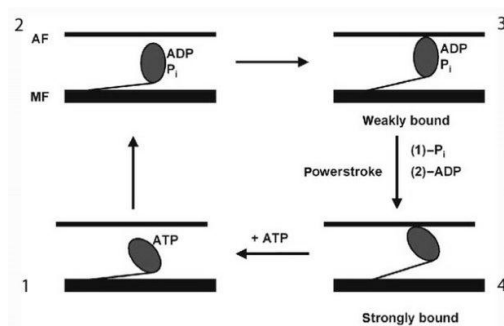


Figure 2: Illustration of the cycle of changes in myosin shape during cross-bridge cycling (1, 2, 3, and 4). ATP hydrolysis releases the energy required for myosin to do its job. AF: actin filament; MF myosin filament (Goody 2003).

During muscle activation, a muscle can deform based on length. Muscle length remains the same during an isometric contraction and varies during a dynamic contraction. A concentric contraction shortens the muscle, whereas during an eccentric contraction the force generated is insufficient to overcome the external load, resulting in a lengthening of the muscle (Johnny Padulo et al. 2013).

The produced force depends on a number of well-documented factors. We only discuss the factors relevant for this study. First, Acto-myosin overlap, where cross-bridges can be formed, is sarcomere-length dependent (Gordon et al. 1966) (Figure 3).

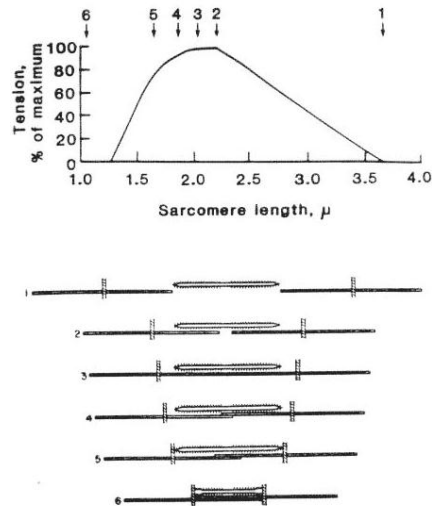


Figure 3: Length-tension relationship of a single frog semitendinosus muscle fiber. The numbers one through six on the length tension curve correspond to the numbers on the schematic diagram of thick and thin filament arrangement. In this way the relationship between thick myosin and thin actin filaments can be compared to the tension at various sarcomere lengths (From Gordon et al., 1966).

During high-velocity shortening, less cross-bridge formation is possible, so less force output is observed (Caputo et al. 1994). Peripheral (muscular) and central (neurological) fatigue reduce the amount of muscle force (Cairns et al. 2005). Lastly when an isometric phase within a muscle contraction is preceded by an eccentric phase, the phenomenon force enhancement (FE) appears during the activation (Herzog 1998). FE will be the focus in this article because it still remains unexplained within the framework of the cross-bridge theory.

When a muscle is stretched while activated and held at a certain final length long enough for the force transients to cease, the steady force achieved is always higher than the steady force that develops when the muscle is activated while already held isometrically at the same final length (Fábio Carderelli Minozzo et al. 2013). FE or residual force enhancement (RFE) defines the difference between an isometric force after an active stretch and a pure isometric contraction at the same final muscle length (Herzog 1998). RFE is composed of 2 elements an passive component (PFE), and an active component (AFE) that is calculated as the difference between RFE and PFE. The active component can be explained by the cross-bridge kinetics and sarcomere length non-uniformity. First, cross-bridge kinetics reflect decreased detachment rates following active muscle stretching, resulting in more attached

cross-bridges and more FE (Ford et al. 1981). Sarcomere length non-uniformity describes a non-uniformity in the length of the sarcomeres within a muscle fiber after an eccentric contraction. Some sarcomeres will overstretch resulting in passive tension force while other sarcomeres will stay in an optimal length and become stronger due to increasing overlap (Hill et al. 1953). FE increases with increasing stretch amplitude (Gavin J. et al. 2007) and longer muscle length (Seiberl et al. 2012), but it is close to independent of stretch velocity (Rassier et al. 2003). Further, it was concluded that FE increases with the level of activation during the active lengthening phase (Oskouei AE et al. 2006). Additionally, FE almost abolished after deactivation (Lee HD et al. 2002), indicating that a physiological origin is less evident.

Passive force enhancement (PFE) is the passive force after deactivation of an actively stretched muscle. The passive force is higher than the force produced after a purely passive stretch or after deactivation from an isometric contraction at the corresponding length (Herzog W. et al. 2003) (Figure 4).

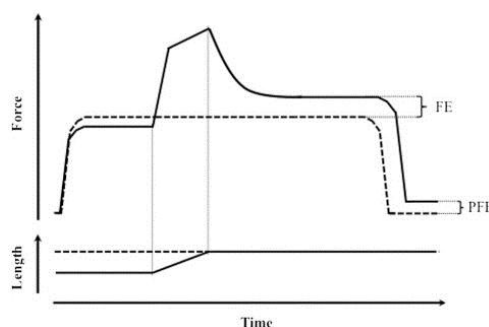


Figure 4: Schematic representation of muscle residual force enhancement. It shows two representative superimposed contractions from the same muscle as it is first activated, stretched to a certain final length, and then isometrically activated and kept at the same final length before being relaxed again. Top panel: force traces. Bottom panel: length traces. FE: force enhancement. PFE: passive force enhancement (Fábio Carderelli Minozzo et al. 2013).

PFE occurs at long lengths, it is long lasting (>25s) and it increases with stretch magnitude and initial muscle length, but it is independent of the speed of stretch (Herzog W. et al 2003). It is suggested that Titin is the structure responsible for most of the passive force in fibers and myofibrils (Granzier H. et al. 2000). It is a molecular spring that runs from the Z-lines of sarcomeres to the M-band (Figure 1). Furthermore, degradation or extraction of titin from myofibrils leads to a rapid drop in passive force (Granzier et al. 1995). PFE is related with an increase in strain in the passive element titin (Noble et al. 1992).

More calcium as a result of membrane damage after eccentric training will increase the stiffness of titin (Labeit et al. 2003, Ingalls et al. 1998). The main interest of this study is to determine if FE improves after an eccentric training. On one hand as a result of increased calcium levels (Barash et al. 2002, Lapier et al. 1995). On the other hand because FE occurs after an eccentric contraction.

Stiffness of titin can explain 25% of the PFE (Joumaa et al. 2008), which leaves 75% unclear. There could be a possibility that the tendons, as a serial elastic component (Figure 5), play a role in this yet unexplainable portion of the PFE. To test the influence of tendons on FE we selected the TS where the m. soleus and m. gastrocnemius medialis as a part of the TS shows an average tendon/fiber ratio of 10.1 and the QF where the m. vastus lateralis and the m. rectus femoris as a part of the QF shows an average tendon/fiber length ratio of 3.9 (Table 1). The TS has a 2.6 larger average tendon/fiber length ratio than the QF.

	TS		QF	
	m. soleus	m. gastrocnemius medialis	m. vastus lateralis	m. rectus femoris
Fiber length (cm)	3,8 ¹ 2,4 ³	4,8 ¹ 4,8 ³	6,6 ² 8,4 ³	6,6 ² 8,2 ³
Tendon length (cm)	27,0 ³	42,5 ³	22,5 ³	41,0 ³
Tendon L/ fiber L ratio	11,3 ³	8,9 ³	2,7 ³	5 ³
Average Tendon L/ fiber L ratio	10,1		3,9	
Taija Finni et al. 2001; 1) Woittiez et al. 1985, 2) Wickiewicz et al. 1983, 3) Hoy M et al. 1990				

Table 1. This table shows the calculation of the tendon/fiber ratio of the m. quadriceps femoris (m. vastus lateralis and m. rectus femoris) and m. triceps surae (m. soleus and m. gastrocnemius medialis).

If tendons would be partially responsible for FE, we need to know how they can store energy. Because the tendon stretches, the muscle is able to function with less or even no change in length, allowing the muscle to generate greater force (Thorpe et al. 1994). During rapid energy-dissipating events, tendons buffer the impact on the muscles by temporarily storing elastic energy, then releasing this energy to the muscle (Thomas J. et al. 2013). During a fast lengthening, tendons will lengthen even more and transfer more power (Kubo et al. 2000). A decrease in tendon stiffness as a result of eccentric training results in larger energy capacity (Witvrouw et al. 2007).

Method

This study was approved by the local ethical commission of UHasselt and the central ethical commission of UZLeuven. Participants: 17 participants were recruited. Inclusion criteria were healthy male subjects without injury of the non-dominant lower extremity and between age of 18 and 30 years old. Every subject was guided by a personal coach to avoid drop out and assure therapy royalty.

Procedure: The aim of this research was to determine the role of the tendons in FE. In addition, the impact of eccentric training on FE was also studied. FE was determined by comparing an eccentric-isometric contraction to a referential isometric contraction, using an isokinetic dynamometer. The eccentric test speed was set at $30^\circ/\text{s}$ and $60^\circ/\text{s}$. To study the role effect of tendons in FE, two muscle groups (QF and TS) with different muscle-tendon ratio were tested. The impact of a four-week eccentric training program on FE was studied as well.

The protocol started with a warming up at 60% of the maximum heart rate ($220 - \text{age}$) for 15 minutes on a treadmill and stretching of the QF and TS. After the warming up an isokinetic dynamometer (Enraf Nonius) was used, which has been proven as a reliable and a valid tool to measure the generated moment of the QF and the TS (Joshua M. et al 2004). Different muscle contractions in positions that exclude gravity resulted in specific results. The maximal isometric tests were performed in sitting position with the knee flexed 90° for the QF and the knee extended 0° and ankle plantar flexion 0° for the TS. At the end there was a cooling down at 60% of the heart rate maximum for 15 minutes on a treadmill.

After the warming up, each muscle group was tested in a systematic order: first a pure isometric contraction (ISO 1) was performed at the reference length, then eccentric contractions were performed with 2 different speeds (ECC $30^\circ/\text{s}$ and ECC $60^\circ/\text{s}$) to end with the same reference isometric contraction (ISO 2). For each contraction type (ISO 1, ECC $30^\circ/\text{s}$, ECC $60^\circ/\text{s}$ and ISO 2), three attempts of about 8s duration were separated with a rest interval of 30s. In between different contraction types, three minutes rest was allowed. This protocol was repeated for both QF and TS. Specific for QF, the isometric contraction were performed at 90° knee angle whereas the eccentric isometric contractions started with an active stretch from 30° of flexion towards 90° where after the contraction was isometrically

persisted at the reference length until 8s of total muscle activation were performed. For the TS after an active stretch from 35° of plantar flexion. To evaluate FE, forces were measured between the fifth and the sixth second after the start of initial muscle activation. (Figure 6).

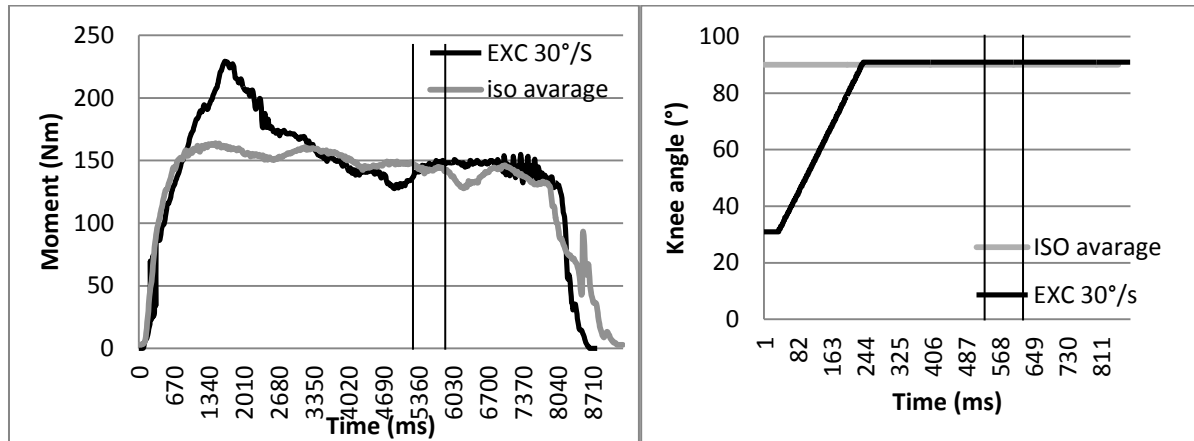


Figure 6: This figure illustrates when forces of the QF were measured and where the eccentric-isometric and isometric muscle contractions are located. The two vertical lines indicate the period of measurement. Left panel: force traces. Right panel: length traces. Black line: eccentric-isometric contraction of 30°/s, grey line: average isometric contraction

After the pre-test, subjects performed a four weeks eccentric training program, consisting of two home-based exercises and one supervised session each week. The home based exercises consisted of lunges, single leg squat and single leg heel drop. The home-based exercises started with three sets and 10 repetitions with supplementary five repetitions each following week and were regularly checked by their personal assistant. The supervised exercises consisted of the home-based exercises and supplementary weight training exercises. The weight training consisted single leg press eccentric and single leg heel drop on the leg press and single knee extension eccentric. The weight training started at 90% 1RM and three sets of 10 repetitions with supplementary 10% 1RM each following week. After four weeks a post-test was performed with the same protocol as the pre-test.

Data analysis

Statistics were performed with SPSS statistics 22. A paired sampled T-test was used to compare two measurements of the same group. We used a parametric test because groups were normal distributed. Within-group comparisons were done for fatigue and training effect of the isometric and eccentric-isometric contractions. The relative force enhancement of the two contraction speeds between the two muscle groups were compared by non-parametric Kruskal-Wallis and Mann-Whitney tests because these groups were not normal distributed. The same tests were used to find a training effect of the relative force enhancement.

First, fatigue was measured by taking the difference between the first and second isometric contraction during both pre- and post-test. Second, the eccentric-isometric measurements and the average pure isometric contraction were compared for both the pre- as the post-test. If there was a difference with a significance level of $p < 0.05$, FE was assumed. Finally, to detect a difference of FE between the two muscle groups and to study the training effect, the relative FE's (Eccentric-isometric/isometric) of the four groups were compared using the Kruskal-Wallis test. The Mann-Whitney test was used to look for differences between groups.

Results

First, differences between the first (ISO 1) and the second (ISO 2) isometric contractions during both pre- and post-tests were evaluated for fatigue. No significant differences between ISO 1 and ISO 2 were found, indicating an unfatigued muscle. Since ISO 1 and ISO 2 can be considered as equal, their mean was used as reference isometric force. The isometric average of the TS was 46 percent less than the isometric average of the QF (Figure 7).

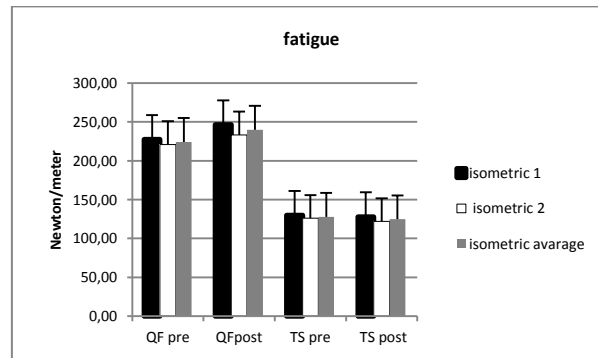


Figure 7: This table shows the fatigue between the first and second isometric tests. QF= m. quadriceps femoris, TS= m. triceps surae, pre= test before training, post= test after training, isometric 1= isometric test in the beginning of the test, isometric 2= test at the end of the test.

Hereafter, relative FE (eccentric-isometric/isometric) of the QF and the TS was evaluated for both speeds and for the pre- and post-test to describe the role of tendons. There was difference between the eccentric-isometric and isometric contraction of the QF at the two speeds, before or after the eccentric training. TS, with a 2.6 larger average tendon/fiber length ratio than the QF (table 1), shows 19 to 99% more FE than QF, which was a statistically significant difference (figure 10).

To evaluate the effect of training on both TS and QF, mean isometric and eccentric (both speeds) data were compared (figure 8 and 9, respectively). The effect of a four week eccentric training on the average isometric contractions of the two muscle groups was observed. There was a significant training effect of 7% between the pre- and post-test of the QF. This effect was not seen in the TS (Figure 8).

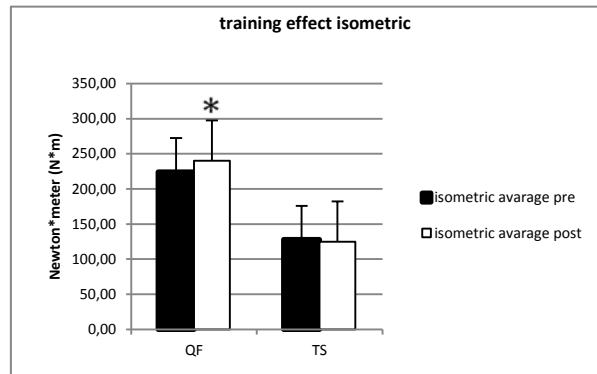


Figure 8: This table shows the mean \pm 1sd of the training effect on the average isometric contractions of the 2 muscle groups. * significantly different from QF iso pre with $P < 0.05$ significance level, QF= m. quadriceps femoris, TS= m. triceps surae, pre= test before training, post= test after training.

Secondly, evaluation of four-weeks eccentric training on the eccentric-isometric contractions of the two muscle groups at a speed of 30°/s and 60°/s showed a significant difference between the pre- and post-test of the QF at 30°/s and the TS at 60°/s. No significant difference was demonstrated between the pre- and post-test of the QF at 60°/s and TS at 30°/s (Figure 9).

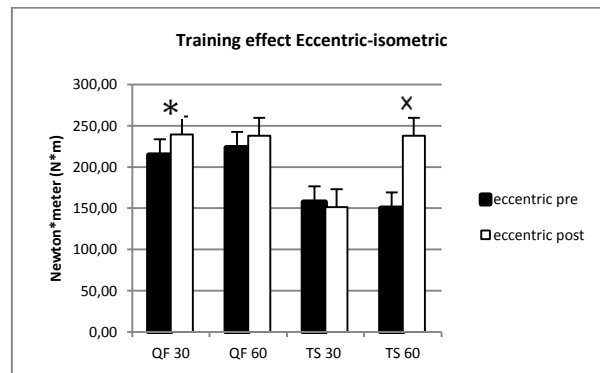


Figure 9: This table shows the mean \pm 1sd of the training effect on the eccentric-isometric contractions of the 2 muscle groups with two speeds. * significantly different from QF 30 pre with $P < 0.05$ significance level, x signification different from TS 60 pre with $P < 0.05$ significance level. QF= m. quadriceps femoris, TS= m. triceps surae, 30= eccentric contraction 30°/s, 60= eccentric contraction 60°/s, pre= tests before training, post= tests after training.

Lastly, the result of four weeks of eccentric training on FE was evaluated. Demonstrating a significant increase for the TS of 80% at a speed of 60°/s. There was no significant training effect of FE for TS 30 (Figure 10).

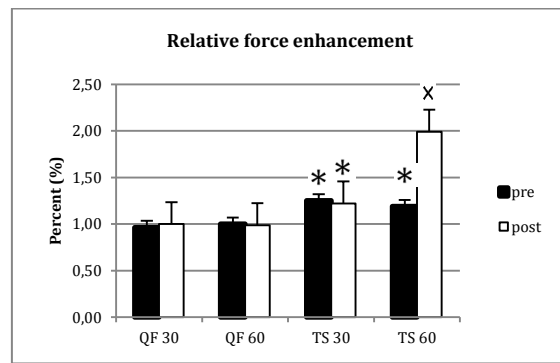


Figure 10: This table shows the mean \pm 1sd of the relative force enhancement (eccentric-isometric/isometric). * significantly different from 1 with $P < 0.05$, ^X significantly different from TS 30 pre, TS 30 post and TS 60 pre with $P < 0.05$ QF= m. quadriceps femoris, TS= m. triceps surae, 30= eccentric contraction 30°/s, 60= eccentric contraction 60°/s, pre= tests before training, post= tests after training.

An overview of the four weeks eccentric training effect of the QF and the TS is illustrated in table 2. There was a training effect of 16 Nm for the QF during the isometric contraction. The eccentric-isometric training effect of the QF 30 amounts 24.5 Nm and a remarkable 88 Nm for TS 60. There is no training effect of the TS 30. However, a training effect on FE of 80% was only found for the TS 60.

Training effect			
Muscle + speed	Isometric	Eccentric-isometric	FE
QF 30°/s	↗	↗	none
QF 60°/s	↗	=	none
TS 30°/s	=	=	=
TS 60°/s	=	↗	↗

Table 2: This table shows the influence of four weeks eccentric training on the isometric contraction, the eccentric-isometric contraction and on force enhancement (FE) on the m. quadriceps femoris (QF) and m. triceps surae (TS) with an eccentric contraction speed of 30°/s and 60°/s.

Discussion

In this study, the effect of a four-week eccentric training program and the tendon/fiber length ratio on force enhancement was evaluated. Determining FE includes calculating the difference between the isometric and eccentric-isometric contraction. Because the eccentric-isometric contraction was tested after the isometric contraction, exhaustion could have influenced the results. Therefore, it was important to test a reference isometric contraction a second time at the end. Statistically, if there was no significant difference between the isometric contraction before (ISO 1) and after (ISO 2) the eccentric isometric contractions, we assumed there was no fatigue. The influence of the tendons on FE was observed by means of testing two different muscle groups, as well as the comparison of two different stretch velocities. It is important to compare the amount of relative FE of the two muscle groups to draw a conclusion, because the QF produces 46 percent more force than the TS. To conclude the final results of the training effect on FE, the effect of training on the isometric and the eccentric-isometric contraction was to be measured separately.

Difference of force enhancement between QF and TS. Role of tendons.

There was no FE measured at QF in this study. These findings are in contrast with the study of Seiberl et al. (2010) where the QF was tested at an isometric position of 100° flexion with stretch amplitude of 20° and a velocity of 60°/s, which resulted in a FE of 5-10%. The amount subjects included in the study were equal but the subjects of Seiberl et al. (2010) performed only three eccentric-isometric contractions and three isometric contractions in a randomized order. Possible reason why FE of the QF was absent in this study could be the larger stretch amplitude of 60°. The larger amplitude could limit the activation as a result of enhanced protective neural inhibition of the muscle (Hahn et al. 2007, Westing S. H. et al. 1989). Co-contraction could also be triggered by the large stretch amplitude and maximal forces in this study resulting in the absent FE of the QF. Co-contraction of the knee flexors is known to occur during isokinetic strength tests of the knee extensors. The amount of co-contraction increases with larger angles of knee flexion and at higher movement velocities. Antagonist co-contraction ranged up to 32% of maximum agonist activity in normal individuals (Snow C. J. et al. 1993).

It is possible that a FE was found at the TS because it contains a 2.6 larger average tendon/fiber length ratio. The stretch of the tendon at a high force affects the fiber length in avoiding excessive lengthening (Arnold et al. 2011). It could be possible that eccentric forces of the TS were not suppressed by a protective neurological inhibition or co-contraction of the dorsal flexor muscles, due to tendons absorbing the majority of the forces. The TS consists of pennate fibers resulting in fewer sarcomeres in series and shorter fiber length (Narici et al. 1999, Liem et al. 2001). The 65 percent shorter fiber length of the TS compared to the QF could explain the FE found at the TS in this study because the fibers undergo a larger stretch amplitude. A pennate muscle like TS can relatively produce more force than a parallel muscle like QF. Because the pennate structure is beneficial for generating force, this could also facilitate a higher FE (Liem et al. 2001). Existence of FE at the TS in this study could be explained by the lesser extent of inhibition and co-contraction, as well as the beneficial effect of tendon and the beneficial muscle architecture of the TS resulting in more force.

The influence of the amount of muscle stretch could explain the FE. The TS was relatively more in stretch position than the m. rectus femoris as a part of the QF (Herzog W. et al 2003). The hip flexion of 90° relatively relaxed the m. rectus femoris in contrast with the knee extension at 0° for the m. gastrocnemius. Testing the QF in a lying position could result in a better comparison for both muscle groups.

Training effect of force enhancement.

The large training effect of FE at the TS 60°/s is remarkable. The isometric force of the TS remained unchanged after training while the eccentric-isometric force of TS 60°/s increased in contrast to TS 30°/s where both contraction types remained unchanged (table 7). The role of the tendon could also be an explanation. During a fast lengthening, tendons could transfer and store more force so higher PFE could be generated in comparison to a slower stretching speed (Kubo et al. 2000). However, this difference in FE between the two movement speeds was noticed only after the eccentric training. Larger movement speeds could effects the FE after eccentric training as a result of decreasing tendon stiffness (Morrisey et al. 2011) because a decrease in tendon stiffness can result in larger energy capacity (Witvrouw et al. 2007). Eccentric training is also known to increase the stiffness of titin too as a result of Ca²⁺ inflow after membrane damage (Barash et al. 2002, Lapier et al. 1995), which could explain

the larger FE at both speeds. The reason for FE to increase only at 60°/s could be stronger tendons after larger movement speeds (Manoj Parimi et al. 2012). In contrast with the study of Rassier et al. (2003), FE could be dependent of the speed of stretch because in this study there was a significant difference between the two velocities after training. Rassier et al. (2003) only studied the lumbrical fibers of a frog without regard to the possible impact of tendons. These findings could confirm the beneficial effect of tendons on force after an eccentric training.

Critical reflection.

With our test protocol, we were able to prevent the negative influence of exhaustion on the results. All the subjects were accurately followed up during the study. There was only one drop out for this study because the measurements of the TS for this subject were not performed well. We could assume the test and training protocol as safe because there were no signs of injuries among the test subjects during or after the study. Testing the QF in a lying position could be an improvement of the protocol. The power of the study could enhance with more subjects and both genders for a larger representation. The training effect could have had a larger impact if the period of training would be increased to eight weeks because there will be a larger muscular adaptation after a longer training period (Alegre et al. 2006).

Implications natural human movement and sport performances.

Several implications of the involvement of tendons and training effect on FE in terms of being beneficial for natural human movement are possible. First, to enhance force production in situations requiring high amounts of force (landings, downstairs walking and fall prevention after stumbling) (Wolfgang Seiberl et al. 2015). Secondly, improving neuromuscular economy and saving of metabolic energy during every day human locomotion or sport performances (Joumaa et al. 2008). During the sport gymnastics the gymnast will perform a landing after a difficult and exhausting performance. During the landing the gymnast will land using an isometric contraction preceded by an eccentric contraction of the QF and TS. The gymnast will be stronger during the isometric contraction and will perform the isometric contraction with less energy lost resulting in more stability.

Conclusion

TS with 2.6 larger average tendon/fiber length ratio shows 19 to 99 percent more FE than QF. Existence of FE at the TS in this study could be explained by the suppressed inhibition and co-contraction due to the beneficial effect of tendon. The beneficial muscle architecture of the TS and because the TS was relatively more in stretched position than the QF could also explain the appearance of FE at the TS.

Eccentric training only influenced the eccentric contraction of TS 60°/s resulting in 80% more FE. Possible explanations are the beneficial influence of tendons. Larger movement speeds could affect the FE after eccentric training as a result of decreasing tendon stiffness.

Increase in stiffness of titin after eccentric training could result in larger FE as well. FE could be dependent of speed of stretch because there was a significant difference between the two velocities after training.

The TS can withstand a higher amount of force after an active stretch of 60°/s as a result of a four week eccentric training program.

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