



**HAL**  
open science

# Effects of eccentric training on mechanical properties of the plantar flexor muscle-tendon complex

Alexandre Fouré, Antoine Nordez, Christophe Cornu

## ► To cite this version:

Alexandre Fouré, Antoine Nordez, Christophe Cornu. Effects of eccentric training on mechanical properties of the plantar flexor muscle-tendon complex. *Journal of Applied Physiology*, 2013, 114 (5), pp.523-537. 10.1152/jappphysiol.01313.2011 . hal-02130794

**HAL Id: hal-02130794**

**<https://hal.science/hal-02130794>**

Submitted on 20 Apr 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



# Effects of eccentric training on mechanical properties of the plantar flexor muscle-tendon complex

Alexandre Fouré,<sup>1,2</sup> Antoine Nordez,<sup>1</sup> and Christophe Cornu<sup>1</sup>

<sup>1</sup>Université de Nantes, Laboratoire "Motricité, Interactions, Performance," UFR STAPS, Nantes, France; <sup>2</sup>Centre de Résonance Magnétique Biologique et Médicale, Université d'Aix-Marseille, Marseille, France

Submitted 21 October 2011; accepted in final form 11 December 2012

**Fouré A, Nordez A, Cornu C.** Effects of eccentric training on mechanical properties of the plantar flexor muscle-tendon complex. *J Appl Physiol* 114: 523–537, 2013. First published December 13, 2012; doi:10.1152/jappphysiol.01313.2011.—Eccentric training is a mechanical loading classically used in clinical environment to rehabilitate patients with tendinopathies. In this context, eccentric training is supposed to alter tendon mechanical properties but interaction with the other components of the muscle-tendon complex remains unclear. The aim of this study was to determine the specific effects of 14 wk of eccentric training on muscle and tendon mechanical properties assessed in active and passive conditions in vivo. Twenty-four subjects were randomly divided into a trained group ( $n = 11$ ) and a control group ( $n = 13$ ). Stiffness of the active and passive parts of the series elastic component of plantar flexors were determined using a fast stretch during submaximal isometric contraction. Achilles tendon stiffness and dissipative properties were assessed during isometric plantar flexion, and passive stiffness of gastrocnemii muscles and Achilles tendon were determined using ultrasonography while ankle joint was passively moved. A significant decrease in the active part of the series elastic component stiffness was found ( $P < 0.05$ ). In contrast, a significant increase in Achilles tendon stiffness determined under passive conditions was observed ( $P < 0.05$ ). No significant change in triceps surae muscles and Achilles tendon geometrical parameters was shown ( $P > 0.05$ ). Specific changes in muscle and tendon involved in plantar flexion are mainly due to changes in intrinsic mechanical properties of muscle and tendon tissues. Specific assessment of both Achilles tendon and plantar flexor muscles allowed a better understanding of the functional behavior of the muscle-tendon complex and its adaptation to eccentric training.

triceps surae muscles; Achilles tendon; passive stiffness; CSA; ultrasound

ECCENTRIC TRAINING IS A MECHANICAL loading often used in clinical context to rehabilitate patients with tendon injuries. Eccentric loading consists in muscle-tendon complex (MTC) lengthening while muscle is contracting, thus it combines effects of stretching and strengthening (3). It was shown that tendinopathies alter tendon mechanical properties when determined in active condition (6), and many positive effects in tendon rehabilitation were found after clinical program including eccentric loadings (2, 28, 42, 47, 52, 81). Most studies examining eccentric effects on tendon have utilized ultrasonography in vivo to determine tendon stiffness during muscle contraction; however, results differ in several previous studies (12, 54, 61) considering the type of the tested population (e.g., healthy volunteers, subjects with tendinopathies) and training characteristics (i.e., intensity, volume, duration). To better

understand the efficiency of eccentric exercises in rehabilitation, adaptations of tendon mechanical properties linked to tendon mechanobiology processes were investigated (85). For example, physiological mechanisms such as collagen turnover were shown to be altered after eccentric training (48–50).

Most of the studies determining the effects of eccentric training only assessed tendon stiffness during isometric contraction (12, 54, 61). Yet tendon dissipation coefficient is representative of a storage-recoil process and was shown to be altered by strength (75) and plyometric (18) training in vivo. In addition, other structures included in the series elastic component (SEC) also play a role in tension transmission and influence the elastic energy storage-recoil process (1). Effects of eccentric training on the global SEC stiffness were already assessed (73). From our results, a specific adaptation of muscle and tendon can be hypothesized (73). Due to technological limitations of noninvasive investigation of muscle stiffness during contraction in vivo, this hypothesis remains to be verified. However, a method developed for isolated muscle (15, 57) allows the determination of specific stiffness for the force-dependent component ( $SEC_1$ ) and force-independent component ( $SEC_2$ ), constituting the plantar flexors SEC during isometric contraction. This method was recently adapted in vivo (17). With regard to previous studies,  $SEC_1$  and  $SEC_2$  were considered to be the active and passive part of the SEC, respectively (17, 19). To our knowledge, no study has yet investigated the effects of eccentric training on the active part of SEC stiffness in vivo, although a decrease in muscle stiffness of the elbow flexors was hypothesized after eccentric training (73). This potential is supposed to be linked to structural changes in muscle such as architecture and/or fiber type composition and has already been shown to result from eccentric training programs (7, 38).

In addition, only a few studies concentrated on adaptations of passive mechanical properties of MTC to eccentric training in vivo (35, 39, 72, 87). Yet it was shown that the passive mechanical properties of MTC play an important role in postural, walking, and running activities (e.g., 30, 80). Mahieu et al. (54) showed that eccentric training decreases the passive torque produced by ankle joint during dorsiflexion. A specific change in muscle and tendon passive stiffness after eccentric training was hypothesized, but specific adaptation between muscle and tendon was not assessed. By means of a recent method determining the stiffness of muscle and tendon of gastrocnemii MTC using ultrasonography during passive motion of ankle joint (36, 37), specific adaptation of muscle, and tendon passive stiffness could be analyzed.

The determination of specific adaptations of muscle and tendon mechanical properties assessed in active and passive conditions to eccentric training may provide important infor-

Address for reprint requests and other correspondence: C. Cornu, Laboratoire "Motricité, Interactions, Performance", UFR STAPS, 25 bis Bd Guy Mollet, 44 322 Nantes cedex 3, France (e-mail: christophe.cornu@univ-nantes.fr).

mation concerning the functional behavior of MTC and the underlying mechanisms to successfully apply eccentric training in rehabilitation programs. On the basis of previously described methods (17–22, 69), the aim of the present study was to determine the effects of eccentric training on mechanical properties of plantar flexors considering: 1) the stiffness of SEC<sub>1</sub> and SEC<sub>2</sub>, 2) the stiffness and dissipative properties of the Achilles tendon during isometric plantar flexion, and 3) the stiffness of gastrocnemii muscles and the Achilles tendon determined during passive motion of the ankle joint.

## METHODS

### Subjects

Twenty-four men volunteered to participate in this study and were randomly assigned to trained [ $n = 11$ , 21.2 (2.7) yr, 177.1 (6.1) cm, 71.1 (5.8) kg] and control groups [ $n = 13$ , 20.5 (1.7) yr, 178.0 (6.5) cm, 68.7 (6.9) kg]. All subjects were involved in regular sport practices [8.8 (6.5) h/wk] and did not change their usual activity during the period of the study. Subjects were fully informed about the nature and the aim of the study before they signed a written informed consent form. Approval for the project was obtained from the local ethics committee. All procedures used in this study were in conformity with the Declaration of Helsinki.

### Eccentric Training

The eccentric training program was based on different kinds of exercises, as defined in the literature (e.g., 2, 54). More precisely, the subjects performed 1) eccentric contraction of the plantar flexor muscles with the leg fully extended as described in Alfredson et al. (2); 2) eccentric contractions by going down from a box of different heights [i.e., from either low (35 cm), medium (50 cm) or high (65 cm) height] performed on one or both feet. All eccentric actions of the plantar flexors were performed either by the right leg or both legs and concentric actions with the left leg only. The intensity level was increased by an elevated number of exercises (i.e., the number of eccentric plantar flexion per exercise) and the jump height. The training program lasted for 14 wk and included 34 sessions of 1 h for a total of ~6,800 eccentric actions (from 200 to 600 per session).

### Experimental Design

Subjects were tested over three sessions performed on different days in a randomized order: 1) a session to assess Achilles tendon and triceps surae muscles geometry; 2) a session to determine Achilles tendon mechanical properties and SEC stiffness in active conditions; 3) a session to assess ankle joint range of motion and the stiffness of gastrocnemii muscles and Achilles tendon during passive motion of the ankle joint.

Subjects performed the three test sessions before (pretest) and 1 wk after the end of the eccentric training period (posttest). Reproducibility of all defined parameters was assessed. Methods were already used in previous studies to determine effects of plyometric exercises (16, 18, 19).

### Achilles Tendon and Triceps Surae Muscles Geometry

Measurements of muscle and tendon cross-sectional area (CSA) were performed by ultrasonographic imaging scans (Philips HD3, Philips Medical Systems, Andover, MA) with an electronic linear array probe (7.5-MHz wave frequency; L9–5, Philips Medical Systems). Measurement of Achilles tendon CSA (CSA<sub>T</sub>) and length was already described in a previous study (18). Intraclass coefficient correlation (ICC) of tendon geometrical parameters ranged from 0.95 to 0.99 ( $n = 8$ ).

The measurements of the triceps surae muscles CSA and architecture were previously described (19) and performed using the same ultrasonographic device and the same probe. Subjects stood on one leg with the ankle and knee joints of the other leg flexed at 90° and fully immersed in a water-filled container. The CSA of triceps surae and gastrocnemii muscles (CSA<sub>TS</sub> and CSA<sub>GAS</sub>, respectively) was averaged across points at 50%, 60%, and 70% from proximal extremity of lower leg length. By using longitudinal ultrasonographic images captured along the belly of each muscle as described in previous studies (40, 41), fascicle length and pennation angle were measured. ICC of muscle architecture and CSA ranged from 0.81 to 0.97 ( $n = 13$  and  $n = 16$  respectively) (19).

### Series Elastic Component Stiffness

The experimental design was already described in previous studies (16, 17, 19). A Biodex System 3 Research (Biodex Medical, Shirley, NY) isokinetic dynamometer was used to measure the external torque, ankle joint angle, and ankle joint angular velocity. Subjects were seated on the isokinetic dynamometer with legs fully extended and their thighs, hip, and shoulders secured and held in position by adjustable lap belts. The ankle joint angle was fixed at 75° (the foot perpendicular to the tibia = 90° with angles less than 90° being in plantar flexion), and hip angle was flexed to 140° (full extension = 180°).

Surface electromyographic (sEMG) signals of the gastrocnemius medialis, gastrocnemius lateralis, soleus, and tibialis anterior muscles were recorded as described previously (19, 20) using active surface electrodes with an interelectrode distance of 10 mm (DE-2.1, Delsys, Boston, MA) placed on the belly of muscles according to surface electromyography for noninvasive assessment of muscle (S.E.N.I.A.M.) recommendations (33). sEMG and mechanical signals were recorded simultaneously and sampled at 1,000 Hz using an analog-to-digital converter (National Instrument, Delsys) and saved on a computer hard drive using EMG-Works 3.1 software (Delsys). In particular, EMG values were determined for a 100-ms period prior to and after the stretching trials to detect potential effects of short latency reflex on EMG signals (19).

Subjects performed 1) a warm up that consisted of submaximal isometric plantar flexions; 2) two maximal voluntary contractions under isometric condition in plantar flexion performed at 75° with 2 min of rest between each trial; 3) a familiarization to the short range stiffness experiment in which subjects had to sustain two submaximal torques at 40 and 80% of their maximal torque. During each trial, a fast stretch into dorsiflexion was applied through a range of motion of 20° (i.e., from 75° to 95°). The acceleration of this stretch was controlled by the Biodex Research Tool kit software. The angular velocity during the stretch reached 250°/s and was constant 60 ms after the beginning of the motion; 4) the short range stiffness experiments (14 trials) described above were then performed at 7 levels of submaximal torque in a random order (two trials at each 10% of maximal torque from 30% to 90% of maximal torque). Between each trial, 2 min of rest was provided.

The torque measured by the dynamometer was corrected with regard to inertia and the weight of the dynamometer attachment (i.e., without the foot being included) to obtain the external torque at the ankle joint. The external torque and the ankle angle were determined when the joint started to move (i.e., when velocity >0) and 60 ms thereafter. A maximal velocity (i.e., ~250°/s) was obtained 60 ms after the beginning of the stretch with a range of motion of ~7°. The MTC stretching velocity and range of motion estimated from published anthropometric data (31) were ~90–110 mm/s and ~2% of the initial length of MTC, respectively. Considering that muscle fiber slack length of gastrocnemii estimated in humans (36) is very close to that reported by Morgan et al. (58, 60) for isolated muscle, it was assumed that stretching velocity was in the same range as those used previously on animals. Because the starting angle was 15° in plantar flexion, the contribution of the parallel elastic component of agonists

and antagonists was neglected. Thus the joint compliance (i.e., inverse of joint stiffness) was considered as the compliance of two springs placed in series, representing compliance of the SEC<sub>1</sub> and SEC<sub>2</sub>. The active component of the series elastic component compliance was thought to be inversely proportional to the torque (57), and the passive component of the series elastic component compliance (C<sub>SEC2</sub>) was assumed to be constant across the range of torque investigated. The relationship between ankle joint compliance and torque can be written as follows:

$$\alpha = C * T = \alpha_0 + C_{SEC2} * T \quad (1)$$

where  $\alpha$  is calculated as the product between external torque (T) produced before the stretch and ankle joint compliance (C), and  $\alpha_0$  represents the compliance index (i.e., the slope of the torque-compliance relationship) of the SEC active part.

A linear regression was applied on the relationship alpha ( $\alpha$ ) – torque (T). Then,  $\alpha_0$  and C<sub>SEC2</sub> were extracted as the Y-intercept and the slope, respectively. Joint stiffness was determined as the ratio of changes in external torque and ankle angle between the beginning of the stretch and 60 ms after the stretch (the determination of instantaneous compliance with regard to the torque-angle relationship during the stretch would have been also possible. This alternative method for the assessment of joint stiffness is developed in APPENDIX A and provides similar results compared with those calculated by the ratio of changes). Joint stiffness and SEC<sub>1</sub> stiffness (S<sub>SEC1</sub>) were determined for two relative torque levels (i.e., 30% and 60% of MVC) and 60 N·m. ICC of series elastic component parameters ranged from 0.88 to 0.96 ( $n = 14$ ) (17).

$$S = T / (T * C_{SEC2} + \alpha_0) \quad (2)$$

The joint stiffness-torque relationship was assessed for each subject and each session (i.e., pretest and posttest). A stiffness index of the active component of the SEC (SI<sub>SEC1</sub>) and a stiffness of the passive component of the SEC (S<sub>SEC2</sub>) were calculated as the inverse of  $\alpha_0$  and C<sub>SEC2</sub>, respectively. Joint stiffness was determined as the ratio of changes in external torque and ankle angle between the beginning of the stretch and 60 ms after the stretch (the determination of instantaneous compliance with regard to the torque-angle relationship during the stretch would have been also possible. This alternative method for the assessment of joint stiffness is developed in APPENDIX A and provides similar results compared with those calculated by the ratio of changes). Joint stiffness and SEC<sub>1</sub> stiffness (S<sub>SEC1</sub>) were determined for two relative torque levels (i.e., 30% and 60% of MVC) and 60 N·m. ICC of series elastic component parameters ranged from 0.88 to 0.96 ( $n = 14$ ) (17).

#### *Achilles Tendon Mechanical Properties during Contraction*

Subjects were in prone position with their legs fully extended. Thighs, hips, and shoulders were secured and held in position by adjustable lap belts as previously described (18).

The session that assessed the mechanical properties of Achilles tendon included the following protocols. 1) A warm up consisting of constant submaximal isometric plantar flexion. 2) Two maximal voluntary isometric contractions in plantar flexion and dorsiflexion, with the knee fully extended at an ankle angle of 90°. The maximal isometric torque in plantar flexion (MVC) was then determined as the maximal value for the two trials. The maximal rate of torque development in plantar flexion (RTD<sub>max</sub>), defined as the maximal slope of the torque-time relationship, was also characterized for the two MVC trials. 3) Familiarization trials to perform a linear increase in isometric torque in plantar flexion, from a relaxed state to 90% of MVC within 5 s, followed by a linear decrease in isometric torque, from 90% of MVC to the rest state within 5 s. Visual feedback was used to regulate and train the subjects for this task. 4) Five trials of constant isometric torque development in plantar flexion as described in *point 3* were then performed by each subject with 2 min of rest between each trial. Displacement of the distal myotendinous junction of the gastrocnemii was measured during the test using ultrasonography. The linear array probe mounted on an externally fixed bracket was strapped onto the skin of subjects to obtain longitudinal ultrasonic images of the distal myotendinous junction of the gastrocnemii.

Ultrasonographic videos were recorded on a hard disk at 25 Hz. To synchronize the torque signal and ultrasonographic images from the videos, the signal of the switch used to start the video was also recorded using the Delsys system. A selection of 40 images, including

20 images equally spaced from both the loading and unloading phases of torque development were collected (Adobe Premiere Elements, Adobe Systems, San Jose, CA) from each trial. Displacements of the myotendinous junction were manually measured on these 40 images using open source digital measurement software (Image J, National Institutes of Health, Bethesda, MD).

The ankle joint torque measured by the dynamometer was converted to tendon force (Ft) using Eq. 3 (6):

$$Ft = T / m_g \quad (3)$$

where  $m_g$  is the moment arm length of gastrocnemii at 90° of ankle joint and knee fully extended, which was estimated from the limb length of each subject (31, 34). Myotendinous junction displacement was corrected with the passive displacement due to joint rotation during the “isometric” contraction as previously described (18, 22). The ratios of the calculated tendon force (Ft) and the corrected elongation ( $\Delta L$ ; i.e., displacement of myotendinous junction) were used to calculate the stiffness of the Achilles tendon.

The Ft- $\Delta L$  relationship is usually curvilinear, consisting of an initial region (toe region), characterized by a large increase in  $\Delta L$  with increasing force and a linear region after the toe region (85). In the present study, the Ft and  $\Delta L$  values from the ascending curve between 50% and 90% of minimal MVC between pretest and posttest were fitted to a linear regression equation, the slope of which was defined as the Achilles tendon stiffness (S<sub>T</sub>) (45). A stiffness index (SI<sub>T</sub>) using an exponential model was also determined as previously described (18). The maximal elongation was defined as  $\Delta L_{max}$ .

Areas under the ascending and descending phases of the curve were calculated and represent the potential elastic energy stored (E<sub>S</sub>) and recoiled energy (E<sub>R</sub>), respectively (53, 65, 66). From these parameters, a dissipation coefficient (DC) was calculated as follows:

$$DC = (E_S - E_R) / E_S \quad (4)$$

EMG signals of the gastrocnemius medialis, gastrocnemius lateralis, soleus and tibialis anterior muscles were recorded during isometric contraction using active surface electrodes. ICC of tendon mechanical properties ranged from 0.94 to 0.99 ( $n = 7$ ) (18).

#### *Ankle Joint Range of Motion, Passive Stiffness of Gastrocnemii Muscles and Achilles Tendon*

*Range of motion and passive torque-angle relationship.* The method used to assess passive mechanical properties of the musculoarticular complex was similar to previous studies (e.g., 16, 67, 76). Isokinetic dynamometer was used to measure the torque produced in resistance to passive stretch, ankle joint angle ( $\theta_a$ ), and ankle joint angular velocity. Subjects were in prone position with legs fully extended and with their thighs, hips, and shoulders secured and held in position by adjustable lap belts. The device enabled us to change the knee angle ( $\theta_k$ ) as described previously (16, 20, 69). The reference angle of the knee joint ( $\theta_k = 0^\circ$ ) corresponded to the knee fully extended. The reference angle of the ankle joint ( $\theta_a = 90^\circ$ ) was defined as the foot perpendicular to the tibia. sEMG signals of triceps surae muscles and tibialis anterior were recorded to ensure that no muscle activity occurred during the passive stretching procedures. sEMG signals were also visualized in real time by the subject and the principal investigator during tests. If during the passive measurements, sEMG values were found to be greater than 1% of the maximal sEMG value determined during maximal voluntary contractions for a given subject, the data were disregarded for analysis (e.g., 56, 66, 68).

Four different tests were performed. 1) Assessment of the maximal ankle joint range of motion in plantar flexion with leg fully extended (RoM<sub>PF</sub>), in dorsiflexion with leg fully extended (RoM<sub>DFext</sub>), and with the knee joint flexed at 80° (RoM<sub>DFflex</sub>). During this test, the foot was passively and manually moved from neutral position ( $\theta_a = 90^\circ$ ) to the maximal RoM determined by the subject when the maximal tolerable stretch was perceived. The foot was then immediately put back into to

the starting position. In each condition, three measurements were performed, and the best trial was considered as the maximal RoM. 2) Five cyclic passive motions at 5°/s from 80% of RoM<sub>PF</sub> to 80% of RoM<sub>Dflex</sub> with knee fully extended. 3) Five cyclic passive repetitions at 5°/s for five randomly tested knee flexion angles ( $\theta_k = 15^\circ, 30^\circ, 45^\circ, 60^\circ, \text{ and } 80^\circ$ ). The range of stretch was increased in proportion with the increase in knee flexion up to passive motions performed from 80% of RoM<sub>PF</sub> to 80% of RoM<sub>Dflex</sub> with knee flexed at 80° to apply Hoang's model (34) improved by Nordez et al. (69). Five minutes of rest between each stretching series of tests were respected. 4) Two maximal voluntary contractions under isometric conditions ( $\theta_k = 0^\circ; \theta_a = 90^\circ$ ) for sEMG normalization purposes.

All of the data were processed using standardized programs computed with Matlab (The Mathworks, Natick, MA). External passive torque and angle position data were filtered using a Butterworth second-order low-pass filter (10 Hz), and recorded torque was corrected from gravity. ICC and variation coefficient of RoM parameters ranged from 0.77 to 0.93 and from 3.3% to 4.4%, respectively ( $n = 6$ ).

*Force-length relationship of the gastrocnemii MTC.* To determine the passive force of the gastrocnemii MTC, an optimization procedure was performed on the differences between the torque-angle relationships obtained at 0°, 15°, 30°, 45°, 60°, and 80° of knee angle. Thus the contribution of the gastrocnemii could be determined directly according to Eq. 5 (69):

$$T_k - T_{80} = m_g * (F_{Gk} - F_{G80}) \quad (5)$$

with  $T_k$  and  $F_{Gk}$  the ankle passive torque and the gastrocnemii passive force determined at different knee angles (0°, 15°, 30°, 45°, and 60°);  $T_{80}$  and  $F_{G80}$  the ankle passive torque and the gastrocnemii passive force determined at 80° of knee angle, respectively,  $m_g$  is the gastrocnemii moment arm assessed using model of Grieve et al. (31). The exponential model used in the present study was similar to the model of Sten Knudsen (64, 69, 82), where  $F_G$  could be calculated as follows:

$$F_G = (1/\beta) * (e^{\beta(l-l_0)} - 1) \quad \text{for } l > l_0 \\ F_G = 0 \quad \text{for } l < l_0 \quad (6)$$

where  $l$  is the gastrocnemii length (i.e., assessed using Grieve's model),  $\beta$  is the parameter determined using the optimization that concerns MTC stiffness, and  $l_0$  the gastrocnemii slack length determined using the optimization procedure. Then, the  $\beta$  parameter was identified as a stiffness index of the gastrocnemii MTC ( $S_{MTC}^{F-L}$ ). In addition, the gastrocnemii MTC length was determined for a force production of 1 N ( $L_{F=1MTC}$ ) (20). Using this exponential model, the maximal gastrocnemii stiffness ( $S_{max}^{F-L}$ ) can be determined using Eq. 7 at the maximal passive force ( $F_{max}$ ) common for both tests:

$$S_{max}^{F-L} = \beta * F_{max} + 1 \quad (7)$$

*Force-length relationships of gastrocnemii muscle and Achilles tendon.* The method used to separate muscle and tendon properties was similar to previous works (20, 36). During experiments in passive conditions described above, the ultrasonographic linear array probe, mounted on an externally fixed bracket, was strapped onto the skin of the subjects to obtain longitudinal ultrasonic images of the distal myotendinous junction of the GM. Preliminary experiments using hypochoogenic wire glued on the skin ensured that the probe remained in a fix position during passive stretching and isometric plantar flexion. The probe was placed at the same position on the lower leg between pretest and posttest. Ultrasonographic videos were recorded on a hard disk at 25 Hz. To synchronize the torque signal and ultrasonographic images from the videos, the signal of the switch used to start the video was also recorded using the Delsys system. Thirty images equally spaced from the loading phases of the fifth cycle of passive stretches performed at 0°, 15°, 30°, 45°, 60°, and 80° of knee flexion were extracted from ultrasonographic videos.

During passive stretching, passive external torque, ankle angle, and displacement of the distal myotendinous junction of the GM were determined during the loading curve of the fifth cycle (i.e., from plantar flexion to dorsiflexion) performed at each knee angle. The MTC length of the gastrocnemii was calculated using published anthropometric data (31). Elongation of the gastrocnemii muscles was determined as the total displacement of the myotendinous junction of the GM.

Length of the gastrocnemii MTC and Achilles tendon was determined for  $\theta_a = 90^\circ$  and  $\theta_k = 0^\circ$  [i.e., calculated using Grieve et al. (31) model and measured using ultrasonography, respectively]. Muscle length was calculated for this position as the difference between MTC and tendon lengths. Length of MTC was determined as function of knee and ankle angles using the model of Grieve et al. (31) on full range of motion for each stretch cycle. Changes in muscle length were determined using displacement of the myotendinous junction of the GM (i.e., elongation of the gastrocnemii muscles determined by ultrasonography) during passive stretches. Thus tendon length was calculated as the difference between MTC and muscle length on the full range of motion of each stretch cycles.

Relationships between  $F_G$  and length of the gastrocnemii muscles and Achilles tendon were characterized. Then, Sten Knudsen model (Eq. 6) was fitted on these two relationships to determine stiffness index and length for a force development of 1 N by both gastrocnemii muscles and Achilles tendon (i.e.,  $S_{muscle}^{F-L}$ ,  $L_{F=1M}$ ,  $S_{tendon}^{F-L}$ , and  $L_{F=1T}$  respectively). ICC of gastrocnemii passive mechanical properties ranged from 0.82 to 0.98 ( $n = 15$ ).

### Statistics

After checking the distribution of data, parametric statistical tests were performed using Statistica software (Statsoft, Tulsa, OK). Descriptive data included means  $\pm$  standard deviation. Two-way multivariate ANOVA (group  $\times$  time) were performed to assess the statistical significance of changes. The critical level of significance in the present study was set at  $P < 0.05$ .

## RESULTS

No significant change was found in the control group between pretest and posttest whatever the parameter assessed (some individual raw data determining MTC mechanical properties under active and passive conditions are shown in APPENDIX B).

### Achilles Tendon and Triceps Surae Muscles Geometry

No significant change was found in MVC, CSA<sub>T</sub>, CSA<sub>GAS</sub>, and CSA<sub>TS</sub> ( $P > 0.05$ ) (Table 1). Although a decrease of 1.7% in GM tendon length was found in trained group ( $P = 0.002$ ), no significant change was found in triceps surae muscles architecture ( $P > 0.05$ ) (Table 1).

### Active and Passive Parts of the Series Elastic Component Stiffness

Mean sEMG activity did not significantly change until a latency of 45 ms following the onset of motion (Fig. 1). At this point, sEMG activity from gastrocnemii and soleus muscles increased for a period of 20–30 ms. Activity from tibialis anterior was unchanged through the recording period. Concerning sEMG data, similar results were observed in a short range experiment performed at baseline and after the eccentric training period.

Although the global angular joint stiffness determined at 60 N/m was significantly lower for the trained group after the eccentric training period ( $-5.4\%$ ,  $P = 0.006$ ) (Fig. 2), no significant change was found in S determined at 30% and 90% of MVC ( $P > 0.05$ ) (Table 2 and Fig. 3).

Table 1. Geometrical parameters of Achilles tendon and triceps surae muscles

	Trained Group		Control Group	
	Pretest	Posttest	Pretest	Posttest
CSA <sub>T</sub> , mm <sup>2</sup>	67.6 ± 7.2	66.6 ± 10.4	59.2 ± 11.6	58.9 ± 9.2
CSA <sub>TS</sub> , mm <sup>2</sup>	3,952 ± 750	3,960 ± 735	3,623 ± 679	3,535 ± 698
CSA <sub>GAS</sub> , mm <sup>2</sup>	1,686 ± 415	1,668 ± 411	1,667 ± 297	1612 ± 294
GL				
Tendon length, cm	22.2 ± 1.9	22.0 ± 1.7	21.9 ± 1.9	22.0 ± 1.6
Pennation angle, °	13.3 ± 1.6	12.6 ± 3.5	12.3 ± 2.4	13.5 ± 1.9
Fascicle length, cm	8.6 ± 1.8	9.5 ± 2.8	9.1 ± 3.1	8.0 ± 1.3
GM				
Tendon length, cm	19.7 ± 2.5	19.2 ± 2.2*	19.4 ± 2.4	19.4 ± 2.2
Pennation angle, °	22.7 ± 2.3	21.6 ± 1.9	23.4 ± 3.0	23.2 ± 1.8
Fascicle length, cm	5.9 ± 0.9	6.2 ± 1.0	5.8 ± 1.1	5.9 ± 0.8
SO				
Tendon length, cm	4.9 ± 1.4	4.4 ± 1.5	4.8 ± 1.3	4.3 ± 4.3
Pennation angle, °	33.5 ± 8.5	31.9 ± 8.4	25.1 ± 7.7	24.3 ± 6.1
Fascicle length, cm	3.1 ± 0.7	3.1 ± 0.8	3.6 ± 1.0	3.7 ± 0.7

Data are means ± SD. CSA<sub>T</sub>: Achilles tendon cross-sectional area; CSA<sub>TS</sub> and CSA<sub>GAS</sub>, mean cross-sectional area of the triceps surae and gastrocnemii muscles, respectively, calculated from measurements at 50, 60, and 70% from proximal extremity of the lower leg length, tendon length, pennation angle, and fascicle length for each muscle of the triceps surae [soleus (SO), gastrocnemius medialis (GM), and gastrocnemius lateralis (GL)]. \* $P < 0.05$ .

Mean alpha-torque relationships of trained subjects determined at baseline and after 14 wk of eccentric training are shown in Fig. 3. A significant interaction ( $P = 0.018$ ) was found between “group” and “time” factors for SI<sub>SECI</sub>. For the trained group, a significant decrease of 10.4% in SI<sub>SECI</sub>

( $0.16 \pm 0.02$  to  $0.14 \pm 0.02^{\circ^{-1}}$ ) without any change in S<sub>SEC2</sub> was observed after training (Fig. 4). No significant change was found in maximal S<sub>SEC1</sub> ( $P > 0.05$ ), whereas a significant decrease was determined for S<sub>SEC1</sub> calculated at 60 N·m ( $P < 0.05$ ) (Table 2).

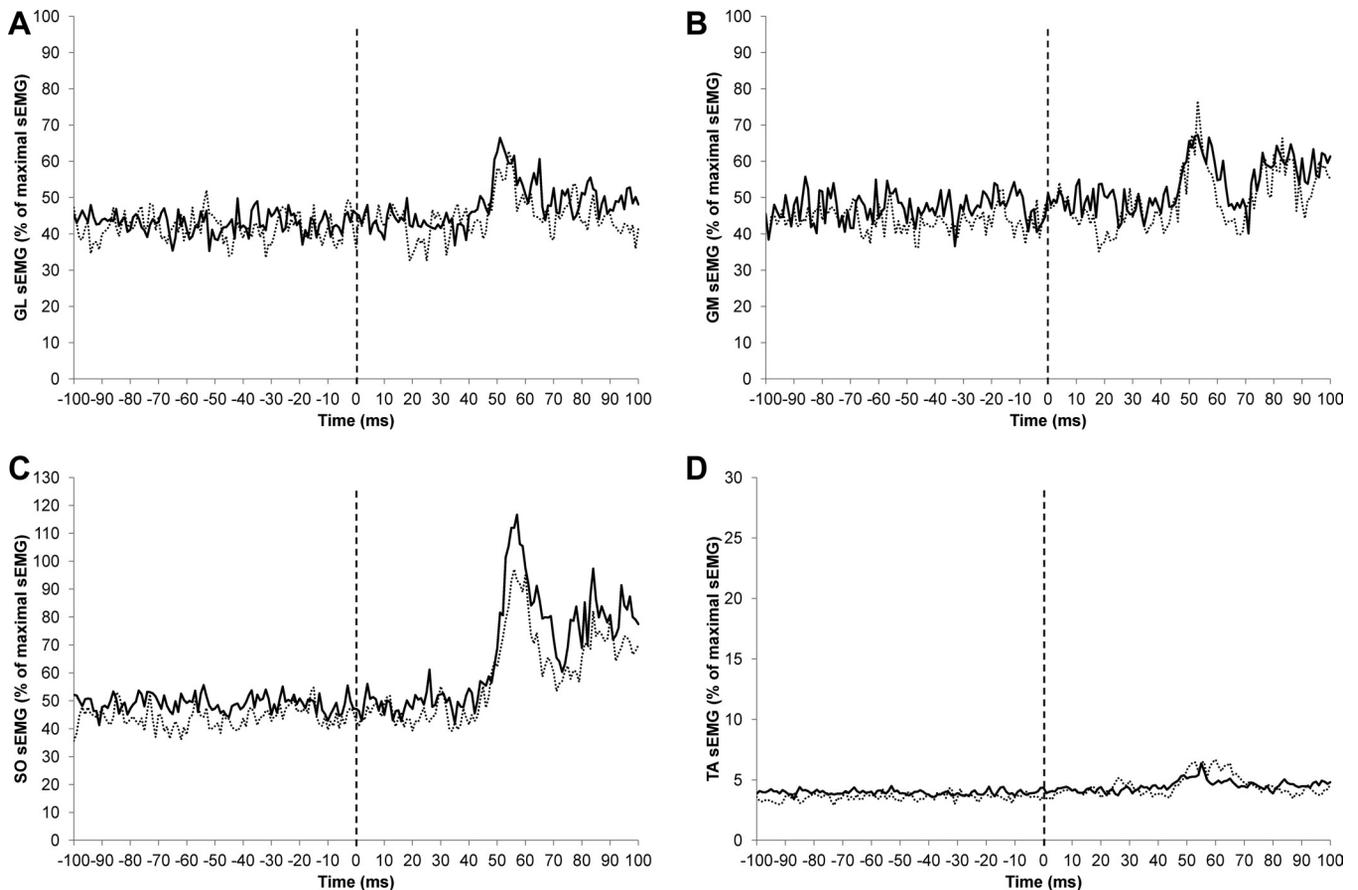


Fig. 1. Mean surface electromyographic (sEMG)-time relationships for gastrocnemius lateralis (GL; A), gastrocnemius medialis (GM; B), soleus (SO; C), and tibialis anterior (TA; D) obtained 100 ms before and after the stretch beginning (vertical dotted line) for the trained group before (solid line) and after (dashed line) the 14 wk of eccentric training.

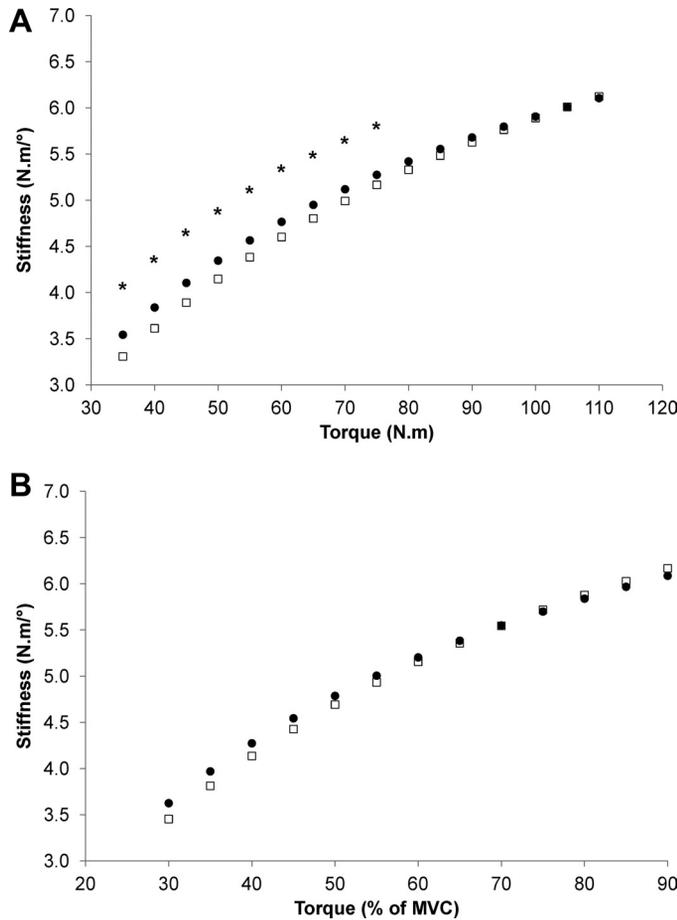


Fig. 2. Mean joint stiffness-torque relationships (A) and joint stiffness-relative torque relationship (B) for the trained group before (●) and after (□) the 14 wk of eccentric training. Error bars were removed for clarity. \* $P < 0.05$ .

### Achilles Tendon Mechanical Properties

For the trained group, no significant change in  $RTD_{max}$  was found ( $1,536 \pm 297$  to  $1,515 \pm 319$  N·m/s,  $P > 0.05$ ). Torque-time and force-elongation relationships are presented in Fig. 5. Linear regression applied on individual Ft- $\Delta L$  and mean sEMG-torque curves showed a very good correlation coefficient (mean  $R^2 = 0.97 \pm 0.02$ ), allowing

Table 2. Active stiffness of plantar flexors muscle-tendon complex mechanical properties

	Trained Group		Control Group	
	Pretest	Posttest	Pretest	Posttest
S				
30% MVC	$3.6 \pm 0.5$	$3.6 \pm 0.6$	$3.5 \pm 0.4$	$3.4 \pm 0.5$
90% MVC	$6.0 \pm 0.8$	$6.0 \pm 1.1$	$6.0 \pm 0.8$	$6.0 \pm 0.7$
60 N·m	$4.7 \pm 0.3$	$4.4 \pm 0.3^*$	$4.6 \pm 0.4$	$4.6 \pm 0.4$
$S_{SEC2}$	$9.2 \pm 1.4$	$10.2 \pm 2.8$	$9.7 \pm 1.9$	$9.8 \pm 1.8$
$S_{SEC1\ 60Nm}$	$9.9 \pm 1.3$	$8.4 \pm 1.5^*$	$9.2 \pm 1.5$	$9.3 \pm 2.4$
$S_{SEC1\ max}$	$19.8 \pm 3.7$	$17.4 \pm 4.2$	$18.5 \pm 3.2$	$18.6 \pm 5.4$

Data are means  $\pm$  SD in N·m· $^{\circ}$  $^{-1}$ . S, global angular joint stiffness determined at 30%, 90% of maximal voluntary contraction and for an absolute level of contraction (60 Nm);  $S_{SEC2}$ , passive part of the series elastic component stiffness;  $S_{SEC1}$ , active part of the series elastic component stiffness determined at 60 N·m and for maximal voluntary contraction ( $S_{SEC1\ 60Nm}$  and  $S_{SEC1\ max}$ , respectively). \* $P < 0.05$ .

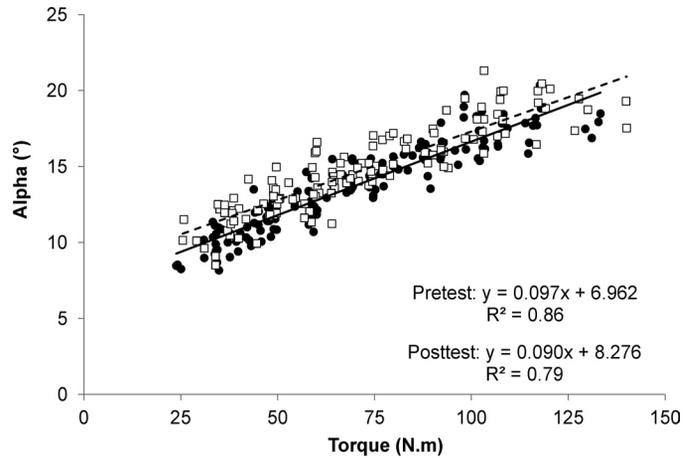


Fig. 3. Mean alpha-torque relationship for the trained group before (● and solid line) and after (□ and dashed line) the 14 wk of eccentric training.

the calculation of  $S_T$ . Mean sEMG-time and sEMG-torque relationships did not significantly change for all muscles between measurements performed at baseline and after eccentric training period (Fig. 6). Thus no significant change

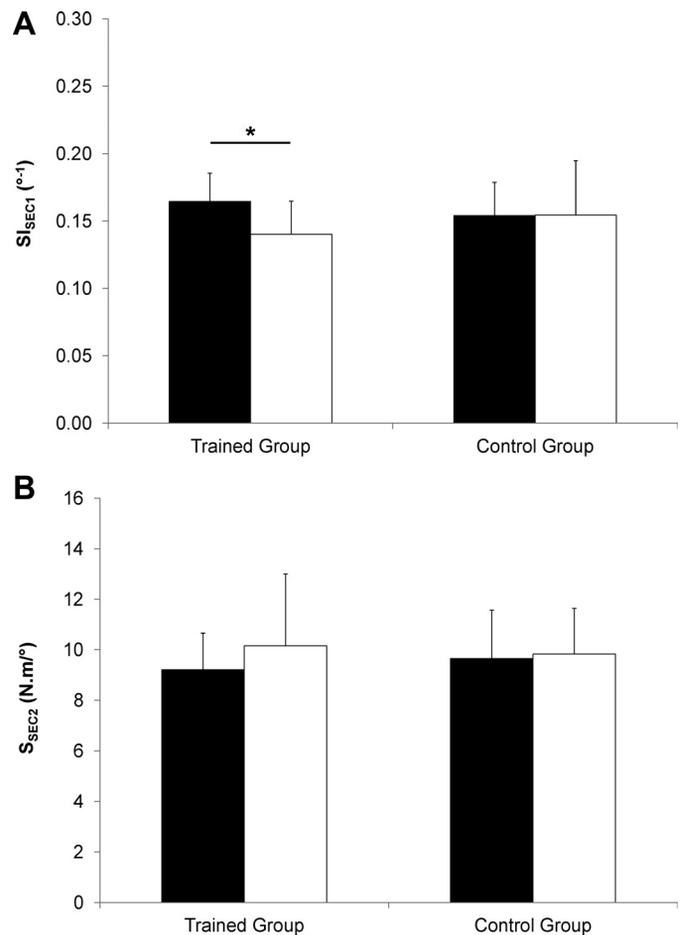


Fig. 4. Stiffness index of the active part of the series elastic component ( $S_{SEC1}$ ; A) and passive part of the series elastic component stiffness ( $S_{SEC2}$ ; B) determined before (solid bars) and after (open bars) the 14 wk of eccentric training for both trained and control groups. Results are presented as mean  $\pm$  standard deviation. \* $P < 0.05$ .

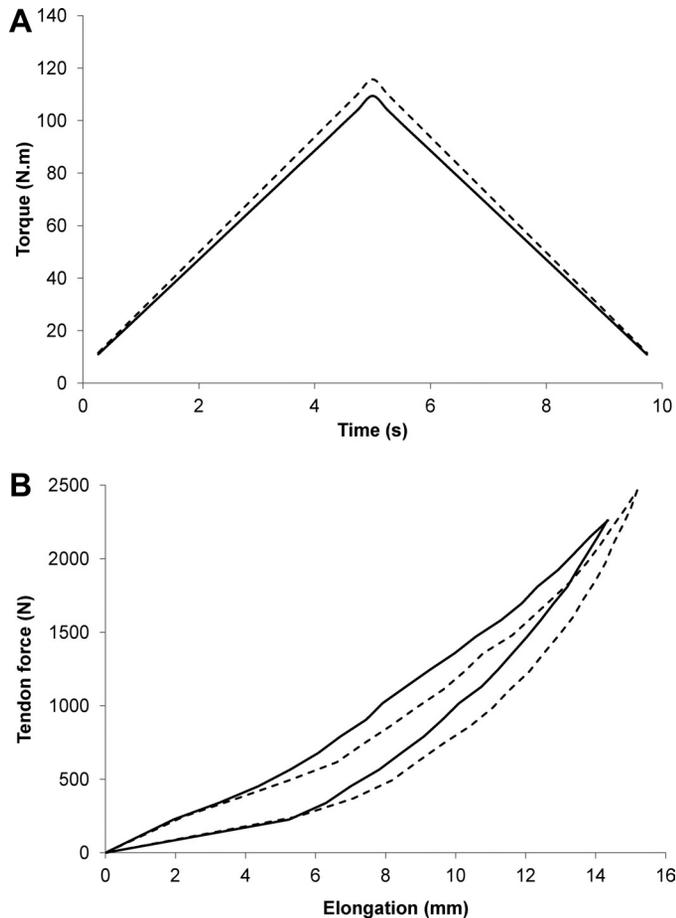


Fig. 5. Mean torque-time relationships (A) and tendon force-elongation relationships (B) obtained during isometric contraction in plantar and dorsi flexion for the trained group before (solid line) and after (dashed line) the 14 wk of eccentric training.

was found in sEMG signals,  $\Delta L_{\max}$ ,  $S_T$ ,  $SI_T$ , and DC ( $P > 0.05$ ) (Table 3).

#### Ankle Range of Motion, Passive Stiffness of Gastrocnemii Muscles, and Achilles Tendon

No significant interaction was found between “group” and “time” factors for  $RoM_{DF_{\text{ext}}}$ ,  $RoM_{PF}$ , and  $RoM_{DF_{\text{flex}}}$  was determined ( $P > 0.05$ ) (Table 4). Also, no significant change could be shown for passive torque-ankle angle relationships whatever the knee flexion angle (Fig. 7A). In addition, no significant change in  $S_{\max}^{F-L}$  (trained group:  $62,451 \pm 25,975$  to  $66,274 \pm 15,705$  N/mm and control group:  $47,681 \pm 16,685$  to  $49,747 \pm 20,009$  N/mm) was observed ( $P > 0.05$ ). Mean passive force-length relationships of the muscle-tendon complex of the gastrocnemii for the trained group at baseline and after eccentric training period are shown in Fig. 7B.

The mean force-length relationships of the Achilles tendon and the gastrocnemii muscle for trained group in pretest and posttest are shown in Fig. 8, A and B, respectively. No significant change in  $SI_{\text{muscle}}^{F-L}$  and  $L_{F=1M}$  ( $P > 0.05$ ) was determined (Table 4), whereas significant increases in  $SI_{\text{tendon}}^{F-L}$  and  $L_{F=1T}$  of 21.8% and 6.4%, respectively, were found in the trained group ( $P = 0.044$  and  $P = 0.040$ , respectively) (Table 4).

## DISCUSSION

The aim of the present study was to examine whether the mechanical properties of plantar flexors muscle and tendon structures were altered with eccentric training. The main purpose was to assess specific mechanical properties of MTC structures in both active and passive conditions by using innovative methods. The effects of eccentric training showed a decrease in the active part of the SEC stiffness of plantar flexors and an increase in Achilles tendon stiffness during passive motion of ankle joint, although training did not change stiffness and dissipative properties of the Achilles tendon during isometric contraction. Furthermore, no significant changes in MTC geometrical properties and sEMG parameters were found, indicating that changes were mainly due to modified intrinsic properties of muscular and tendinous tissues.

The results of this study showed that ankle range of motion measured under passive condition was unchanged after the eccentric training program. Mahieu et al. (54) found an increase in dorsiflexion range of motion with the leg fully extended in a healthy population despite no significant interaction for statistical analysis between “group” and “time” factors. Our results are in accordance with Silbernagel et al. (79) who showed no significant change in ankle joint range of motion after 12 wk of eccentric training in subjects with Achilles tendinopathies.

Only one study assessed the effects of eccentric training on passive stiffness of the ankle joint (54). It was shown that passive ankle joint torque plays an important role in daily activities (63, 80, 88) and that functional performances are influenced by elastic properties of the passive musculoarticular complex, including structures such as muscles, tendons, skin, subcutaneous tissue, fascia, ligaments, joint capsule, and cartilage (76, 89). During passive stretches, the intrinsic subcellular cytoskeletal proteins (i.e., titin, desmin) (86), the associated connective tissues (epimysium, perimysium, and endomysium), and the tendons (32) were probably the main tissues lengthened (29). The measurement of the passive force-length relation of human muscle in vivo is challenging as the muscle must be “isolated” from other structures (34, 36, 37). Thus force obtained during passive stretches is lower than during slow walking when exclusively the passive behavior of the gastrocnemii muscle-tendon is considered. In the current study, a decrease in passive torque was shown for dorsiflexion of the ankle joint, indicating a specific adaptation of muscle and tendon stiffness for passive conditions. The specific passive stiffness of gastrocnemii muscles and Achilles tendon was examined. An increase in Achilles tendon stiffness was determined, whereas no significant change in stiffness of gastrocnemii muscle was found.

Eccentric training had no significant effect on tendon stiffness and dissipative properties for isometric contraction. This result is in accordance with the study of Mahieu et al. (54) using a similar training program. Other studies showed an increase in tendon stiffness (e.g., 12); however, additional loads during eccentric loadings have been used. Appropriate mechanical loading can result in positive changes in tendinous structures and may lead to improved functional behavior, whereas excessive loading may induce tendon degeneration (54). To our knowledge, no previous study assessed the effects of eccentric loading on dissipative properties of tendon. No

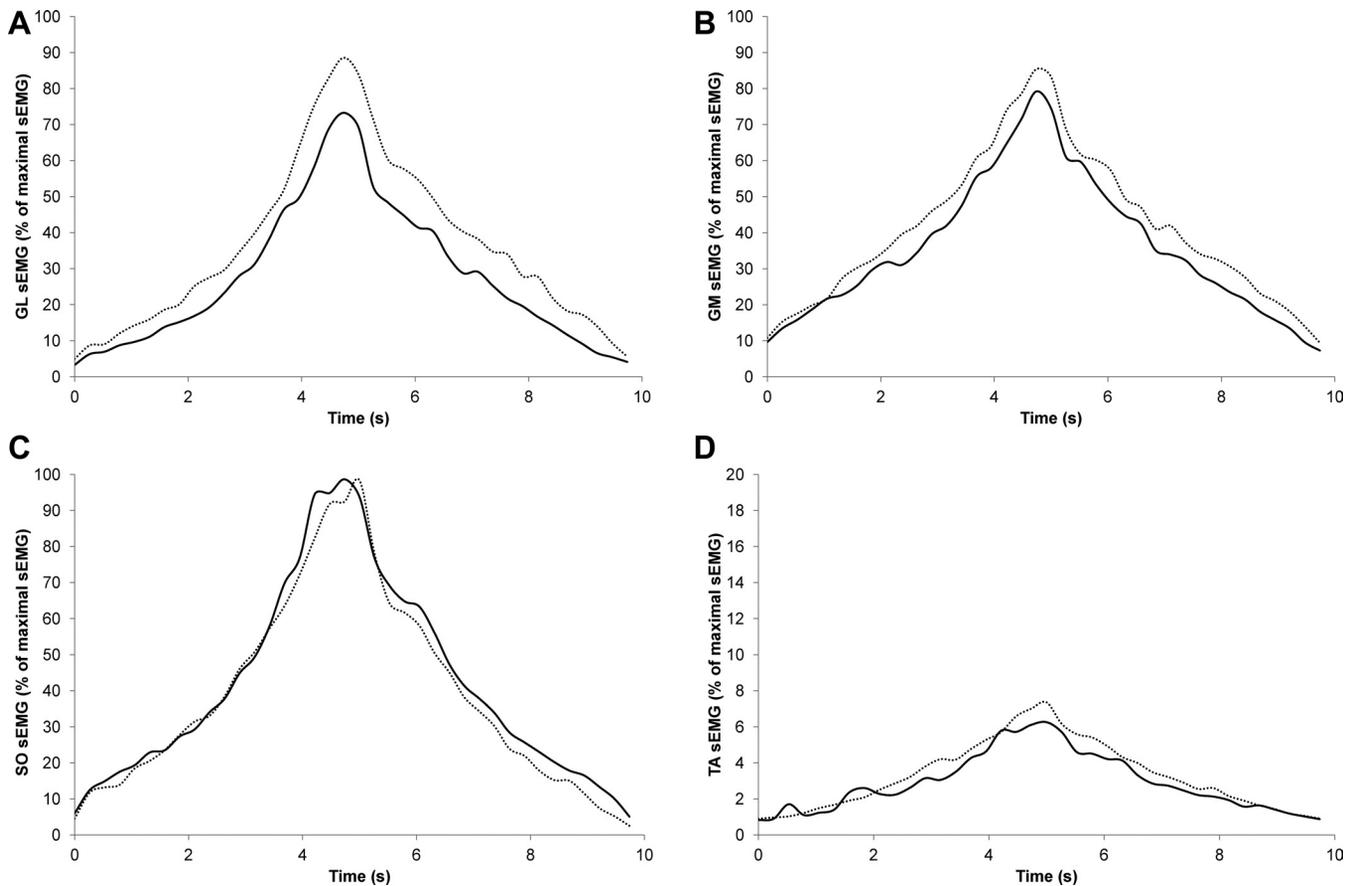


Fig. 6. Mean sEMG-time relationships for GL (A), GM (B), SO (C), TA (D) obtained during isometric contraction in plantar and dorsiflexion for the trained group before (solid line) and after (dotted line) the 14 wk of eccentric training.

change in the tendon's DC was found in the present study, indicating that eccentric training did not change the capacity to dissipate potential elastic energy during lengthening. Yet, a previous study showed a decrease in the tendon DC after strength training in elderly subjects (75). However, eccentric training combines stretching and strengthening effects (3). Our results are in accordance with those findings obtained in studies assessing effects of chronic stretching and low-load resistance training (45, 46). Interestingly, in a previous study, a decrease in DC of Achilles tendon was found after 14 wk of plyometric training (18). Plyometric contraction consists in an eccentric action followed by a concentric action to restore potential elastic energy stored during the first phase. Eccentric contraction performed alone consists in the storage of elastic energy that is dissipated. Changes in tendon DC after plyometric and eccentric trainings were shown to be coherent with the func-

tional behavior of MTC induced by plyometric and eccentric contractions.

During contraction a decrease in joint stiffness for an absolute level of torque (i.e., 60 N·m) was assessed, which is in accordance with the results of Pousson et al. (73) who found an increase in SEC compliance of elbow flexors. Specific adaptations of active and passive parts of the SEC were characterized more precisely in the current study. As it was hypothesized in a former study (73), a decrease in the stiffness of the active part of the SEC was determined, whereas no significant change was found in the SEC passive part stiffness. Our results could be explained by an increase in muscle sarcomere in series, which has already been shown in animal studies (51, 59) and put forward in recent studies determining the effects of eccentric training in vivo (10, 54). In addition, structural changes in muscle (e.g., fiber type transition) were taken into account as a possible factor in former studies (4, 23, 73) as well as the fact that fast muscle fibers are more compliant than slow ones (71).

However, some methodological considerations have to be considered with regard to the assessment of the mechanical properties of MTC. Assumptions linked to the alpha method were abundantly discussed in previous studies (17, supplementary material of Ref. 20). As mentioned before, the stiffness of SEC<sub>2</sub> was assumed to be constant, and SEC<sub>1</sub> stiffness was considered as proportional to torque on the full range of torque investigated (i.e., between 30% and 90% MVC). Studies have

Table 3. *Achilles tendon mechanical properties*

	Trained Group		Control Group	
	Pretest	Posttest	Pretest	Posttest
$\Delta L_{\max}$ , mm	14.4 ± 2.6	15.2 ± 2.9	15.9 ± 2.9	15.7 ± 2.0
$S_T$ , N/mm	215.8 ± 55.0	251.1 ± 109.2	220.1 ± 83.9	222.2 ± 84.9
$SI_T$ , mm <sup>-1</sup>	0.076 ± 0.049	0.096 ± 0.050	0.097 ± 0.063	0.084 ± 0.064
DC, %	27.8 ± 13.7	26.3 ± 11.2	33.6 ± 11.9	36.5 ± 13.4

Data are means ± SD.  $\Delta L_{\max}$ , maximal Achilles tendon elongation;  $S_T$ , Achilles tendon stiffness; DC, dissipation coefficient.

Table 4. Ankle joint range of motion and passive stiffness of the gastrocnemii muscle and Achilles tendon

	Trained Group		Control Group	
	Pretest	Posttest	Pretest	Posttest
RoM <sub>PF</sub> , °	61 ± 6	63 ± 4	59 ± 10	58 ± 8
RoM <sub>DFext</sub> , °	49 ± 4	52 ± 6	51 ± 8	50 ± 7
RoM <sub>DFflex</sub> , °	60 ± 6	62 ± 7	58 ± 10	58 ± 12
Force-length relationships				
SI <sub>MTC</sub> <sup>F-L</sup> , m <sup>-1</sup>	87.5 ± 12.9	89.2 ± 11.2	84.6 ± 11.0	83.8 ± 16.4
L <sub>F=1 MTC</sub> , m	0.372 ± 0.019	0.373 ± 0.018	0.371 ± 0.026	0.366 ± 0.031
SI <sub>muscle</sub> <sup>F-L</sup> , m <sup>-1</sup>	168.1 ± 44.0	153.8 ± 27.7	150.6 ± 34.8	142.0 ± 39.9
L <sub>F=1 M</sub> , m	0.247 ± 0.026	0.246 ± 0.027	0.251 ± 0.017	0.248 ± 0.020
SI <sub>tendon</sub> <sup>F-L</sup> , m <sup>-1</sup>	152.9 ± 16.6	185.9 ± 32.6*	165.6 ± 21.8	169.9 ± 38.4
L <sub>F=1 T</sub> , m	0.170 ± 0.023	0.174 ± 0.024*	0.168 ± 0.025	0.167 ± 0.028

Data are means ± SD. RoM<sub>PF</sub>, maximal range of motion of the ankle joint in plantar flexion with leg fully extended; RoM<sub>DFext</sub>, maximal range of motion of the ankle joint in dorsiflexion with leg fully extended; RoM<sub>DFflex</sub>, maximal range of motion of the ankle joint in dorsiflexion with knee flexed at 80°. Ankle joint angle = 0° with foot perpendicular to the tibia. Knee angle = 180° with leg fully extended. Stiffness index and length at a passive force of 1 N of the gastrocnemii muscle-tendon complex, Achilles tendon and gastrocnemii muscle (SI<sub>MTC</sub><sup>F-L</sup>, L<sub>F=1 MTC</sub>; SI<sub>muscle</sub><sup>F-L</sup>, L<sub>F=1 M</sub>; and SI<sub>tendon</sub><sup>F-L</sup>, L<sub>F=1 T</sub>, respectively) determined from force-length relationships. \*P < 0.05.

shown that the onset of a change in EMG activity, as a result of the short latency stretch reflex, generally occurs between 40 and 60 ms (11, 70). An analysis on sEMG signal was performed before and after the beginning of the stretch using a method similar to that described by Cronin et al. (11). Com-

pared with the results of Cronin et al., the short latency reflex occurred later. This difference could be explained by the ankle angle used before the stretch (i.e., 15° in plantar flexion, whereas 0° was used in the study of Cronin et al.). In the current study, reflex activity was shown to start at least 45 ms or more after the beginning of the stretch. In the literature, the

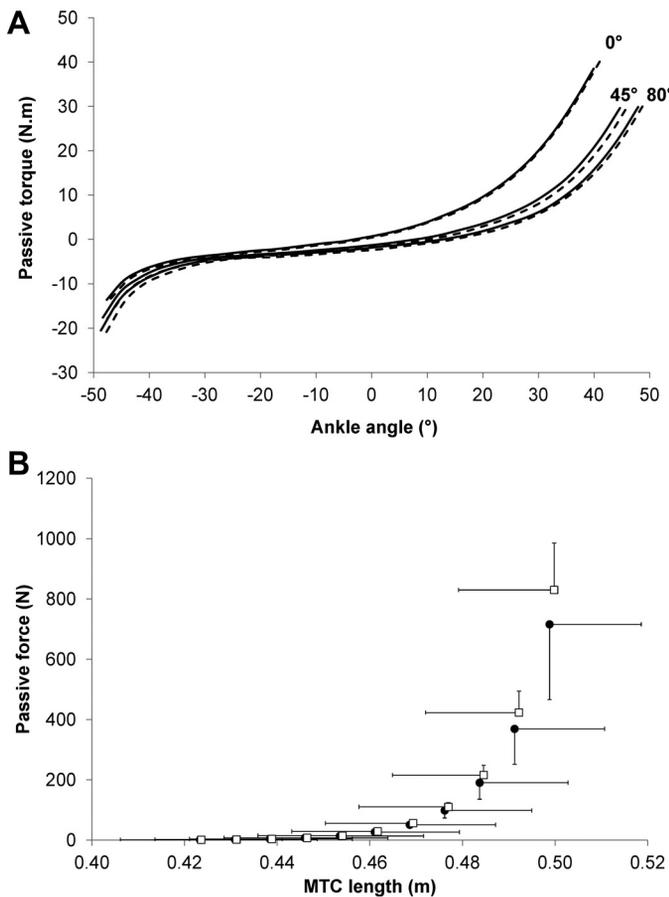


Fig. 7. Mean relationships between passive torque and ankle angle obtained during passive stretching of ankle joint performed at 0°, 45°, and 80° of knee flexion angle (A) and mean force-length relationships of the gastrocnemii muscle-tendon complex determined in passive condition (B) for the trained group before (solid line and ●) and after (dashed line and □) the 14 wk of eccentric training.

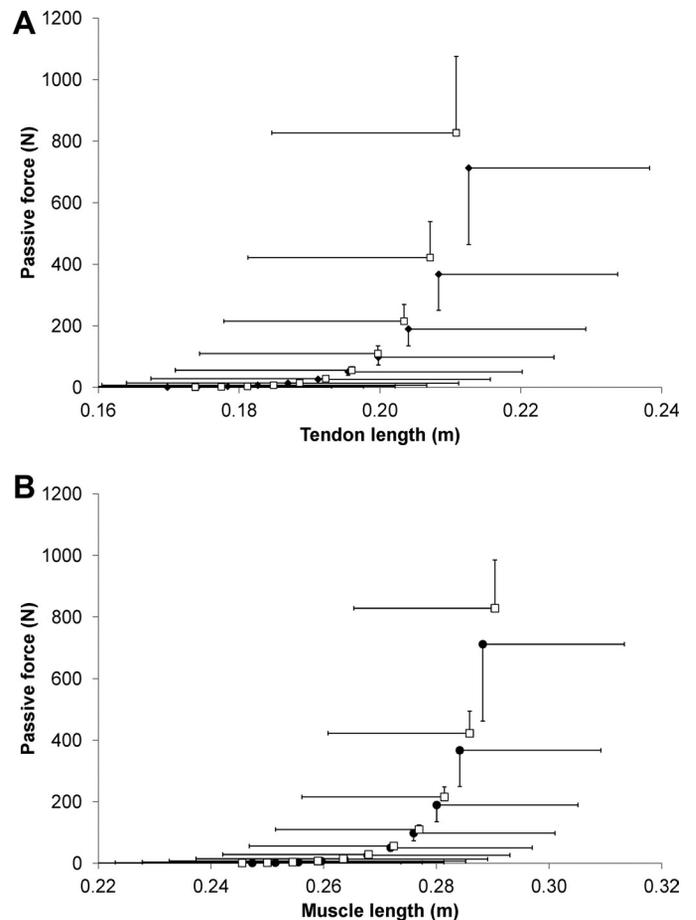


Fig. 8. Mean force-length relationships of the Achilles tendon (A) and the gastrocnemii muscle (B) determined in passive condition for the trained group before (●) and after (□) the 14 wk of eccentric training.

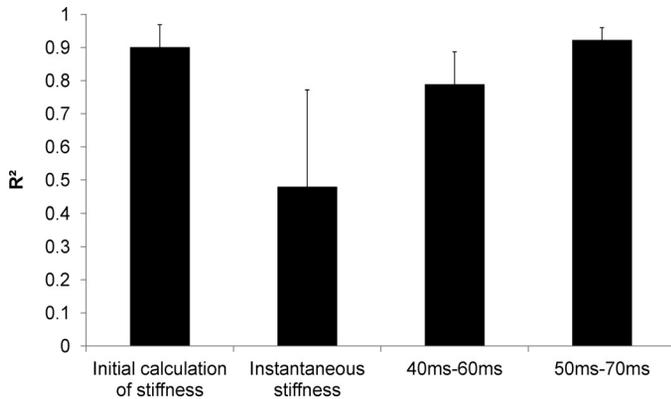


Fig. 9. Mean values of regression coefficient ( $R^2$ ) of the linear fit on alpha-torque relationships using stiffness calculated as exposed in the present study, instantaneous stiffness determined 60 ms after the beginning of the stretch, mean instantaneous stiffness values calculated between 40 and 60 ms, and between 50 and 70 ms after the beginning of the stretch.

electromechanical delay for the plantar flexors is between 16 ms (at  $15^\circ$  in plantar flexion) during electrically evoked contractions (62) and 24 ms (at  $0^\circ$ ) during voluntary contractions (90). Therefore, the influence of reflex activity on external torque and stiffness assessed in the present study is likely to be minimal. Furthermore, no significant change at the onset of the reflex activity was shown after our eccentric training protocol.

In addition, the assumption that tendon stiffness remains constant at high forces might be inconsistent when using an exponential equation for the length-tension properties of the tendon. Nevertheless, the force level for passive stretches was lower than for the contraction. It is well known that the tendon force-length relationship can be considered as biphasic consisting of a toe region (nonlinear part, characterized by a large increase in length with small increments in force) and followed by a linear region (85). Most notably, Proske and Morgan (74) concluded that “above 20–30% of maximal isometric tension, tendon stiffness is more nearly constant than proportional to the tension,” indicating that the toe region comprises this range of force. In our study, torque ranged from 0 to 25% of MVC in passive condition, thus corresponding to the toe region. This justifies the use of an exponential model for the length-tension properties of the tendon for passive conditions (27). On the contrary, in the short range stiffness experiment, torque ranged from 30% to 90% of MVC, corresponding to the linear region. This justifies the hypothesis of the constant tendon compliance for the alpha method (supplementary material of Ref. 20). Note that this last assumption is in accordance with the linear regression to model the tendon force-length relationship obtained by using ultrasonography during contractions.

In addition, we assume that  $S_{SEC1}$  is proportional to torque. Linear relationships were reasonably plotted between sEMG and torque for plantar flexor muscles ( $R^2 = 0.96$  and  $0.98$  for the trained group on pretest and posttest, respectively) on the range of torque investigated (i.e., from 30% to 90% MVC) and no significant difference in muscle activation levels was found between pretest and posttest. Thus the results of eccentric training are likely not to be influenced by our hypothesis that  $S_{SEC1}$  is proportional to torque.

Moreover, recent studies observed a potential lateral transmission of tension laterally between muscles. Bojsen-Moller

et al. (9) indirectly showed some intermuscle force transmission between gastrocnemii and soleus in humans (9). However, in this last study, displacements were measured instead of force. Due to the nonlinear force-displacement relationship of the muscle, large displacements can be observed at low force transmission. Only one recent study quantified the intermuscle force transmission between gastrocnemii and soleus in humans (83). By using an elegant model, this study estimated the magnitude of force transmitted from the gastrocnemii to the soleus and showed that this magnitude is negligible ( $\sim 5$  N). In addition, another study stated that the shear elastic modulus measured using supersonic imaging provide an estimate of passive muscle tension. By using this technique, it was shown that shear elastic modulus-length relationships were similar whatever the knee angle during passive dorsiflexion (55). Although further studies are required to confirm this finding, the hypotheses used in the Hoang’s model can be considered as being reasonable because there is currently not enough evidence to contest its validity.

Another methodological consideration concerns the relative contribution of the triceps surae to the active ankle torque, which is challenging to determine noninvasively in vivo. To our knowledge, the only studies assessing the inclusion of the triceps surae are invasive in nature, for instance by using optic

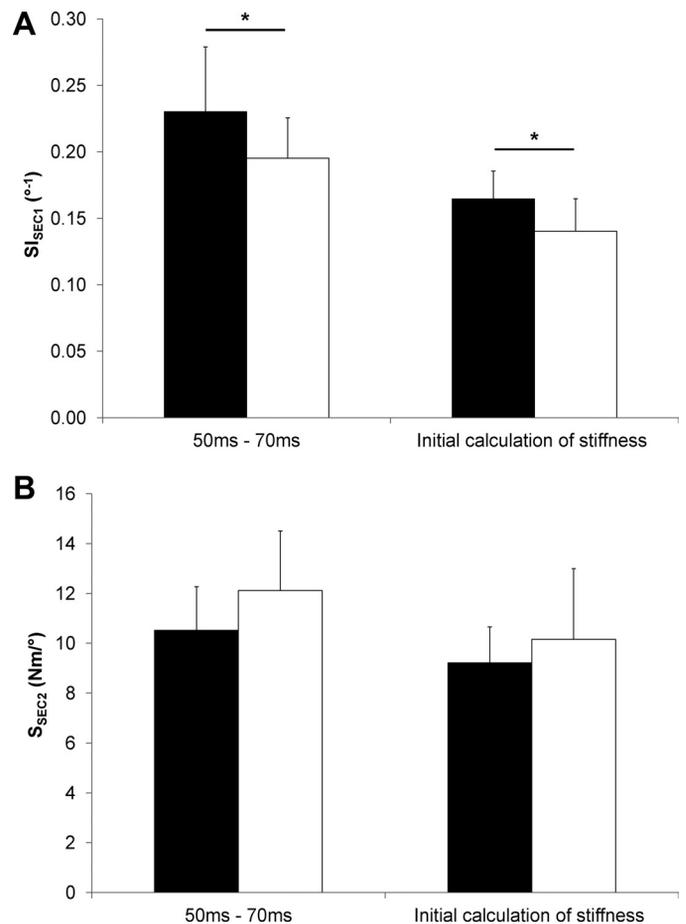


Fig. 10. Mean values of  $S_{SEC1}$  and  $S_{SEC2}$  determined considering instantaneous stiffness averaged on the range 50–70 ms after the beginning of the stretch and considering method exposed in the manuscript for the trained group before (solid bars) and after (open bars) training.  $*P < 0.05$ .

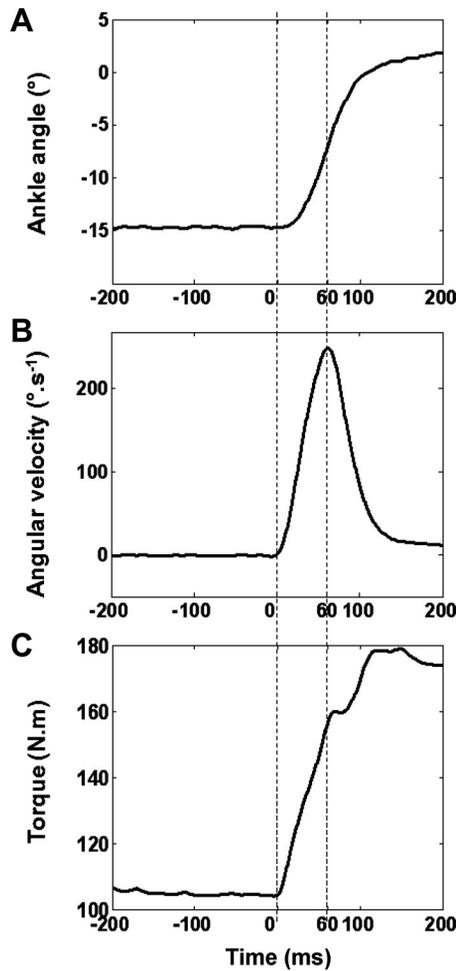


Fig. 11. Typical raw data obtained during a trial of the short range stiffness experiment with ankle angle (A), angular velocity (B), and external torque (C). After the isometric contraction, triceps surae was quickly stretched. The first 60 ms (vertical dotted line) of the stretch were used to determine the joint stiffness.

fiber sensors (e.g., 5). Arndt et al. (5) indicate that the relative contribution of the triceps surae is increased when the knee is extended (i.e., the same position as for the present study). The authors indicate that under those conditions the relative contribution of the triceps surae is  $\sim 80\%$ . Due to limitation of accuracy by using this method and the inclusion of only one subject (13, 14), these results should be considered with caution. Nevertheless, the finding (i.e.,  $\sim 80\%$  triceps surae contribution to ankle torque) is in accordance with estimations provided by other studies (24, 77, 84). Thus, the contribution of the five other muscles (i.e., flexor hallucis longus, tibialis posterior, flexor digitorum longus, peroneus longus, peroneus brevis) to active ankle plantar flexion torque could be considered as negligible compared with the triceps surae muscles contribution (84). The muscle contribution to active torque is supposed to be almost proportional to the physiological cross-sectional area (PCSA) (24, 25, 26). In addition, both muscle CSA and muscle architecture (i.e., muscle thickness, fascicle length and pennation angle) and sEMG activity level did not significantly change after the training period for the trained group, indicating that the relative contribution of muscles remain unchanged. Thus, for instance, a change in PCSA of the

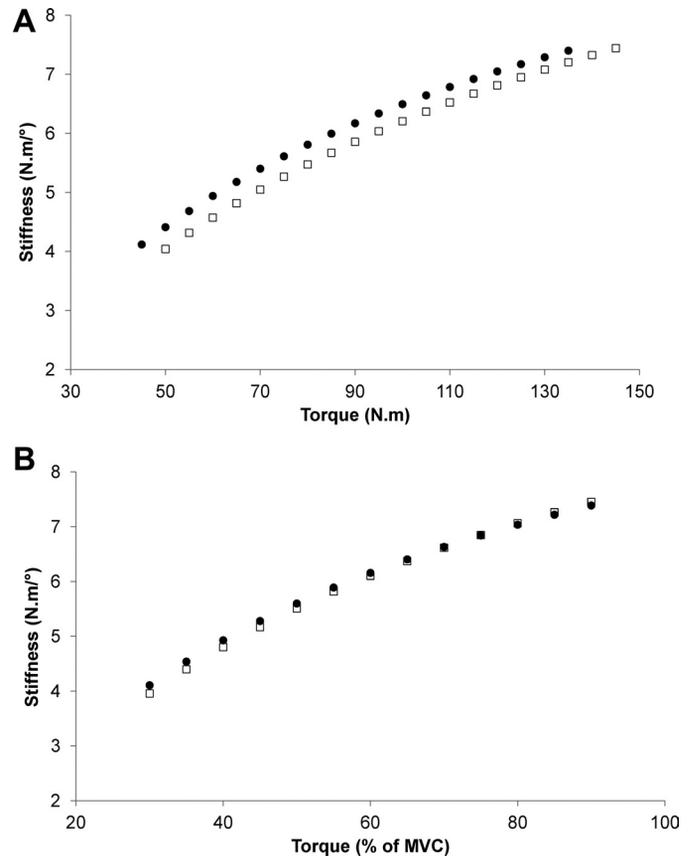


Fig. 12. Joint stiffness-torque relationships (A) and joint stiffness-relative torque relationship (B) for a representative trained subject before (●) and after (□) the 14 wk of eccentric training. Error bars were removed for clarity.

other muscles of 10% (to the best of our knowledge no study investigated changes in geometric parameters of other muscles after chronic intervention) should induce a change in relative contribution of  $\sim 2\%$ . Therefore, its influence on the contribution of the total plantar flexion torque production is likely to be minimal. Thus it could be assumed that changes in the dissipative coefficient were mainly associated with changes in the dissipative properties of the tendon rather than being linked to muscle function.

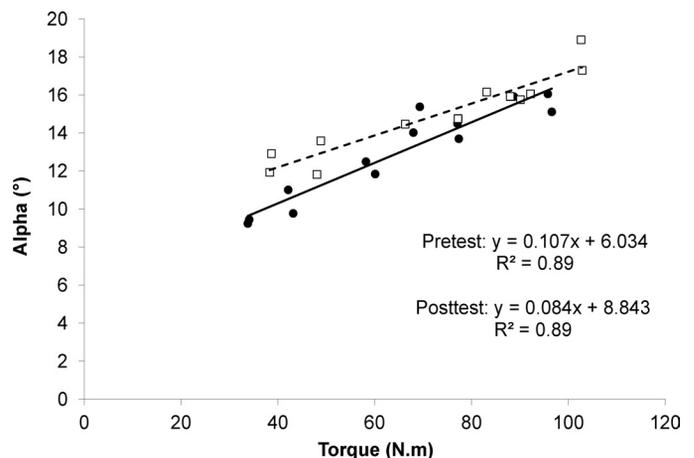


Fig. 13. Alpha-torque relationship for a representative trained subject before (● and solid line) and after (□ and dashed line) the 14 wk of eccentric training.

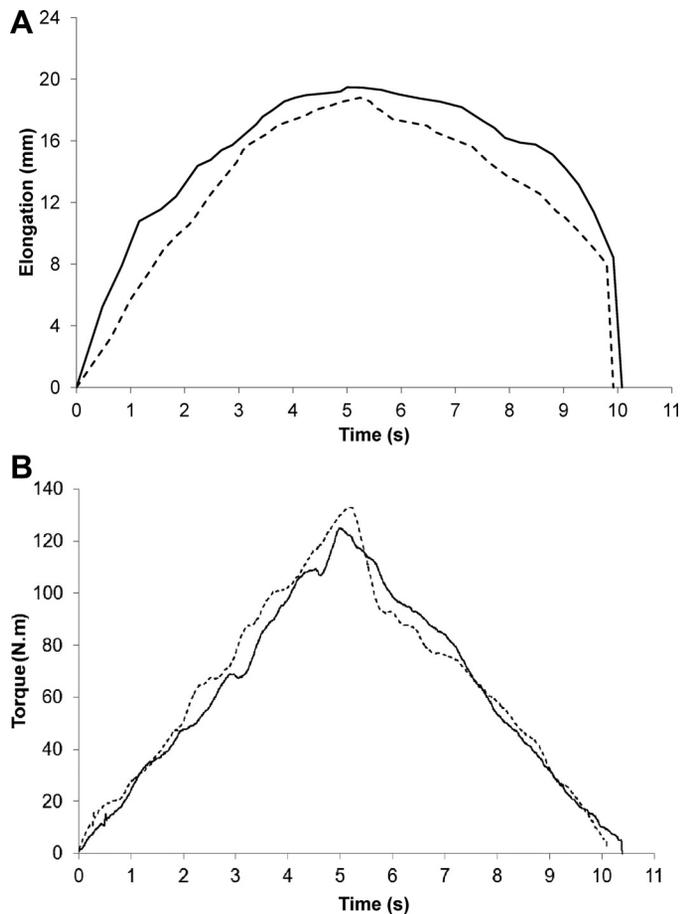


Fig. 14. Elongation-time relationships (A) and torque-time relationships (B) obtained during isometric contraction in plantar and dorsiflexion for a representative trained subject before (solid line) and after (dashed line) the 14 wk of eccentric training.

Interestingly, specific adaptations of tendon were found in stiffness determined in active and passive conditions. Indeed, no significant changes in  $S_T$  and  $SI_T$  were found, whereas an increase in  $SI_{tendon}^{F-L}$  occurred after 14 wk of eccentric training. Although the mechanical properties of the same structure were assessed, different adaptations occurred specifically when tendon stiffness is assessed in active and passive conditions. Similar results were found following plyometric training, showing an increase in Achilles tendon stiffness for the active condition but without any changes during passive motion of the ankle joint (18, 20). Two main hypotheses could explain the different findings for active and passive tendon stiffness. First, during contraction of the triceps surae muscle group, higher stress is applied on tendon structures than during passive motion, and changes in tendon stiffness due to the training can depend on the stress level. Second, the stress applied can be qualitatively different. Indeed, shearing movements were shown between the soleus and gastrocnemii during an isometric plantar flexion (8). Because different muscle structures are implied in tension production for muscle contractions and passive joint motion (i.e., mainly cross bridges during contraction and parallel elements during passive motion), it could be expected that components of Achilles tendon are not identically stressed due to their specific mechanical behavior. Several studies focused on the role the extracellular matrix (ECM)

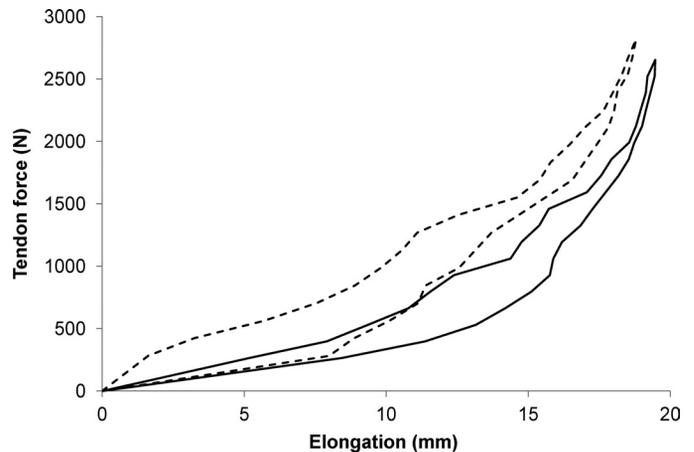


Fig. 15. Tendon force-elongation relationships obtained during isometric contraction in plantar and dorsiflexion for a representative trained subject before (solid line) and after (dashed line) the 14 wk of eccentric training.

is playing with regard to mechanical properties of the tendon (e.g., 43, 44). The ECM is made of a variety of substances (i.e., mainly collagen fibrils and proteoglycans). In addition to the proteoglycans, the hydrophilic ECM consists of a variety of other proteins such as noncollagen glycoproteins (e.g., 78). It is known that the force transmission of the muscle-tendon com-

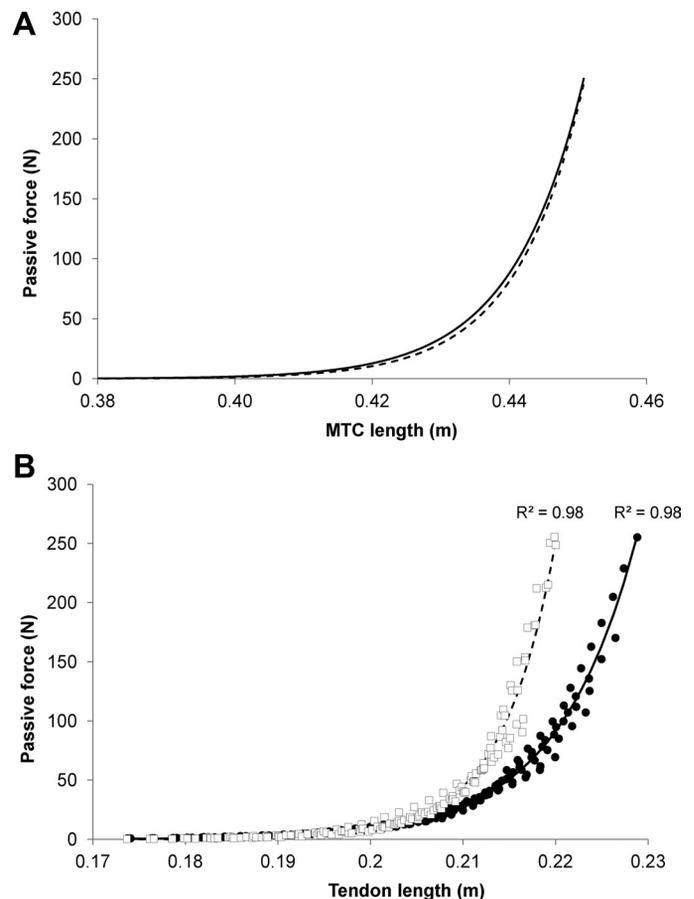


Fig. 16. Force-length relationships of the gastrocnemii muscle-tendon complex (A) and the Achilles tendon (B) determined in passive condition for a representative trained subject before (solid line and ●) and after (dashed line and □) the 14 wk of eccentric training.

plex is dependent on the structural integrity between individual muscle fibers and the ECM as well as the fibrillar arrangement of the tendon and its allowance for absorption and loading of energy (43). Thus, considering the fact that change in tendon stiffness is specific to the stress level and/or tendon stretching velocity, an increase in stiffness of different substructures within ECM could be effective. However, further studies are needed to compare mechanical tendon properties at the same level of tension in active and passive conditions and to determine more precisely the specific adaptations of these substructures according to the type (e.g., higher shearing stress during contraction) and level of applied stress.

In summary, the present study concentrated on the effects of eccentric training on specific mechanical properties of plantar flexor muscles and the Achilles tendon in both active and passive conditions. The major effect of eccentric training can be seen in the decrease in the active part of the SEC stiffness leading to an increase in energy that could be stored during eccentric contraction. Eccentric loading abundantly used in tendinopathies rehabilitation programs did not significantly affect tendon mechanical properties. Adaptations in mechanical properties of plantar flexor muscles and the Achilles tendon seem to be more protective to lower the risk of muscle and/or tendon injuries (i.e., no change in dissipative properties of tendon and decrease in SEC<sub>1</sub> stiffness). However, differences in adaptation to training of the Achilles tendon stiffness determined in active and passive conditions remain unclear. Further studies are needed to precisely identify the specific adaptations of tendon structures with regard to the type and level of stress applied to the tendon during passive motion and muscle contraction. Such an approach might allow a better understanding of specific physiological mechanisms potentially involved in changes of tendon mechanical properties.

#### APPENDIX A

In active condition, the joint stiffness was calculated as the ratio of changes in external torque and ankle angle between the beginning of the stretch and 60 ms after. It would also have been possible to determine instantaneous compliance considering the torque-angle relationship during the stretch. For the only time point for which no significant angular acceleration occurred (i.e., 60 ms after the beginning of the stretch in our experimental design), instantaneous stiffness was determined with regard to the torque angle relationship. However, the instantaneous stiffness was slightly noisy with the filters used, which are usually considered to be appropriate (17). Thus the alpha-torque relationship obtained using this calculation was not appropriate. Therefore, instantaneous stiffness was averaged on time ranges to limit the influence of noise but also of inertia and reflex influence during the stretch. This additional processing was performed for the trained group before and after eccentric training. The mean  $R^2$  values of the alpha-torque relationships are shown in Fig. 9.

The values indicate that time range between 50 and 70 ms after the beginning of the stretch reached a good compromise considering inertial and reflex influences. In addition, analyses performed in this time range provide similar quality of fits as those exposed in the present study when determining the alpha-torque relationship. Thus the influence of training was determined using this additional approach (Fig. 10).

Results showed that changes are similar for both  $SI_{SEC1}$  and  $S_{SEC2}$ . Therefore, the method using the instantaneous stiffness is an interesting alternative and the results presented in Fig. 10 strengthen the results concerning the effects of eccentric training obtained in the present study.

#### APPENDIX B

In addition to mean relationships, some raw data and traces of  $I$  angle and torque during the rapid stretch used in the alpha method (Figs. 11, 12, and 13), 2) EMG and measures of myotendinous junction displacement during isometric contractions (Figs. 14 and 15), and 3) the passive force-length relationships (Fig. 16) of a representative trained subject.

#### GRANTS

This study was supported by grants from the Association Française contre les Myopathies (Grant no. 13923), Nantes Métropole and the Recherche et Sport en Pays de la Loire network.

#### DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

#### AUTHOR CONTRIBUTIONS

Author contributions: A.F. performed experiments; A.F. and A.N. analyzed data; A.F., A.N., and C.C. interpreted results of experiments; A.F. prepared figures; A.F. drafted manuscript; A.F., A.N., and C.C. edited and revised manuscript; A.F., A.N., and C.C. approved final version of manuscript; A.N. and C.C. conception and design of research.

#### REFERENCES

- Alexander RM, Bennet-Clark HC. Storage of elastic strain energy in muscle and other tissues. *Nature* 265: 114–117, 1977.
- Alfredson H, Pietila T, Jonsson P, Lorentzon R. Heavy-load eccentric calf muscle training for the treatment of chronic Achilles tendinosis. *Am J Sports Med* 26: 360–366, 1998.
- Allison GT, Purdam C. Eccentric loading for Achilles tendinopathy—strengthening or stretching? *Br J Sports Med* 43: 276–279, 2009.
- Almeida-Silveira MI, Perot C, Pousson M, Goubel F. Effects of stretch-shortening cycle training on mechanical properties and fibre type transition in the rat soleus muscle. *Pflügers Arch* 427: 289–294, 1994.
- Arndt AN, Komi PV, Bruggemann GP, Lukkariniemi J. Individual muscle contributions to the in vivo achilles tendon force. *Clin Biomech* 13: 532–541, 1998.
- Arya S, Kulig K. Tendinopathy alters mechanical and material properties of the Achilles tendon. *J Appl Physiol* 108: 670–675, 2010.
- Blazevich AJ, Cannavan D, Coleman DR, Horne S. Influence of concentric and eccentric resistance training on architectural adaptation in human quadriceps muscles. *J Appl Physiol* 103: 1565–1575, 2007.
- Bojsen-Moller J, Hansen P, Aagaard P, Svantesson U, Kjaer M, Magnusson SP. Differential displacement of the human soleus and medial gastrocnemius aponeuroses during isometric plantar flexor contractions in vivo. *J Appl Physiol* 97: 1908–1914, 2004.
- Bojsen-Moller J, Schwartz S, Kalliokoski KK, Finni T, Magnusson SP. Intermuscular force transmission between human plantarflexor muscles in vivo. *J Appl Physiol* 109: 1608–1618, 2010.
- Brockett CL, Morgan DL, Proske U. Human hamstring muscles adapt to eccentric exercise by changing optimum length. *Med Sci Sports Exerc* 33: 783–790, 2001.
- Cronin NJ, Peltonen J, Ishikawa M, Komi PV, Avela J, Sinkjaer T, Voigt M. Effects of contraction intensity on muscle fascicle and stretch reflex behavior in the human triceps surae. *J Appl Physiol* 105: 226–232, 2008.
- Duclay J, Martin A, Duclay A, Cometti G, Pousson M. Behavior of fascicles and the myotendinous junction of human medial gastrocnemius following eccentric strength training. *Muscle Nerve* 39: 819–827, 2009.
- Erdemir A, Piazza SJ, Sharkey NA. Influence of loading rate and cable migration on fiberoptic measurement of tendon force. *J Biomech* 35: 857–862, 2002.
- Erdemir A, Hamel AJ, Piazza SJ, Sharkey NA. Fiberoptic measurement of tendon forces is influenced by skin movement artifact. *J Biomech* 36: 449–455, 2003.
- Ettema GJ, Huijings PA. Skeletal muscle stiffness in static and dynamic contractions. *J Biomech* 27: 1361–1368, 1994.
- Fouré A, Nordez A, Guette M, Cornu C. Effects of plyometric training on passive stiffness of gastrocnemii and the musculo-articular complex of the ankle joint. *Scand J Med Sci Sports* 19: 811–818, 2009.

17. **Fouré A, Nordez A, Cornu C.** In vivo assessment of both active and passive parts of the plantarflexors series elastic component stiffness using the alpha method: a reliability study. *Int J Sports Med* 31: 51–57, 2010.
18. **Fouré A, Nordez A, Cornu C.** Plyometric training effects on Achilles tendon stiffness and dissipative properties. *J Appl Physiol* 109: 849–854, 2010.
19. **Fouré A, Nordez A, McNair P, Cornu C.** Effects of plyometric training on both active and passive parts of the plantarflexors series elastic component stiffness of muscle-tendon complex. *Eur J Appl Physiol* 111: 539–548, 2011.
20. **Fouré A, Nordez A, Cornu C.** Effects of plyometric training on passive stiffness of gastrocnemii muscles and Achilles tendon. *Eur J Appl Physiol* 112: 2849–2857, 2012.
21. **Fouré A, Cornu C, McNair PJ, Nordez A.** Gender differences in both active and passive parts of the plantar flexors series elastic component stiffness and geometrical parameters of the muscle-tendon complex. *J Orthop Res* 30: 707–712, 2012.
22. **Fouré A, Cornu C, Nordez A.** Is tendon stiffness correlated to the dissipation coefficient? *Physiol Meas* 33: N1–9, 2012.
23. **Friden J.** Changes in human skeletal muscle induced by long-term eccentric exercise. *Cell Tissue Res* 236: 365–372, 1984.
24. **Fukunaga T, Roy RR, Shellock FG, Hodgson JA, Edgerton VR.** Specific tension of human plantar flexors and dorsiflexors. *J Appl Physiol* 80: 158–165, 1996.
25. **Fukunaga T, Kawakami Y, Kuno S, Funato K, Fukashiro S.** Muscle architecture and function in humans. *J Biomech* 30: 457–463, 1997.
26. **Fukunaga T, Miyatani M, Tachi M, Kouzaki M, Kawakami Y, Kanehisa H.** Muscle volume is a major determinant of joint torque in humans. *Acta Physiol Scand* 172: 249–255, 2001.
27. **Fung YC.** Biomechanics: mechanical properties of living tissues. New York: Springer-Verlag, 1981.
28. **Fyfe I, Stanish WD.** The use of eccentric training and stretching in the treatment and prevention of tendon injuries. *Clin Sports Med* 11: 601–624, 1992.
29. **Gajdosik RL, Vander Linden DW, McNair PJ, Riggin TJ, Albertson JS, Mattick DJ, Wegley JC.** Slow passive stretch and release characteristics of the calf muscles of older women with limited dorsiflexion range of motion. *Clin Biomech* 19: 398–406, 2004.
30. **Gajdosik RL, Vander Linden DW, McNair PJ, Riggin TJ, Albertson JS, Mattick DJ, Wegley JC.** Viscoelastic properties of short calf muscle-tendon units of older women: effects of slow and fast passive dorsiflexion stretches in vivo. *Eur J Appl Physiol* 95: 131–139, 2005.
31. **Grieve DW, Cavanagh PR, Pheasant S.** Prediction of gastrocnemius length from knee and ankle joint posture. In: *Biomechanics VI-A*, edited by Asmussen E and Jorgensen K. Baltimore, MD: University Park, 1978, p. 405–412.
32. **Herbert RD, Moseley AM, Butler JE, Gandevia SC.** Change in length of relaxed muscle fascicles and tendons with knee and ankle movement in humans. *J Physiol* 539: 637–645, 2002.
33. **Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G.** Development of recommendations for SEMG sensors and sensor placement procedures. *J Electromyogr Kinesiol* 10: 361–374, 2000.
34. **Hoang PD, Gorman RB, Todd G, Gandevia SC, Herbert RD.** A new method for measuring passive length-tension properties of human gastrocnemius muscle in vivo. *J Biomech* 38: 1333–1341, 2005.
35. **Hoang PD, Herbert RD, Gandevia SC.** Effects of eccentric exercise on passive mechanical properties of human gastrocnemius in vivo. *Med Sci Sports Exerc* 39: 849–857, 2007.
36. **Hoang PD, Herbert RD, Todd G, Gorman RB, Gandevia SC.** Passive mechanical properties of human gastrocnemius muscle tendon units, muscle fascicles and tendons in vivo. *J Exp Biol* 210: 4159–4168, 2007.
37. **Hoang PD, Saboisky JP, Gandevia SC, Herbert RD.** Passive mechanical properties of gastrocnemius in people with multiple sclerosis. *Clin Biomech* 24: 291–298, 2009.
38. **Hortobagyi T, Hill JP, Houmard JA, Fraser DD, Lambert NJ, Israel RG.** Adaptive responses to muscle lengthening and shortening in humans. *J Appl Physiol* 80: 765–772, 1996.
39. **Janecki D, Jarocka E, Jaskolska A, Marusiak J, Jaskolski A.** Muscle passive stiffness increases less after the second bout of eccentric exercise compared to the first bout. *J Sci Med Sport* 14: 338–343, 2011.
40. **Kawakami Y, Ichinose Y, Fukunaga T.** Architectural and functional features of human triceps surae muscles during contraction. *J Appl Physiol* 85: 398–404, 1998.
41. **Kawakami Y, Muraoka T, Ito S, Kanehisa H, Fukunaga T.** In vivo muscle fibre behaviour during counter-movement exercise in humans reveals a significant role for tendon elasticity. *J Physiol* 540: 635–646, 2002.
42. **Kingma JJ, de Knikker R, Wittink HM, Takken T.** Eccentric overload training in patients with chronic Achilles tendinopathy: a systematic review. *Br J Sports Med* 41: e3, 2007.
43. **Kjaer M.** Role of extracellular matrix in adaptation of tendon and skeletal muscle to mechanical loading. *Physiol Rev* 84: 649–698, 2004.
44. **Kjaer M, Magnusson P, Krogsgaard M, Boysen Moller J, Olesen J, Heinemeier K, Hansen M, Haraldsson B, Koskinen S, Esmarck B, Langberg H.** Extracellular matrix adaptation of tendon and skeletal muscle to exercise. *J Anat* 208: 445–450, 2006.
45. **Kubo K, Kanehisa H, Fukunaga T.** Effects of resistance and stretching training programmes on the viscoelastic properties of human tendon structures in vivo. *J Physiol* 538: 219–226, 2002.
46. **Kubo K, Kanehisa H, Miyatani M, Tachi M, Fukunaga T.** Effect of low-load resistance training on the tendon properties in middle-aged and elderly women. *Acta Physiol Scand* 178: 25–32, 2003.
47. **Kulig K, Lederhaus ES, Reischl S, Arya S, Bashford G.** Effect of eccentric exercise program for early tibialis posterior tendinopathy. *Foot Ankle Int* 30: 877–885, 2009.
48. **Langberg H, Skovgaard D, Petersen LJ, Bulow J, Kjaer M.** Type I collagen synthesis and degradation in peritendinous tissue after exercise determined by microdialysis in humans. *J Physiol* 521: 299–306, 1999.
49. **Langberg H, Rosendal L, Kjaer M.** Training-induced changes in peritendinous type I collagen turnover determined by microdialysis in humans. *J Physiol* 534: 297–302, 2001.
50. **Langberg H, Ellingsgaard H, Madsen T, Jansson J, Magnusson SP, Aagaard P, Kjaer M.** Eccentric rehabilitation exercise increases peritendinous type I collagen synthesis in humans with Achilles tendinosis. *Scand J Med Sci Sports* 17: 61–66, 2007.
51. **Lynn R, Morgan DL.** Decline running produces more sarcomeres in rat vastus intermedius muscle fibers than does incline running. *J Appl Physiol* 77: 1439–1444, 1994.
52. **Maffulli N, Walley G, Sayana MK, Longo UG, Denaro V.** Eccentric calf muscle training in athletic patients with Achilles tendinopathy. *Disabil Rehabil* 30: 1677–1684, 2008.
53. **Maganaris CN.** Tensile properties of in vivo human tendinous tissue. *J Biomech* 35: 1019–1027, 2002.
54. **Mahieu NN, McNair P, Cools A, D'Haen C, Vandermeulen K, Witvrouw E.** Effect of eccentric training on the plantar flexor muscle-tendon tissue properties. *Med Sci Sports Exerc* 40: 117–123, 2008.
55. **Maisetti O, Hug F, Bouillard K, Nordez A.** Characterization of passive elastic properties of the human medial gastrocnemius muscle belly using supersonic shear imaging. *J Biomech* 45: 978–984, 2012.
56. **McNair PJ, Dombroski EW, Hewson DJ, Stanley SN.** Stretching at the ankle joint: viscoelastic responses to holds and continuous passive motion. *Med Sci Sports Exerc* 33: 354–358, 2001.
57. **Morgan DL.** Separation of active and passive components of short-range stiffness of muscle. *Am J Physiol Cell Physiol* 232: C45–C49, 1977.
58. **Morgan DL, Proske U, Warren D.** Measurements of muscle stiffness and the mechanism of elastic storage of energy in hopping kangaroos. *J Physiol* 282: 253–261, 1978.
59. **Morgan DL.** New insights into the behavior of muscle during active lengthening. *Biophys J* 57: 209–221, 1990.
60. **Morgan DL, Whitehead NP, Wise AK, Gregory JE, Proske U.** Tension changes in the cat soleus muscle following slow stretch or shortening of the contracting muscle. *J Physiol* 522: 503–513, 2000.
61. **Morrissey D, Roskilly A, Twycross-Lewis R, Isinkaye T, Screen H, Wledge R, Bader D.** The effect of eccentric and concentric calf muscle training on Achilles tendon stiffness. *Clin Rehabil* 25: 238–247, 2011.
62. **Muraoka T, Muramatsu T, Fukunaga T, Kanehisa H.** Influence of tendon slack on electromechanical delay in the human medial gastrocnemius in vivo. *J Appl Physiol* 96: 540–544, 2004.
63. **Muraoka T, Muramatsu T, Takeshita D, Kanehisa H, Fukunaga T.** Estimation of passive ankle joint moment during standing and walking. *J Appl Biomech* 21: 72–84, 2005.
64. **Nordez A, Cornu C, McNair P.** Acute effects of static stretching on passive stiffness of the hamstring muscles calculated using different mathematical models. *Clin Biomech* 21: 755–760, 2006.
65. **Nordez A, McNair P, Casari P, Cornu C.** Acute changes in hamstrings musculo-articular dissipative properties induced by cyclic and static stretching. *Int J Sports Med* 29: 414–418, 2008.

66. **Nordez A, Casari P, Cornu C.** Effects of stretching velocity on passive resistance developed by the knee musculo-articular complex: contributions of frictional and viscoelastic behaviours. *Eur J Appl Physiol* 103: 243–250, 2008.
67. **Nordez A, Casari P, Mariot JP, Cornu C.** Modeling of the passive mechanical properties of the musculo-articular complex: acute effects of cyclic and static stretching. *J Biomech* 42: 767–773, 2009.
68. **Nordez A, McNair PJ, Casari P, Cornu C.** Static and cyclic stretching: their different effects on the passive torque-angle curve. *J Sci Med Sport* 13: 156–160, 2009.
69. **Nordez A, Foure A, Dombroski EW, Mariot JP, Cornu C, McNair PJ.** Improvements to Hoang et al.'s method for measuring passive length-tension properties of human gastrocnemius muscle in vivo. *J Biomech* 43: 379–382, 2010.
70. **Obata H, Kawashima N, Akai M, Nakazawa K, Ohtsuki T.** Age-related changes of the stretch reflex excitability in human ankle muscles. *J Electromyogr Kinesiol* 20: 55–60, 2009.
71. **Petit J, Filippi GM, Emonet-Denand F, Hunt CC, Laporte Y.** Changes in muscle stiffness produced by motor units of different types in peroneus longus muscle of cat. *J Neurophysiol* 63: 190–197, 1990.
72. **Porter MM, Andersson M, Hellstrom U, Miller M.** Passive resistive torque of the plantar flexors following eccentric loading as assessed by isokinetic dynamometry. *Can J Appl Physiol* 27: 612–617, 2002.
73. **Pousson M, Van Hoecke J, Goubel F.** Changes in elastic characteristics of human muscle induced by eccentric exercise. *J Biomech* 23: 343–348, 1990.
74. **Proske U, Morgan DL.** Tendon stiffness: methods of measurement and significance for the control of movement. A review. *J Biomech* 20: 75–82, 1987.
75. **Reeves ND, Narici MV, Maganaris CN.** Strength training alters the viscoelastic properties of tendons in elderly humans. *Muscle Nerve* 28: 74–81, 2003.
76. **Riemann BL, DeMont RG, Ryu K, Lephart SM.** The Effects of sex, joint angle, and the gastrocnemius muscle on passive ankle joint complex stiffness. *J Athl Train* 36: 369–375, 2001.
77. **Sale D, Quinlan J, Marsh E, McComas AJ, Belanger AY.** Influence of joint position on ankle plantarflexion in humans. *J Appl Physiol* 52: 1636–1642, 1982.
78. **Scott JE.** Proteoglycan: collagen interactions and subfibrillar structure in collagen fibrils. Implications in the development and ageing of connective tissues. *J Anat* 169: 23–35, 1990.
79. **Silbernagel KG, Thomee R, Thomee P, Karlsson J.** Eccentric overload training for patients with chronic Achilles tendon pain—a randomised controlled study with reliability testing of the evaluation methods. *Scand J Med Sci Sports* 11: 197–206, 2001.
80. **Silder A, Heiderscheit B, Thelen DG.** Active and passive contributions to joint kinetics during walking in older adults. *J Biomech* 41: 1520–1527, 2008.
81. **Stanish WD, Rubinovich RM, Curwin S.** Eccentric exercise in chronic tendinitis. *Clin Orthop Relat Res*: 65–68, 1986.
82. **Sten-Knudsen O.** Torsional elasticity of the isolated cross striated muscle fibre. *Acta Physiol Scand* 28: 1–240, 1953.
83. **Tian M, Herbert RD, Hoang PD, Gandevia SC, Bilston LE.** Myofascial force transmission between the human soleus and gastrocnemius muscles during passive knee motion. *J Appl Physiol* 113: 517–523, 2012.
84. **van Zandwijk JP, Bobbert MF, Harlaar J, Hof AL.** From twitch to tetanus for human muscle: experimental data and model predictions for m. triceps surae. *Biol Cybern* 79: 121–130, 1998.
85. **Wang JH.** Mechanobiology of tendon. *J Biomech* 39: 1563–1582, 2006.
86. **Waterman-Storer CM.** The cytoskeleton of skeletal muscle: is it affected by exercise? A brief review. *Med Sci Sports Exerc* 23: 1240–1249, 1991.
87. **Whitehead NP, Allen TJ, Morgan DL, Proske U.** Damage to human muscle from eccentric exercise after training with concentric exercise. *J Physiol* 512: 615–620, 1998.
88. **Whittington B, Silder A, Heiderscheit B, Thelen DG.** The contribution of passive-elastic mechanisms to lower extremity joint kinetics during human walking. *Gait Posture* 27: 628–634, 2008.
89. **Wright V.** Stiffness: a review of its measurement and physiological importance. *Physiotherapy* 59: 107–111, 1973.
90. **Wu YK, Lien YH, Lin KH, Shih TT, Wang TG, Wang HK.** Relationships between three potentiation effects of plyometric training and performance. *Scand J Med Sci Sports* 20: 80–86, 2009.