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Effects of plyometric training on passive stiffness of *gastrocnemii* muscles and Achilles tendon

Alexandre Fouré · Antoine Nordez ·
Christophe Cornu

Abstract Plyometric training is commonly used to improve athletic performance; however, it is unclear how each component of the muscle–tendon complex (MTC) is affected by this intervention. The effects of 14 weeks of plyometric training on the passive stiffness of the *gastrocnemii* muscles and Achilles tendon was determined simultaneously to assess possible local adaptations of elastic properties. The passive force–length relationship of the *gastrocnemii* MTC and elongation of the *gastrocnemii* muscles were determined using ultrasonography during passive cyclic stretching in 19 subjects divided into trained ($n = 9$) and control ($n = 10$) groups. An upward trend in stiffness of the *gastrocnemii* MTC ($P = 0.09$) and a significant increase in the intrinsic *gastrocnemii* muscle stiffness were found ($P < 0.05$). In contrast, no significant change in *gastrocnemii* tendon stiffness, or in muscle and tendon geometry, was determined ($P > 0.05$). Considering the lack of change in *gastrocnemii* muscle geometry, the change in the *gastrocnemii* muscle stiffness may be mainly due to a change in the intrinsic mechanical properties of the muscular tissues.

Keywords Range of motion · Jump · Stiffness · *Gastrocnemius* muscle–tendon complex

Introduction

Plyometric training is conventionally used by athletes to improve jumping and sprinting abilities (e.g., Markovic 2007; Ronnestad et al. 2008). During plyometric exercise, the muscle–tendon complex (MTC) stores potential elastic energy during the eccentric phase and restores a part of this energy during the concentric phase (Komi 1992). Thus, the efficiency of a stretch–shortening cycle is influenced by MTC mechanical properties, and a recent study has shown that the increase in jump performance after plyometric training is mainly a consequence of change in MTC mechanical properties, rather than changes in muscle activation strategies (Kubo et al. 2007). It has been shown that the Achilles tendon stiffness determined during muscle contractions increases as a result of plyometric training (Burgess et al. 2007; Fouré et al. 2010; Wu et al. 2010). In contrast, it was shown that such training induces a decrease in muscle stiffness determined during contractions in animals (Almeida-Silveira et al. 1994; Pousson et al. 1991), with studies performed in vivo also showing the same results (Fouré et al. 2011).

As it was shown that passive ankle joint torque plays an important role in various tasks, such as standing and walking (Muraoka et al. 2005; Silder et al. 2008; Whittington et al. 2008), functional performances are also influenced by elastic properties of the passive musculo-articular complex, including structures such as muscles, tendons, skin, subcutaneous tissue, fascia, ligaments, joint capsule and cartilage (Riemann et al. 2001; Wright 1973). Nevertheless, few studies have focused on the effects of training protocol, specifically plyometric training, on musculo-articular complex passive stiffness. Passive cyclic stretches are conventionally performed to obtain passive torque–angle relationships, from which the mechanical

properties of the musculo-articular complex can be extracted (e.g., Magnusson 1998; Mahieu et al. 2008; Nordez et al. 2009a). Recently, a mathematical model developed by Hoang et al. (2005) and improved by Nordez et al. (2010) was used to assess passive force–length relationship of the *gastrocnemii* MTC.

In a previous study, it was shown that 8 weeks of plyometric training increased the *gastrocnemii* MTC stiffness (Fouré et al. 2009). This increase in passive MTC stiffness was hypothesized as being mainly due to changes in *gastrocnemii* muscle stiffness, rather than to Achilles tendon, considering that no significant change was found in tendon stiffness during an isometric contraction (Fouré et al. 2009).

However, the hypothesis could be discussed with respect to two main arguments. Firstly, the passive muscle stiffness was not measured directly. Hoang et al. (2007b) showed that ultrasonography could be used to assess muscle and tendon force–length relationships, and this method has been very useful in determining the plyometric training effects on passive muscle stiffness. Secondly, the tendon stiffness was assessed during an isometric contraction, while MTC stiffness was measured during passive stretching. Yet, the force–length relationship of tendon is non-linear, and the stiffness measured under the high forces generated during isometric contractions unlikely represents the stiffness of the tendon when subject to lower forces involved in passive movement of the MTC (Ettema and Huijing 1989; Lieber and Friden 2000; Morse et al. 2008). Thus, to discuss the possible specific adaptations of the MTC structures, it appears relevant to assess muscle and tendon stiffness under passive conditions, as performed by Hoang et al. (2007b).

The aim of the present study was to determine the effects of plyometric training on the passive force–length relationship of both *gastrocnemii* muscles and Achilles tendon, and the possible specific adaptations of the *gastrocnemii* MTC mechanical properties as hypothesized in a previous study (Fouré et al. 2009). The cross-sectional areas of muscle and tendon were also measured to obtain passive muscle and tendon stress–strain relationships.

Materials and methods

Subjects

Nineteen males volunteered to participate in this study and were assigned to either a trained group ($n = 9$, 19.6 ± 1.8 years, 177.3 ± 6.2 cm, 68.1 ± 6.4 kg) or control group ($n = 10$, 22.1 ± 3.7 years, 177.4 ± 5.4 cm, 71.0 ± 8.1 kg). All subjects were involved in regular sport practices (10.7 ± 6.1 h/wk) and maintained 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. This study was conducted according to the Helsinki Statement and was approved by the local ethics committee.

The plyometric training program, jump tests, geometry of the Achilles tendon and *gastrocnemii* muscles are detailed in two previous studies (Fouré et al. 2010, 2011). It lasted 14 weeks, including 34 1-h sessions for a total of 6,800 jumps (from 200 to 600 jumps per session).

Experimental design

All subjects in the trained group participated in a testing session before (pre-tests) and 1 week after the end of the plyometric training period (post-tests). Untrained subjects were retested 15 weeks after their baseline evaluation. Subjects were tested to determine the ankle joint ranges of motion and passive mechanical properties of the *gastrocnemii* MTC. Functional parameters (i.e., jump performances) and MTC geometry measurements have been also determined and presented in previous studies (Fouré et al. 2010, 2011).

Geometrical parameters of Achilles tendon and *gastrocnemii* muscles

Cross-sectional area measurements of the Achilles tendon (CSA_{AT}), and *gastrocnemii* muscles (CSA_{GAS}) were carried out by ultrasonographic imaging scans (Philips HD3, Philips Medical Systems, Andover, MA, USA) with an electronic linear array probe (7.5-MHz wave frequency; L9-5, Philips Medical Systems, Andover, MA, USA) as described previously (Fouré et al. 2010, 2011). The cross-sectional area of *gastrocnemii* muscles was determined at 50, 60 and 70% of lower leg length. A mean *gastrocnemii* muscle cross-sectional area was then determined from measurement performed on the three levels of the lower leg.

Range of motion and passive torque–angle relationship

The method to assess passive mechanical properties of the musculo-articular complex was similar to that in previous studies (e.g., Nordez et al. 2009a; Riemann et al. 2001). A Biodex system three research[®] (Biodex Medical, Shirley, NY, USA) isokinetic dynamometer was used to measure the torque produced in resistance to passive stretch (T), ankle joint angle (θ_a) and ankle joint angular velocity. Subjects lay prone, legs fully extended with thighs, the hip, and shoulders secured by adjustable lap belts and held in position (Fig. 1). The right ankle joint was securely strapped to a footplate connected to the level arm of the

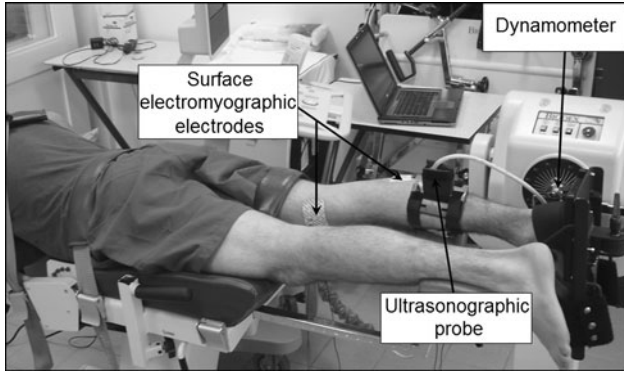


Fig. 1 Subject position during ankle passive stretches. A computer recorded simultaneously electromyographic, ultrasonographic and mechanic data

dynamometer. The input axis of the dynamometer was carefully adjusted to the axis of rotation of the right ankle joint. The device enabled us to change the knee angle (θ_k) as described by Fouré et al. (2009). 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.

Surface electromyographic (sEMG) signals of the medial *gastrocnemius* (GM), lateral *gastrocnemius* (GL), *soleus* (SO) and *tibialis anterior* (TA) muscles 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. Active surface electrodes with an inter-electrode distance of 10 mm (DE-2.1, Delsys[®] Inc, Boston, MA, USA) were placed on muscles according to SENIAM recommendations (Hermens et al. 2000). One reference electrode was placed on the medial femoral epicondyle. sEMG and mechanical (T , θ_a and ω) signals were sampled at 1,000 Hz using an A/D converter (National Instrument, Delsys[®] Inc, Boston, MA, USA) and stored on a hard drive using EMGWorks 3.1 software (Delsys[®] Inc, Boston, MA, USA) for further analysis. 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, its data was disregarded for analysis (e.g., McNair et al. 2001; Nordez et al. 2008, 2009b).

Pre- and post-tests included: (1) Assessment of the maximal ankle joint range of motion (RoM) in plantar flexion with the leg fully extended ($\text{RoM}_{\text{PF}}^{k_0}$), in dorsiflexion with the leg fully extended ($\text{RoM}_{\text{DF}}^{k_0}$) and with the knee joint flexed at 80° ($\text{RoM}_{\text{DF}}^{k_{80}}$). 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 muscles had reached the maximum perceived

tolerable stretch. The foot was then immediately returned 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 $5^\circ/\text{s}$ from 80% of $\text{RoM}_{\text{PF}}^{k_0}$ to 80% of $\text{RoM}_{\text{DF}}^{k_0}$ with knee fully extended. (3) Five cyclic passive repetitions at $5^\circ/\text{s}$ for five randomly tested knee flexion angles ($\theta_k = 15^\circ, 30^\circ, 45^\circ, 60^\circ$ and 80°). The range of stretch was increased proportionally with increase in knee flexion up to passive motions performed from 80% of $\text{RoM}_{\text{PF}}^{k_0}$ to 80% of $\text{RoM}_{\text{DF}}^{k_0}$ with knee flexed at 80° to apply Hoang's model (Hoang et al. 2005) improved by Nordez et al. (2010). Five minutes of rest between each stretching series were allowed. (4) Two maximal voluntary contractions under isometric conditions ($\theta_k = 0^\circ$; $\theta_a = 90^\circ$) for sEMG normalization purposes.

All data were processed using standardized programs computed with Matlab[®] (The Mathworks, Natick, USA). External passive torque and angle position data were filtered using a Butterworth second-order low pass filter (10 Hz), and recorded torque values were corrected for gravity.

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 $0^\circ, 15^\circ, 30^\circ, 45^\circ, 60^\circ$ and 80° of knee angle. Thus, the contribution of the *gastrocnemii* could be determined directly according to the Eq. 1 (Nordez et al. 2010):

$$T_k - T_{80} = m_G (F_{Gk} - F_{G80}) \quad (1)$$

with T_k and F_{Gk} the ankle passive torque and the *gastrocnemii* passive force determined at different knee angles ($k = 0^\circ, 15^\circ, 30^\circ, 45^\circ$ 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 the *gastrocnemii* moment arm assessed using the model of Grieve et al. (1978). The exponential model used in the present study was similar to the model of Sten-Knudsen (Nordez et al. 2006, 2010; Sten-Knudsen 1953) where F_G could be calculated using Eq. 2:

$$F_G = \frac{1}{\alpha} \left(e^{\alpha(l-l_0)} - 1 \right) \quad \text{for } l > l_0$$

$$FG = 0 \quad \text{for } l < l_0 \quad (2)$$

In which l is the *gastrocnemii* length assessed using model of Grieve et al. (1978), α is the parameter determined using the optimization that concerns MTC stiffness, l_0 the *gastrocnemii* slack length determined using the optimization and e the exponential function. The two parameters of

the Eq. 2 (i.e., l_0 and α) were determined by minimizing the squared difference between the experimental and the modeled (Eqs. 1, 2) responses using Matlab (The Mathworks, Natick, USA) and the optimization toolbox (Levenberg–Maquard algorithm). Nevertheless, as previously described by Hoang et al. (2005), l_0 determined with optimization was not necessarily physiologically relevant. Indeed, due to the exponential modeling, a low passive tension, but higher than zero, was developed on a large range of the force–length relationship. Thus, a *gastrocnemii* MTC length for a force production of 1 N ($L_{F=1 \text{ MTC}}$) was determined. Although $L_{F=1 \text{ CMT}}$ is more reproducible than l_0 , these parameters are not true values of the slack length and this point is discussed later.

Using this exponential model, the maximal *gastrocnemii* stiffness (S_{max}^{F-L}) can be determined using Eq. 3 at the maximal passive force (F_{max}) common for both tests:

$$S_{\text{max}}^{F-L} = \alpha \times F_{\text{max}} \quad (3)$$

Then, the α parameter was identified as a stiffness index of the *gastrocnemii* MTC (SI_{MTC}^{F-L}).

Force–length relationships of *gastrocnemii* muscles and Achilles tendon

The echographic 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. 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 stretches, passive external torque, ankle angle and displacement of the distal myotendinous junction of the GM were determined during the loading aspect 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 (Grieve et al. 1978; Hoang et al. 2005). Elongation of the *gastrocnemii* muscles was determined as the total displacement of the myotendinous junction of the GM.

The length of the *gastrocnemii* MTC and tendon was determined for $\theta_a = 90^\circ$ and $\theta_k = 0^\circ$ [i.e., calculated using Grieve et al. (1978) model and measured using ultrasonography, respectively]. Muscle length was calculated, for this position, as the difference between MTC and tendon

lengths. Then, the length of MTC was determined as function of knee and ankle angles using the same anthropometric model 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 cycle.

Relationships between F_G and length of the *gastrocnemii* muscles and Achilles tendon were determined. Next, the Sten-Knudsen model (Eq. 2) was fitted to these two relationships to determine the stiffness index and length for a force development of 1 N by both *gastrocnemii* muscles and Achilles tendon (i.e., SI_{muscle}^{F-L} , $L_{F=1 \text{ M}}$, SI_{tendon}^{F-L} and $L_{F=1 \text{ T}}$, respectively).

Stress–strain relationships of *gastrocnemii* muscles and Achilles tendon

Sten-Knudsen model (Eq. 2) was also fitted to the stress–strain relationships in all subjects. The intrinsic stiffness index of the *gastrocnemii* muscles and Achilles tendon were then determined (i.e., $SI_{\text{muscle}}^{\sigma-\epsilon}$ and $SI_{\text{tendon}}^{\sigma-\epsilon}$ respectively).

Reproducibility

The reproducibility of ankle joint range of motion, *gastrocnemii* MTC passive stiffness index and length, and the Achilles tendon cross-sectional area determined in the present study were investigated at the same time of the day with 2 days of rest in between in our previous studies (Fouré et al. 2010, 2009; Nordez et al. 2010). The reproducibility of the Achilles tendon passive stiffness index and length, *gastrocnemii* muscle passive stiffness index and length, and muscle cross-sectional area were also determined and are shown in Table 1. Intraclass correlation coefficients and coefficients of variation ranged from 0.82 to 0.98 and from 1.3 to 9.9%, respectively. These results support the reliability of the methods used.

Statistics

After checking the distribution of data, parametric statistical tests were performed using Statistica[®] software (Statsoft Inc., Tulsa, OK, USA). Two-way multivariate analyses of variance (ANOVA) (group \times time) were performed to assess the statistical significance of changes in jump performances, ranges of motion, *gastrocnemii* muscles and Achilles tendon cross-sectional area and passive mechanical properties of the *gastrocnemii* MTC, muscles

and Achilles tendon. A Newman–Keuls post hoc analysis was conducted when appropriate. The critical level of significance in the present study was set to $P < 0.05$.

Results

Cross-sectional area of the Achilles tendon and *gastrocnemii* muscles

No significant effect of training was determined after plyometric training on CSA_{GAS} and CSA_T ($P > 0.05$) (Table 2). For the control group, no significant change in geometrical parameters was observed ($P > 0.05$).

Range of motion and passive torque–angle relationship

An interaction was found between “group” and “time” factors for ankle joint $RoM_{DF}^{k_0}$. An increase of 7.3%

($P < 0.05$) was only found for the trained group. No significant change in $RoM_{PF}^{k_0}$ and $RoM_{DF}^{k_{80}}$ was determined ($P < 0.05$) for both groups (Table 2).

No significant change was found in passive torque–angle relationships of ankle joint for both groups ($P > 0.05$).

Force–length relationships of *gastrocnemii* MTC

From *gastrocnemii* MTC force–length relationships (Fig. 2a), upward trends were found for the trained group in SI_{MTC}^{F-L} ($P = 0.09$) and $L_{F=1}$ MTC ($P = 0.06$) between pre- and post-tests (Fig. 3). No significant change in F_{max} (trained group: 525 ± 165 to 492 ± 165 N and control group: 539 ± 220 to 595 ± 217 N) and S_{max}^{F-L} (trained group: 444.13 ± 177.54 to 452.00 ± 218.25 N/mm and control group: 470.00 ± 193.74 to 511.41 ± 195.01 N/mm) was found in both groups ($P > 0.05$).

Table 1 Reproducibility of Achilles tendon, *gastrocnemii* MTC and muscle mechanical and geometrical parameters

	Test 1	Test 2	ICC	CV (%)	SEM
SI_{MTC}^{F-L} (m^{-1})	94.0 (12.9)	90.1 (17.3)	0.87	6.1	5.6
$L_{F=1}$ MTC (m)	0.418 (0.026)	0.414 (0.025)	0.96	1.3	0.005
SI_{muscle}^{F-L} (m^{-1})	160.9 (44.3)	145.5 (35.6)	0.82	9.9	16.9
$L_{F=1}$ M (m)	0.255 (0.023)	0.252 (0.023)	0.97	1.6	0.006
SI_{tendon}^{F-L} (m^{-1})	189.6 (28.8)	175.0 (30.1)	0.83	7.8	12.2
$L_{F=1}$ T (m)	0.157 (0.018)	0.154 (0.023)	0.98	1.9	0.005
CSA_{GAS} (mm^2)	1673 (509)	1685 (504)	0.98	5.1	76

ICC intraclass correlation coefficient, CV coefficient of variation, SEM standard error of measurement, SI_{MTC}^{F-L} and $L_{F=1}$ MTC stiffness index and length of *gastrocnemii* MTC for a passive force of 1 N, respectively, SI_{muscle}^{F-L} and $L_{F=1}$ M stiffness index and length of *gastrocnemii* muscles for a passive force of 1 N, respectively, SI_{tendon}^{F-L} and $L_{F=1}$ T stiffness index and length of Achilles tendon for a passive force of 1 N, respectively, CSA_{GAS} cross-sectional area of the *gastrocnemii* muscles averaged on the cross-sectional areas determined at 50, 60 and 70% of the lower leg length defined as the distance between the center of the lateral malleolus and the popliteal crease

Table 2 : Effects of plyometric training on ankle joint flexibility, Achilles tendon and *gastrocnemii* muscle cross-sectional areas

	Trained group		Control group	
	Pre-test	Post-test	Pre-test	Post-test
$RoM_{PF}^{k_0}$ (°)	53.6 (4.5)	53.4 (8.8)	62.1 (9.3)	59.4 (12.4)
$RoM_{DF}^{k_0}$ (°)	42.5 (5.7)	45.9 (8.5) [†]	51.8 (9.1)	48.7 (7.7)
$RoM_{DF}^{k_{80}}$ (°)	55.5 (9.3)	56.2 (10.6)	55.0 (11.2)	53.5 (12.4)
CSA_T (mm^2)	55.6 (12.2)	57.3 (13.1)	53.8 (9.7)	55.3 (8.6)
CSA_{GAS} (mm^2)	1536 (537)	1615 (463)	1752 (364)	1659 (368)

$RoM_{PF}^{k_0}$ Maximal range of motion of the ankle joint in plantar flexion with leg fully extended, $RoM_{DF}^{k_0}$ Maximal range of motion of the ankle joint in dorsiflexion with leg fully extended, $RoM_{DF}^{k_{80}}$ 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. CSA_T Achilles tendon cross-sectional area, CSA_{GAS} cross-sectional area of the *gastrocnemii* muscles averaged on the cross-sectional areas determined at 50, 60 and 70% of the lower leg length defined as the distance between the center of the lateral malleolus and the popliteal crease. Post hoc test: [†] $P < 0.05$

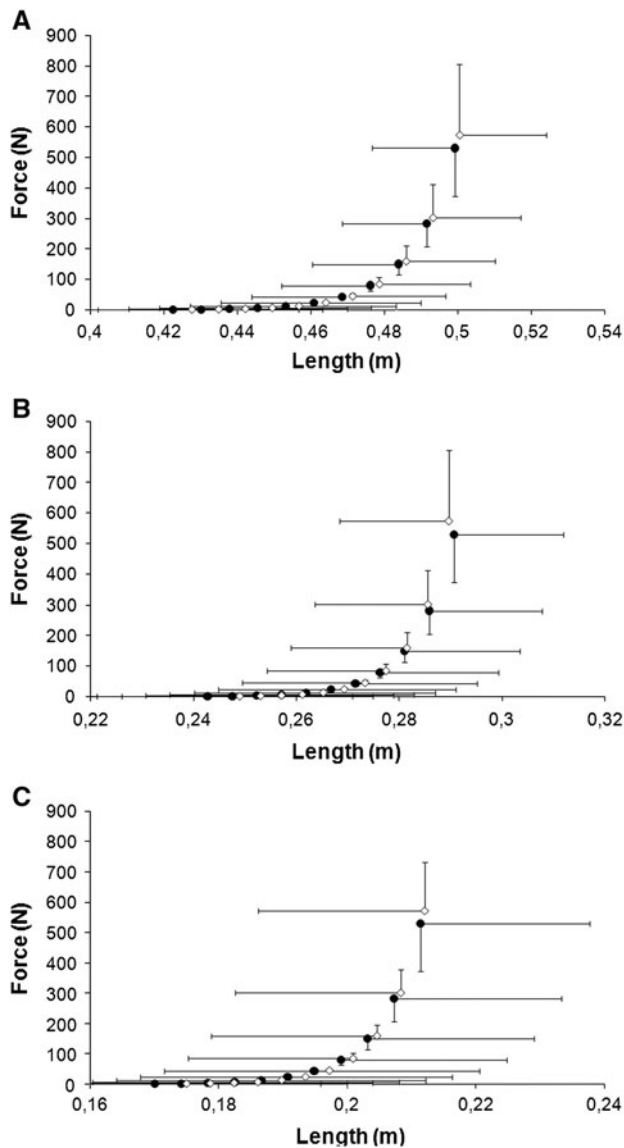


Fig. 2 Mean force-length relationships of the *gastrocnemii* muscle-tendon complex (a), muscle (b) and the Achilles tendon (c) for the trained group between pre-test (filled circles) and post-test (diamonds)

Force-length relationships of muscle and tendon of the *gastrocnemii*

The force-length relationships of the *gastrocnemii* muscles and Achilles tendon for trained group in pre- and post-tests are shown in Fig. 2b and c respectively. An upward trend in SI_{muscle}^{F-L} ($P = 0.08$) and a significant increase in $L_{F=1\text{ M}}$ ($P = 0.02$) were observed (Fig. 3). No significant change in SI_{tendon}^{F-L} and $L_{F=1\text{ T}}$ was found in the trained group (Fig. 2) and all the control group parameters ($P > 0.05$).

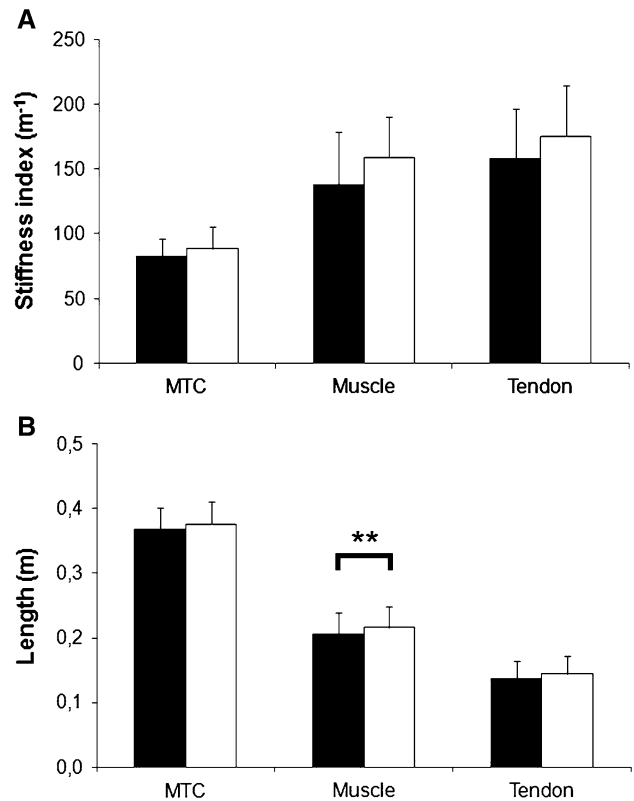


Fig. 3 Stiffness index (a) and length for a passive force of 1 N (b) determined from force-length relationships for *gastrocnemii* muscle-tendon complex (MTC), muscle and Achilles tendon for the trained group between pre-test (filled rectangles) and post-test (open rectangles). Post hoc test: $**P < 0.05$

Stress-strain relationships of *gastrocnemii* muscles and Achilles tendon

From the stress-strain relationships, a significant increase of 26.1% in $SI_{\text{muscle}}^{\sigma-\epsilon}$ was determined for the trained group ($P < 0.05$) (Table 3), and no significant change in $SI_{\text{tendon}}^{\sigma-\epsilon}$ was found in both groups ($P > 0.05$).

Discussion

The aim of this study was to determine the effects of plyometric training on the passive stiffness of the *gastrocnemii* MTC components. The major finding was the significant increase in intrinsic stiffness of the *gastrocnemii* muscles determined non-invasively in vivo after 14 weeks of plyometric training.

Concerning the functional parameter, the flexibility of the ankle joint was increased when the leg was fully extended. The maximal range of motion in dorsiflexion increased by 7.3% (i.e., about 3.5°) after plyometric training for the trained group. No significant change was found in our

Table 3 Effects of plyometric training on stiffness and length parameters of *gastrocnemii* muscles and tendon

		Trained group		Control group	
		Pre-test	Post-test	Pre-test	Post-test
Force–length relationships	SI_{MTC}^{F-L} (Nm^{-1})	82.8 (13.1)	88.6 (17.2)	87.4 (7.8)	85.5 (8.9)
	SI_{muscle}^{F-L} (Nm^{-1})	137.7 (41.1)	159.1 (31.0)	151.3 (31.4)	142.4 (28.2)
	SI_{tendon}^{F-L} (Nm^{-1})	158.1 (38.4)	175.3 (39.5)	169.7 (23.4)	176.7 (34.3)
Stress–strain relationships	$SI_{muscle}^{\sigma-\epsilon}$ (MPa)	29.1 (13.5)	35.0 (11.4) [†]	32.6 (6.2)	30.2 (6.3)
	$SI_{tendon}^{\sigma-\epsilon}$ (MPa)	21.8 (8.4)	25.5 (8.5)	23.9 (4.9)	25.5 (9.3)

Stiffness index of the Achilles tendon, *gastrocnemii* muscles and *gastrocnemii* muscle–tendon complex (SI_{tendon}^{F-L} , SI_{muscle}^{F-L} and SI_{MTC}^{F-L} , respectively) determined from force–length relationships; intrinsic stiffness index of the Achilles tendon and *gastrocnemii* muscles ($SI_{tendon}^{\sigma-\epsilon}$ and $SI_{muscle}^{\sigma-\epsilon}$, respectively) determined from stress–strain relationships. Results are presented as mean (standard deviation). Post hoc test: [†] $P < 0.05$

previous study after 8 weeks of plyometric training, although an upward trend of 10.3% (i.e., 3°) was observed in the maximal range of motion in dorsiflexion with leg fully extended (Fouré et al. 2009). The longer training protocol performed in this study could explain, in part, the significant increase in ankle joint range of motion compared to previous studies (Fouré et al. 2009; Mahieu et al. 2008).

The effect of plyometric training on muscle and tendon behaviors during passive motion has never been previously investigated. Nevertheless, specific changes in the length of muscle and tendon structures during ankle passive motion have been recently assessed in several studies (Abellana et al. 2009; Hoang et al. 2007b, 2009; Morse et al. 2008). When the knee is fully extended, the relative contributions of the *gastrocnemii* muscles and Achilles tendon represent about 50% of the total MTC length change (Hoang et al. 2007b; Morse et al. 2008). Our results are similar to those of the previous studies in this regard. During passive stretches, sEMG activity was carefully controlled. The sEMG activities of agonist (i.e., *soleus* and *gastrocnemii*) and antagonist (i.e., *tibialis anterior*) muscles were below 1% MVC throughout the passive stretches even when the joint was close to 80% RoM. A slow stretch velocity (i.e., 5°/s) and a limited range of motion (i.e., 80% RoM) were used to avoid any stretch reflex onset in sEMG signal (McNair et al. 2001; Nordez et al. 2009a, b, 2010). In addition, it seems that muscle fibers transmit force not only to tendon, but also to adjacent structures, including other muscles (Huijing 2003). Thus, some transmission of force to adjacent structures could occur (Maas et al. 2005; Maas and Sandercock 2008). Nevertheless, observations on humans in vivo suggest that intermuscular force transmission is normally negligible (Hoang et al. 2007a, b). Considering that only knee joint flexion angle was changed between the various conditions, it could be assumed that the major part of the passive torque difference was due to the *gastrocnemii* MTC (Herbert et al. 2008).

The specific force of the *gastrocnemii* MTC has been already determined in previous studies (Hoang et al. 2005, 2007a, b, 2009; Nordez et al. 2010). The mean maximal

force values determined in this work was similar (Fouré et al. 2009; Hoang et al. 2005; Nordez et al. 2010). To determine *gastrocnemii* MTC length and lever arm, the model of Grieve et al. (1978) was used. Using this anthropometric model is likely to provide a good estimate of average MTC length and lever arm, but do not take into account specific subject characteristics which may differ from the average. Mis-specification of lever arms of atypical individuals could distort estimates of force–length relationships (Hoang et al. 2005). Nevertheless, this issue was previously discussed as relying on the accuracy of estimations of changes in muscle–tendon length with joint angle (Herbert et al. 2002). In addition, it could be assumed that, during this 14 weeks period of plyometric training, no change in lower leg length and lever arm occurred. Therefore, a potential misestimation of the muscle length and lever arm using Grieve et al.’s model would not have any influence on interpretation of our results concerning the effects of plyometric training. As well, we found no significant change in *gastrocnemii* MTC force–length relationship with training. Thus, the stiffness index (i.e., SI_{MTC}^{F-L}) extracted from the model of Sten-Knudsen (Nordez et al. 2006, 2010; Sten-Knudsen 1953), independent of the force, showed a non-significant upward trend ($P = 0.09$).

The force–length relationships were fitted with the Sten-Knudsen model to determine α representing a stiffness index and l_0 the *gastrocnemii* slack length (i.e., Eq. 2) (Nordez et al. 2010). The use of an exponential model for the determination of the slack length was found to be reproducible; however, the value of l_0 was too small to be physiologically possible. Using anthropometric data (Grieve et al. 1978), it was found the mean slack length corresponded to an ankle angle of 93° in plantar flexion (i.e., foot perpendicular to the tibia = 0° and knee fully extended), which is not included in the physiological range of motion. Hence, strains determined from this slack length (i.e., for MTC, muscle and tendon) were too high. However, the aim of the present study was to determine the effect of plyometric training and to assess the change in l_0 .

Considering the reproducibility of the slack length measurements (Table 1), the error in slack length determination was assumed to have negligible effect on interpretations and conclusions posited in this work. To improve the slack length assessment, the determination of the MTC, muscle and tendon length was done for 1 N ($L_{F=1}$), a very small force considering the range of force observed during passive stretches. The mean length calculated for 1 N seems more representative of the physiological slack length, which corresponds to an ankle angle of about 50° in plantar flexion (i.e., with knee fully extended). $L_{F=1}$ was specific to each subject and not arbitrarily determined as the length measured with the joint in its mid-position (Magnusson et al. 2003) or when the net joint torque is zero (De Monte et al. 2006; Muraoka et al. 2002). As $L_{F=1}$ was reproducible, it was used in the present study for analyses. Thus, the method used provides the opportunity to explore effects of plyometric training on *gastrocnemii* MTC passive stiffness and length in more depth. While no significant change in SI_{tendon}^{F-L} was found after 14 weeks of plyometric training, a non-significant upward trend in SI_{muscle}^{F-L} was observed ($P = 0.07$). This upward trend could be due to an increase in muscle and/or intrinsic tissues' mechanical properties. Considering that no significant change in mean CSA_{GAS} was determined, changes in intrinsic mechanical properties of muscle tissues occurred with an increase of 26.1% in $SI_{muscle}^{\sigma-\varepsilon}$ after our plyometric training protocol. This can probably be due to an increase in muscle collagen concentration, which has already been shown on isolated muscle after jump training (Ducomps et al. 2003).

Then, a different change occurred in passive stiffness of muscle and tendon after plyometric training. Considering the model of Zajac (1989), an increase in muscle passive properties (PEC_1) was found, while the passive stiffness of tendon (PEC_2) was unchanged (Fig. 4). These results are in addition to those obtained in the same population after the same plyometric training on the stiffness of the series elastic component (Fouré et al. 2011) and Achilles tendon mechanical properties (Fouré et al. 2010). A decrease in the active part of the series elastic (SEC_1) stiffness was previously found (Fouré et al. 2011) whereas, an increase in PEC_1 stiffness was observed in the present study. However, PEC_1 and SEC_1 do not represent the behavior of the same structures within the muscle (Fig. 4), and a specific adaptation of active and passive structures within the muscle could be considered. Concerning the Achilles tendon, an increase was previously observed in the stiffness of Achilles tendon and the passive part of the series elastic component (SEC_2) stiffness during an isometric contraction (Fouré et al. 2010, 2011), while no significant change in PEC_2 stiffness was shown in the present study. Different adaptations occurred specifically when tendon stiffness was assessed in active and

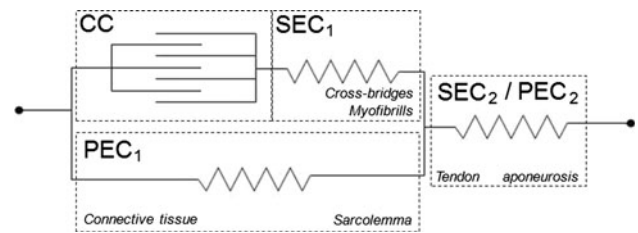


Fig. 4 Zajac's model illustrating the interaction between the contractile component (CC) and parallel (PEC) and series elastic components (SEC). In this model, muscle and tendon structures (i.e., SEC_1/PEC_1 and SEC_2/PEC_2 , respectively) are dissociated (Zajac 1989)

passive conditions. Thus, mechanical loading performed on tendon during passive joint motion and isometric contraction should involve different structures within the tendon.

In summary, the present study determined the effects of 14 weeks of plyometric training, with consideration to dissociated change in passive stiffness of the *gastrocnemii* MTC, muscle and Achilles tendon. This dissociation allowed for the assessment of specific adaptations of each component belonging to the *gastrocnemii* MTC non-invasively, after 14 weeks of plyometric training. Passive structures of the *gastrocnemii* muscle were more sensitive to plyometric actions than tendinous tissues. Further studies are needed to determine the potential physiological mechanisms involved in changes of tendon mechanical properties assessed in active and passive conditions. In addition, with involvement of active mechanical properties of MTC in muscle tension transmission and potential elastic energy storage–recoil process being well known, the contribution of passive mechanical properties in functional behavior of MTC needs to be determined more clearly.

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