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ORIGINAL ARTICLE

Effects of plyometric training on both active and passive parts of the plantarflexors series elastic component stiffness of muscle–tendon complex

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Abstract The aims of this study were to determine the effects of plyometric training on both active and passive parts of the series elastic component (SEC) stiffness, and on geometrical parameters [i.e., muscle architecture, muscle and tendon cross-sectional area (CSA)] of the plantarflexors muscle–tendon complex to assess possible specific adaptations of the elastic properties. Nineteen subjects were randomly divided into a trained group and a control group. Active and passive components of the SEC stiffness were determined using a fast stretch during submaximal voluntary isometric plantarflexor activity. Geometrical parameters of the *triceps surae* muscles and the Achilles tendon were determined using ultrasonography. A significant increase in the passive component of the SEC stiffness was found ($p < 0.05$). In contrast, a significant decrease in the active part of the SEC stiffness was observed ($p < 0.05$). No significant changes in plantarflexor muscles CSA, architecture and Achilles tendon CSA were seen ($p > 0.05$). Thus, plyometric training led to specific adaptations within each part of the SEC. Theses adaptations could increase both the efficiency of the energy storage–recoil process and muscular tension transmission leading to an increase in jump performances.

Keywords Stiffness · Cross-sectional area · Muscle architecture · Achilles Tendon · Jump training

Introduction

The stretch shortening cycle is a mechanism of the human muscle–tendon complex (MTC) for improving both the performance and economy of motion. It primarily involves the mechanical properties of MTC and utilizes an elastic energy storage–recoil process and muscular tension transmission (Komi 1992). Plyometric training has been shown to increase performance in jumping activities (e.g., Fouré et al. 2009; Kyrolainen et al. 2005; Spurrs et al. 2003). These increases in performance have traditionally been explained by MTC mechanical properties changes (i.e., involvement of elastic energy storage-recoil process and muscular tension transmission) as well as the optimization of neural properties (i.e., stretch reflex, muscle-activation strategies). Of these explanations, it has been recently shown that improvements in jump performance after plyometric training are more likely a consequence of changes in the mechanical properties of the MTC rather than muscle activation strategies (Kubo et al. 2007).

A number of authors (e.g., Cornu et al. 1997; Grosset et al. 2009; Kubo et al. 2007; Pousson et al. 1995; Spurrs et al. 2003) have noted that one of the mechanical properties that undergo changes as a result of such training is musculotendinous stiffness. Musculotendinous stiffness refers to the degree of resistance offered by tissues in response to specific lengthening. Several methods can be

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used to determine musculotendinous stiffness, most through indirect measurements that assess how a joint resists externally imposed displacements (Latash and Zatsiorsky 1993) and such measurements are often termed joint stiffness, and where quick-release and short range methods are utilized, it was assumed that the musculotendinous stiffness is the major part of the joint stiffness and that the other components could be considered as negligible in stiffness measurements (e.g., Blanpied and Smidt 1992; Goubel and Pertuzon 1973). There is conflicting evidence in the literature showing that both increases and decreases in stiffness may lead to improvements in performance. In respect to jumping performance following plyometric training, Kubo et al. (2007) recently reported an increase of 63.4% in joint stiffness assessed during drop jumps as a result of 12 weeks of plyometric training, a finding consistent with earlier studies by Spurrs et al. (2003) and Pousson et al. (1995) that assessed stiffness using an oscillation technique and a quick-release method, respectively. In contrast, Cornu et al. (1997) found a decrease of 32.7% in ankle joint stiffness after 7 weeks of plyometric training using sinusoidal perturbations. Similarly, Grosset et al. (2009) reported that 10 weeks of plyometric training led to a decrease of 21% in musculotendinous stiffness assessed using the quick-release method.

These contrasting findings may reflect a number of issues. First, the measurement techniques used to evaluate stiffness, particularly whether the technique utilized was more suited or applicable to determine a specific component of musculotendinous stiffness. Hills model type (Hill 1938) shows that the stiffness of the series elastic component (SEC) is composed of a passive part (i.e., mainly tendon and aponeuroses) and an active part (i.e., contractile elements) (Huxley and Simmons 1971). Secondly, these specific components may respond differently to training. It may be that plyometric training induces specific changes in different elements of the MTC. There is some evidence to support this conjecture. Using an invasive technique, Malisoux et al. (2006) found an increase in Young's modulus of type II muscle fibers myosin heavy chain isoforms only, as a result of 8 weeks of stretch shortening cycle training. These authors also noted a significant increase in cross-sectional area (CSA) of the muscle fibers and the proportion of type II muscle fibers. Other authors have focused on tendon stiffness. For instance, Burgess et al. (2007) and Wu et al. (2009) found an increase in Achilles tendon stiffness after 6 and 8 weeks of plyometric training, respectively, while Kubo et al. (2007) and Fouré et al. (2010a) found no significant change in Achilles tendon stiffness 12 and 8 weeks of training, respectively. To our best knowledge, no studies have determined the effects of a plyometric training program simultaneously and non-invasively on both active and passive parts of the SEC stiffness.

The assessment of muscle mechanical properties remains difficult to perform non-invasively in vivo. However, a recent study by Fouré et al. (2010a) adapted the alpha method, which was previously developed in isolated muscle (Morgan 1977) to determine the stiffness of both components of the SEC simultaneously in vivo. Thus, Fouré et al. (2010a) work provides the opportunity to explore the effects of plyometric training on musculotendinous stiffness in more depth.

Specifically, the aims of the current study were to determine the effects of plyometric training on both parts of the SEC stiffness non-invasively in vivo (Fouré et al. 2010a) to clarify possible local adaptations (1) between muscle and tendon structures mechanical properties within the *triceps surae* muscle group; and (2) between muscular and tendinous intrinsic mechanical properties and geometrical parameters (i.e., CSA and architecture) of the *triceps surae* MTC.

Methods

Subjects

Nineteen males volunteered to participate in this study and were randomly assigned to trained [$n = 9$, 18.8 (0.9) years, 177.3 (6.2) cm, 68.4 (6.5) kg] and control groups [$n = 10$, 18.9 (1.0) years, 179.8 (5.4) cm, 73.3 (8.0) kg]. All subjects were involved in regular sport practices [10.5 (6.2) h week^{-1}] 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. This study was conducted according to the Helsinki Statement (last modified in 2004) and was approved by the local ethics committee.

Training

The plyometric training program was based on the different kinds of jumps, as defined in the literature (e.g., Cornu et al. 1997; Pousson et al. 1990; Spurrs et al. 2003). More precisely, the subjects performed: (1) squat jumps (SJ) defined as vertical jumps without prior counter movement, (2) vertical counter movement jumps (CMJ), (3) drop jumps [i.e., hopping, jumps from either low (35 cm), medium (50 cm) or high (65 cm) platforms], (4) a series of repetitive jumps over 40 cm high barriers using one foot or both feet. The program was progressed by increasing the number of exercises, the number of jumps per exercise and the intensity of the exercises (e.g., the height was increased). The training program lasted for 14 weeks and included 34 sessions of 1 h for a total of approximately 6,800 jumps (from 200 to 600 jumps per session).

Experimental design

Subjects were tested over three sessions performed on different days in a randomized order: (i) a jump test session to determine performances in SJ, CMJ and reactive jump (RJ), (2) a session to assess the ankle joint stiffness called the "short range stiffness experiment", (3) a session to assess Achilles tendon CSA, *triceps surae* muscles CSA and architecture. Subjects performed the three test sessions before (pretests) and over 1 week after the end of the plyometric training period (posttests).

Jump performance session

Performances in SJ, CMJ and RJ were determined for all subjects, using a Bosco jumping mat (Ergojump, Globus Italia, Codogne, Italy). The SJ was performed with a start angle fixed at 90° of knee flexion. The RJ consists of eight maximal jumps performed consecutively only using ankle joint movements (i.e., without knee or hip flexion). The maximal heights in SJ and CMJ and the average height in RJ were determined as the best from three trials. During all jump tests, subjects were instructed to put their hands on their hips. The test was repeated if the subject did not follow the instructions concerning jump procedures (i.e., hands positions, knee flexion during RJ).

Active and passive parts of the SEC stiffness

A Biodex system 3 research® (Biodex medical, Shirley, NY, USA) isokinetic dynamometer was used to measure the external torque produced, ankle joint angle and ankle joint angular velocity. Subjects were seated, legs fully extended with thighs, the hip and shoulders secured by adjustable lap belts and held in position as described in previous studies (Fouré et al. 2009; Nordez et al. 2009). The right ankle joint was strapped securely to a footplate connected to the lever arm of the dynamometer. The input axis of the dynamometer was aligned to the presumed rotational axis of the right ankle joint. The ankle joint angle was fixed at 75° (the foot perpendicular to the tibia = 90° with angles <90° being in plantarflexion), and hip angle was flexed to 140° (full extension = 180°).

Subjects performed: (1) a warm up which consisted of submaximal isometric plantarflexor activation, (2) two maximal voluntary contractions under isometric conditions in plantarflexion performed at 75° with 2 min of rest between each trial. The maximal isometric torque in plantarflexion (MVC) was utilized in subsequent analyses, (3) a familiarization to the short range stiffness experiment in which subjects had to sustain two submaximal torques at 40 and 80% of their MVC. In each of these trials, a fast stretch into dorsiflexion was then 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 and the angular velocity during the stretch reached 250°/s, (4) the short range stiffness experiments (14 trials) outlined above were then performed at seven levels of submaximal torque in a random order (2 trials at each 10% of MVC from 30 to 90% of MVC). Between each trial, 2 min of rest was provided.

Surface electromyographic (sEMG) signals of the lateral *gastrocnemius* (GL), medial *gastrocnemius* (GM), and *soleus* (SO) muscles were recorded. 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 (i.e., external torque, ankle angle and angular velocity) 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 analyses. 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.

Thereafter, the data processing was similar to that of Fouré et al. (2010a). The torque measured by the dynamometer was corrected for inertia and the weight of the dynamometer attachment to obtain the external torque at the ankle joint. The external torque and the ankle angle were determined when the joint commenced movement (i.e., when velocity > 0) and 60 ms thereafter. The joint compliance (i.e., inverse of joint stiffness) was considered as the compliance of two springs placed in series, one representing compliance of the active component, and the other, the passive component of the SECs. The active component of the SEC compliance was thought to be inversely proportional to the torque (Morgan 1977) and the passive component of the series elastic component compliance (C_{SEC2}) was assumed to be constant across the range of torque investigated. The influence of this second assumption on the results is assessed in the electronic supplementary material 1. The relationship between ankle joint compliance and torque can be written as follows:

$$\alpha = C \times T = \alpha_0 + C_{SEC2} \times T \qquad (1)$$

where α is calculated as the product between external torque (T) and ankle joint compliance (C), and α_0 represents the elastic extension with the torque-dependent component of the SEC.

A linear regression was applied on the relationship alpha (α) − torque (T). Then, α_0 and C_{SEC2} were extracted as the Y-intercept, and the slope, respectively. These two parameters (i.e., α_0 and C_{SEC2}) were used to calculate the joint stiffness (S) using Eq. 2:

$$S = \frac{T}{T \times C_{SEC2} + \alpha_0} \quad (2)$$

The joint stiffness-torque relationship was assessed for each subject and each session (i.e., pre and posttests). A stiffness index of the active component of the SEC (SI_{SEC1}) and a stiffness of the passive component of the SEC (S_{SEC2}) were calculated as the inverse of α_0 and C_{SEC2}, respectively.

CSA and architecture measurement session

Achilles tendon geometrical parameters

Measurements of the Achilles tendon cross-sectional area (CSA_{AT}) 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). Subjects lay in a prone position on an examination couch with legs fully extended and the ankle joint angle set at 90°. A water bag was placed over the posterior aspect of the ankle. The measurement of CSA_{AT} was performed in a transversal plane with the transducer perpendicular to the Achilles tendon at the level of the medial malleolus (Ying et al. 2003). Images were saved on a hard disk and CSA_{AT} was determined using open-source digital measurement software (Image J, NIH, Bethesda, MD, USA). The CSA_{AT} were averaged over at least three images.

Triceps surae muscles CSA

Measurement of the plantarflexor muscles CSA was 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 (Fig. 1). Using a specific guide, 12 images were taken transversally (4 images on each side of the lower leg) on 3 levels of the lower leg length, this being defined as the distance between the centre of the lateral malleolus and the popliteal crease. The cross-sectional area of *triceps surae* muscles (CSA_{TS}) was averaged across points at 50, 60 and 70% of lower leg length. More specifically, images were saved on a hard disk and then, at each point of the lower leg length, all images were assembled to obtain a full lower leg CSA image using powerpoint software format (Powerpoint 2007, Microsoft Corp., Redmond, WA, USA). From these images of the lower leg (Fig. 2), the CSA of *triceps surae* muscles was determined using open-source digital measurement software (Image J, NIH, Bethesda, MD, USA).

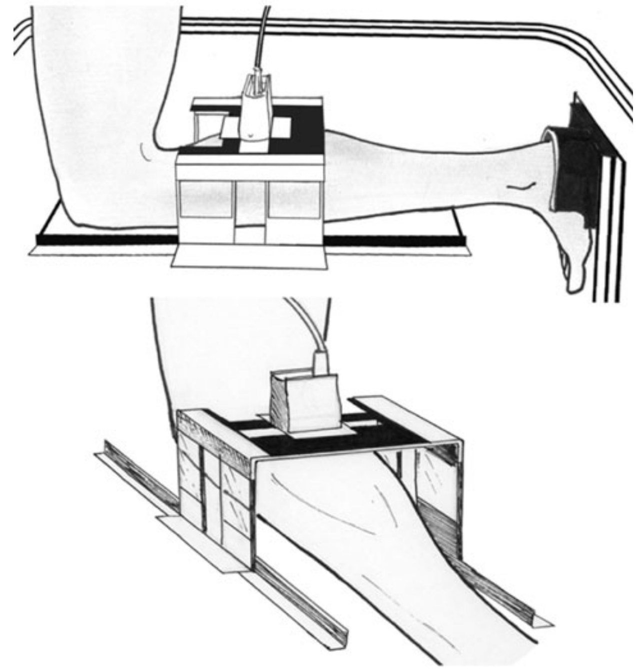

Fig. 1 Subject position for ultrasound scanning in the water-field container (cut away). The subjects were kneeling and water covered the entire lower leg. The foot was rigidly stabilized at 90° of ankle flexion. Knee angle was maintained at 90° of knee flexion by having the leg supported at the end of the water-field container. Ultrasound images were acquired transversally on each side of the lower leg using a specific probe guide

Triceps surae muscles architecture

Muscle architectural parameters were measured on the three muscles of the *triceps surae* (i.e., SO, GM and GL). Subjects lay in a prone position on an examination couch with legs fully extended and their ankle angle fixed at 90°. Using longitudinal ultrasonographic images captured along the belly of each muscle as detailed in previous studies (Kawakami et al. 1998, 2002), fascicule length and pennation angle were measured. Fascicle length was defined as the length of the fascicular path between the superficial and deep aponeurosis. In some cases, the fascicles extended off the acquired image. The length of the missing portion was estimated by linear extrapolation. This was done by measuring the linear distance from the identifiable end of a fascicle to the intersection of a line drawn from the fascicle and a line drawn from the superficial aponeurosis (e.g., Blazevich et al. 2007). The pennation angle was determined on each image as the angle between fascicle and

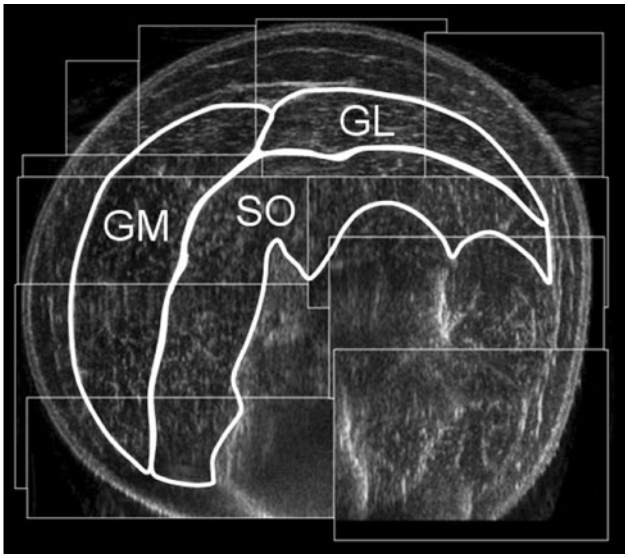

Fig. 2 Typical ultrasonographic images of the triceps surae muscles obtained at 70% of the lower leg length. The lateral gastrocnemius (*GL*), the medial gastrocnemius (*GM*) and the soleus (*SO*) are labeled and outlined

deep aponeurosis (Fig. 3). Each measurement was averaged across three fascicules on at least three images.

Reliability

The reliability of the stiffness parameters (i.e., joint stiffness values, SI_{SEC1} and S_{SEC2}) have been previously determined and shown to be good (ICCs higher than 0.88 and CVs lower than 6.0 Fouré et al. (2010a). A pilot study was conducted for the current study to assess the reliability of the methods used to determine the geometrical properties of plantarflexors MTC. Data from two repeated testing sessions completed at the same time of the day with a 2-day interval were examined. Intraclass correlation coefficients (ICC) (2, *k*) (Fleiss 1986) were calculated, and are presented in Table 1 (ICC ranged from 0.82 to 1.00). In addition, the standard error of measurement and coefficient of variation associated with each ICC were calculated (Table 1). The results supported the reliability of the methods proposed in the present study.

Statistics

After checking the distribution of data, parametric statistical tests were performed using Statistica® software (Statsoft Inc., Tulsa, OK, USA). Descriptive data included means (SD). Two-way multivariate analyses of variance (ANOVA) (group × time) were performed to assess the statistical significance of changes in jumps performances, joint stiffness, SI_{SEC1}, S_{SEC2}, CSA_{AT}, CSA_{TS} and architectural parameters of *triceps surae* muscles. A Newman–Keuls post hoc analysis was conducted where appropriate. The critical level of significance in the present study was set at $p < 0.05$.

Results

Jump performances

A significant interaction ($p < 0.05$) between "group" and "time" factors was found for SJ, CMJ and RJ performances (Table 2). For the trained group, a significant increase in height was shown in SJ (mean +11.0%, $p < 0.001$), CMJ (mean +7.4%, $p < 0.02$) and RJ (mean +27.7%, $p < 0.001$). For the control group, no significant change in these parameters was observed ($p > 0.05$).

Active and passive components of the SEC stiffness

A significant interaction ($p < 0.05$) was found between "group" and "time" factors for SI_{SEC1} and S_{SEC2}. Mean

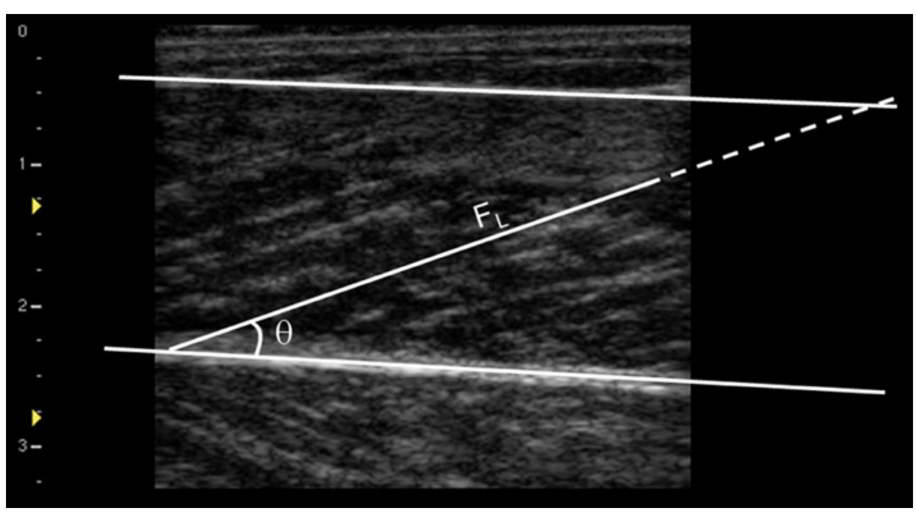

Fig. 3 Typical ultrasonographic image of the medial *gastrocnemius* obtained on one subject. *Lines* delineating the deep aponeurosis and visible fascicles are used to determine fascicle length (F_L) and pennation angle (θ)

Table 1 Intraclass correlation coefficient (ICC), variation coefficient (CV) and standard error of measurement (SEM) calculated to establish day to day reliability for Achilles tendon cross-sectional area (CSA_{AT}), cross-sectional area of the triceps surae muscles (CSA_{TS}) meaning 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, architecture parameters (pennation angle and fascicule length) for lateral gastrocnemius (GL), medial gastrocnemius (GM) and soleus (SO)

	Day to day reliability (2, *k*)	ICC	CV	SEM	*N*
	CSA_{AT} (mm^2)	0.99	2.2	0.8	8
	CSA_{TS} (mm^2)	0.97	4.8	165	16
GL	Pennation angle (°)	0.86	6.4	0.9	13
	Fascicule length (cm)	0.81	6.9	0.5	13
GM	Pennation angle (°)	0.96	4.3	1.1	13
	Fascicule length (cm)	0.91	4.4	0.2	13
SO	Pennation angle (°)	0.91	10.9	2.8	13
	Fascicule length (cm)	0.85	12.1	0.5	13

N number of subjects

relationships between ankle joint stiffness and external torque for both trained and control group are presented in Fig. 4. The joint stiffness values at high torque levels were significantly higher in the posttest as compared to the pretest for the trained group ($p < 0.05$) (Fig. 4). For the trained group, a significant decrease of 10.4% in SI_{SEC1} (Fig. 5a) and a significant increase of 13.2% in S_{SEC2} was observed after training (Fig. 5b). For the control group, no significant change was observed ($p > 0.05$).

Electromyographic activity

Mean EMG activity recorded before and after the stretching protocol is shown in Fig. 6. EMG activity was not observed to change until a latency of 45 ms following the onset of motion. At this point, EMG activity from *gastrocnemius* and *soleus* muscles increased for a 20–30 ms period. Activity from *tibialis anterior* was unchanged through the recording period.

Geometrical parameters of the triceps surae MTC

After plyometric training, no significant effect of training was observed in CSA_{TS}, CSA_{AT} and architectural parameters ($p > 0.05$) (Table 3). For the control group, no significant change in geometrical parameters was observed ($p > 0.05$).

Discussion

The aims of this study were to determine the effects of 14 weeks of plyometric training on jumping performance, together with biomechanical and muscle architectural properties of the plantarflexor MTC. With respect to the former, the increase in jump performances (between 7.4 and 27.7% according to the jump type) after the plyometric training for the trained group was in agreement with the published results. A recent meta-analysis reported an increase of 4.7 and 8.7% in SJ and CMJ performances, respectively, after 4 to 24 weeks of plyometric training (Markovic 2007). Therefore, our jump results demonstrated the efficacy of our training program.

In the present study, an increase in joint stiffness at higher levels of torque was found. Other studies have also found increases between 8.2 and 63.4% (i.e., depending on the stiffness measurement methods used) in global ankle stiffness (Kubo et al. 2007; Pousson et al. 1995; Spurrs et al. 2003; Toumi et al. 2004). However, there are contrasting findings. For instance, both Cornu et al. (1997) and Grosset et al. (2009) have noted decreases in stiffness after plyometric training.

In the current study, measurements of both active and passive components of the SEC stiffness were performed from a global measurement simultaneously in vivo using a new methodology (Fouré et al. 2010a). With regard to the specific adaptations of each component of the SEC stiffness, the decrease in the active component of the SEC stiffness (i.e., located in muscular structures) after plyometric training is in agreement with the findings in isolated

Table 2 Jump performances (SJ squat jump, CMJ counter movement jump and RJ reactive jump) in trained and control groups before (pretest) and after (posttest) 14 weeks of plyometric training

	Trained group		Control group	
	Pretest	Posttest	Pretest	Posttest
SJ maximal height (cm)	37.5 (4.4)	41.5 (4.2)‡	34.7 (7.8)	35.5 (8.3)
CMJ maximal height (cm)	44.5 (4.8)	47.5 (3.8)†	40.3 (7.8)	39.5 (6.9)
Average height on 8 RJ (cm)	32.3 (5.1)	40.6 (3.0)‡‡	27.8 (2.8)	25.2 (4.2)

The results are presented as mean (standard deviation)

Post hoc test: $^{†}p < 0.02$; $^{‡}p < 0.01$; $^{‡‡}p < 0.001$

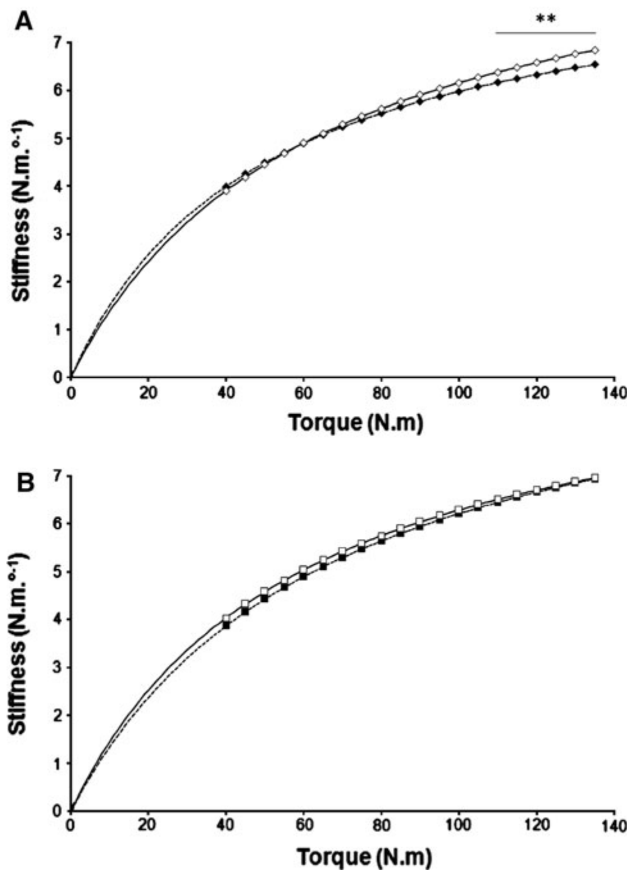

Fig. 4 Mean joint stiffness–torque relationships obtained before (*filled diamond*) and after (*open diamond*) 14 weeks of plyometric training for both trained (**a**) and control (**b**) groups. **Statistically significant difference between pretest and posttest values ($p < 0.05$)

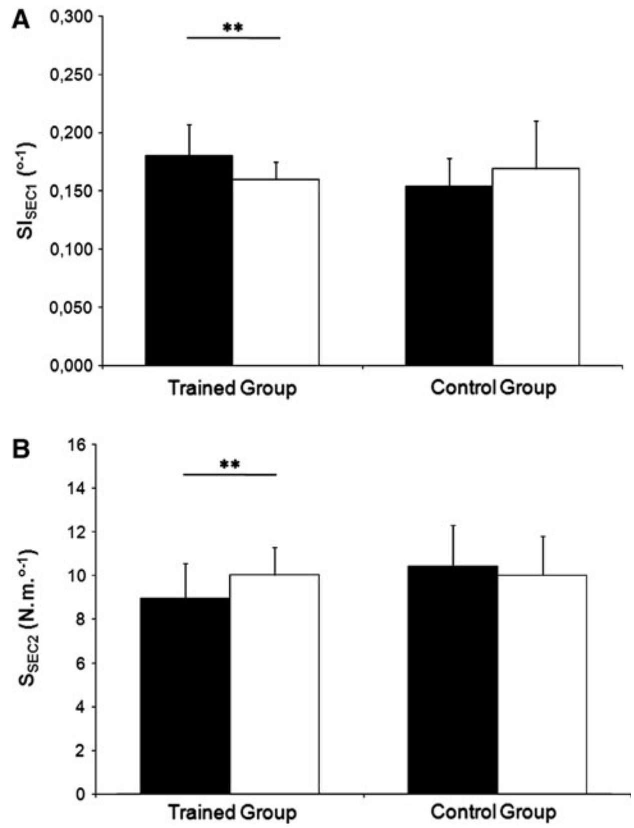

Fig. 5 **a** Mean ± standard deviation of the stiffness index of the active part of the series elastic component (SI_{SEC1}) and **b** mean ± standard deviation of the passive part of the series elastic component stiffness (S_{SEC2}) determined before (*filled bar*) and after (*open bar*) 14 weeks of plyometric training for both trained and control groups. **Statistically significant difference between pretest and posttest values ($p < 0.05$)

muscle (Almeida-Silveira et al. 1994; Pousson et al. 1991). While speculative, considering the lack of change in *triceps surae* muscles architecture and the CSA, the change in stiffness is most likely due to changes in the intrinsic mechanical properties of the muscle fibers. As hypothesized in previous studies (Cornu et al. 1997; Malisoux et al. 2006; Pousson et al. 1991), a fiber type transition phenomenon could occur. Supporting this conjecture in rat soleus muscle, plyometric training can induce a relative increase in type II fibers (Almeida-Silveira et al. 1994) which are more compliant than type I fibers (Goubel and Marini 1987). From a practical standpoint, the decrease in the active component of the SEC stiffness probably allows a better storage of elastic energy during the eccentric phase of the stretch-shortening cycle.

The increase in the passive component of the SEC stiffness (i.e., mainly located in tendon structures) found in the present study is in agreement with previous work studying effects of plyometric training on Achilles tendon (Burgess et al. 2007; Wu et al. 2009). In addition, the lack of change in CSA_{AT} after training is also similar to the findings of Kubo et al. (2007). Thus, it seems likely that the observed increases in the SEC tendon stiffness may result from intrinsic structural changes (e.g., increases in cross linkages between collagen fibrils), rather than changes in the gross geometrical parameters of the tendon.

With respect to the methodology utilized in the current study, initially, the alpha technique was developed to separate both muscle and tendon stiffness behavior in isolated muscle–tendon preparations (Morgan 1977; Morgan et al. 1978). This method assumes that tendon stiffness remains constant throughout the range of force (Morgan, 1977). In the Electronic Supplementary Material 1, the effects of the assumption of constant stiffness of the SEC_1 for force levels higher than 30% of MVC is quantified. Using data from the same subjects who were participants in the present study (Fouré et al. 2010b), where Achilles tendon stiffness was assessed using ultrasonography during increased isometric plantarflexion, it is clearly shown that a nonlinear model slightly, but significantly improves the calculations of tendon stiffness, SI_{SEC1} and S_{SEC2} using the alpha method. However, it can also be concluded that the alpha method is

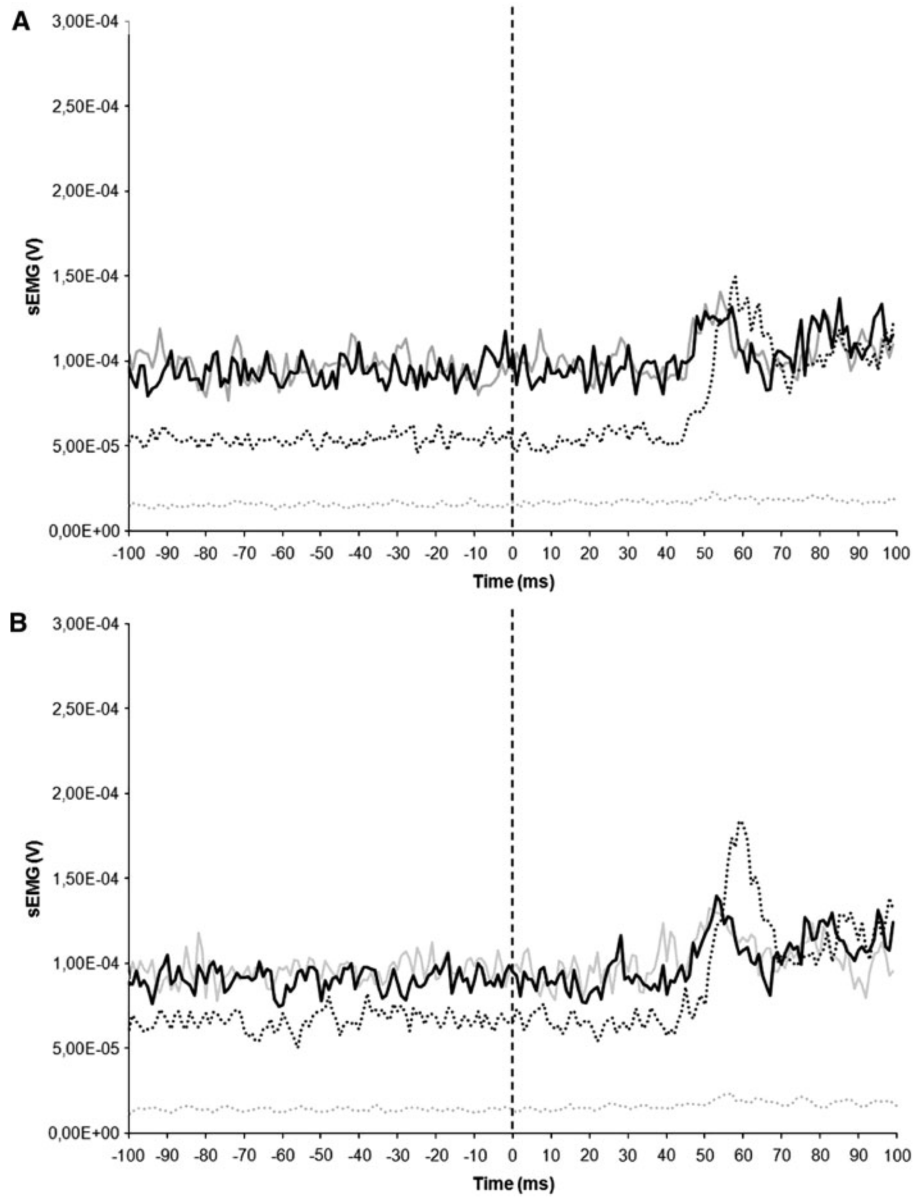

Fig. 6 Mean sEMG–time relationships for each muscles: *gastrocnemius lateralis* (*gray line*), *gastrocnemius medialis* (*black line*), *soleus* (*dotted black line*) and *tibialis anterior* (*dotted gray line*) obtained for data 100 ms before and after the beginning of the stretch (*solidus*) on all valid trials for the trained group before (**a**) and after (**b**) 14 weeks of plyometric training

only slightly affected by the constant stiffness hypothesis (i.e., mean error of +3.4% for the SI_{SEC1} and −4.3% for S_{SEC2}), indicating that the linear model can be utilized in the alpha method in vivo. This result confirms the conclusion of Proske and Morgan (1987) that, for ex vivo muscle, "above 20–30% of maximal isometric tension, tendon stiffness is more nearly constant than proportional to the tension".

Some consideration should be given to neural signals affecting the current findings. In the current study, the method utilized assumes that change in muscular activation has no impact on the measurement of stiffness. From a theoretical perspective, studies have 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 (Cronin et al. 2008; Obata et al. 2010). An analysis on sEMG signal was performed on the data before and after the beginning of the stretch using a similar method to that described by Cronin et al. (2008). When compared with the results of Cronin et al., the short latency reflex occurred later and with smaller amplitude (Fig. 6). This difference could be explained by the ankle angle used before the stretch (i.e., 15° in plantarflexion, whereas 0° was used in the study of Cronin et al.). In the current study, reflex activity was shown to occur at least 45 ms or more after the beginning of the stretch (Fig. 6). In the literature, the electromechanical delay for the plantarflexors is between 16 ms (at 15° in plantarflexion) during electrically evoked contractions (Muraoka et al. 2004) and 24 ms (at 0°) during voluntary contractions (Wu et al. 2009). Therefore, the influence of such activity on the external torque and

Table 3 Achilles tendon cross-sectional area (CSA_{AT}), mean cross-sectional area of the triceps surae muscles (CSA_{TS}) calculated from CSA determined at 50, 60 and 70% of the lower leg length, pennation angle and fascicule length for each muscle of the triceps surae (soleus [SO], gastrocnemius medialis [GM] and gastrocnemius lateralis [GL]) with gain between pre and posttests for both control and trained groups

	Trained group	Control group		
	Pretest	Posttest	Pretest	Posttest
CSA_{AT} (mm^2)	55.6 (12.2)	57.3 (13.1)	53.8 (9.7)	55.3 (8.6)
CSA_{TS} (mm^2)	3,432 (538)	3,659 (487)	3,900 (612)	3,783 (646)
GL				
Pennation angle (°)	11.6 (3.6)	12.3 (2.9)	11.9 (1.6)	13.8 (1.4)
Fascicule length (cm)	8.9 (2.5)	8.6 (0.9)	8.7 (1.0)	7.7 (1.0)
GM				
Pennation angle (°)	24.4 (3.2)	23.1 (2.2)	23.5 (3.0)	23.1 (1.9)
Fascicule length (cm)	5.5 (0.6)	5.9 (0.7)	5.6 (0.7)	5.7 (0.5)
SO				
Pennation angle (°)	26.0 (4.6)	23.9 (6.2)	26.3 (5.8)	23.7 (4.3)
Fascicule length (cm)	3.6 (0.8)	4.1 (0.9)	3.5 (0.8)	3.9 (0.7)

The results are the mean (standard deviation)

stiffness assessed in the present study is likely to be minimal. In addition, a recent study showed that plyometric training did not change the short latency reflex apparition delay (Potach et al. 2009).

In summary, the present study has determined effects on both active and passive component of the SEC stiffness, and on geometrical properties of *triceps surae* MTC as a result of plyometric training. This type of training may enhance the elastic energy storage via the decrease in the active component of the SEC stiffness, but also increases muscular tension transmission and recoil of elastic energy due to an increase in the passive component of the SEC stiffness leading to an increase in MTC mechanical efficiency and consequently higher functional performance associated with this training program. Further research is needed to determine the likely physiological mechanisms involved in specific adaptations of the different structures within the MTC.

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