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Intrinsic Ankle and Hopping Leg-Spring Stiffness in Distance Runners and Aerobic Gymnasts

Authors

G. Rabita¹, A. Couturier¹, D. Lambertz^{2,3}

Affiliations

¹ National Institute of Sport, Expertise and Performance, Research Department, Paris, France

² Federal University of Pernambuco, Physical Education Department, Recife, Brazil

³ CNRS UMR 6600, Biomechanics and Bioengineering, Technological University, Compiègne, France

Key words

- musculotendinous elasticity
- spring-mass model
- hopping
- elite sportsmen

Abstract

The objective of this study was to examine the contribution of intrinsic ankle stiffness to leg-spring stiffness in high level athletes using various musculotendinous solicitations. 8 aerobic gymnasts (G), 10 long-distance runners (R) and 7 controls (C) were evaluated using quick-release and sinusoidal perturbation tests in order to quantify their respective plantarflexor musculotendinous (SI_{MT}), ankle musculoarticular active (SI_{MA}) and passive (K_p) stiffness. Leg-spring stiffness (K_{leg}) was measured during vertical hopping.

Runners and gymnasts presented significantly higher SI_{MT} values ($P < 0.01$) than controls: 60.4 (± 14.1) $\text{rad}^{-1} \cdot \text{kg}^{2/3}$ for G, 72.7 (± 23.8) $\text{rad}^{-1} \cdot \text{kg}^{2/3}$ for R and 38.8 (± 6.5) for C. In addition, normalized K_{leg} was not significantly different between G, R and C. It appeared that intrinsic ankle stiffness had no influence on leg-spring stiffness. The adaptation of SI_{MT} seems to concern specifically the active part of the series elastic component in runners. The results suggested that the number of stretch-shortening cycles during daily practice sessions, rather than their intensity, act as the determinant for this component.

Introduction

The human body can be modelled using a simple spring-mass system during running or hopping tasks [11, 35]. This model consists of a body mass supported by a linear spring which represents one or both legs according to the alternative or simultaneous characteristics of the stretch-shortening cycle (SSC) exercise. Leg-spring stiffness, is defined as the ratio of maximal ground reaction force to maximal leg compression at the midpoint of the contact phase [11]. Regulation of this stiffness has been shown to depend on neuromuscular factors [3, 25] and intrinsic mechanical properties of musculotendinous (MT) structures [4, 21].

Intrinsic elastic properties are usually evaluated under pseudo-isolated conditions and at distinct anatomical levels. Musculoarticular (MA) stiffness corresponds to the combined elastic properties of tendon, muscle, ligament and articular structures of the whole joint. MA stiffness is most often evaluated by subjecting the joint to sinusoidal perturbations. More specifically, the MT unit represents both active (muscle fibres) and passive (tendon) fractions of the series elastic component in the modified Hill muscle model [19, 40]. MT stiffness is usually assessed by the

quick-release method which consists of a sudden and fast release of the isometrically contracted muscles. The plasticity of these structures has been widely documented in humans, either directly after hyperactivity [7, 13, 16, 28], hypoactivity [9, 32] or in the disease state [8, 24]. In contrast to the numerous studies which focused exclusively on tendon structures [2, 26, 27, 39], very few investigations have been carried out to determine the effects of intensive sport activity on MT and MA elastic properties in high level sportsmen. In our previous study [38], higher MT stiffness in elite long and triple jumpers compared with occasional sportsmen was observed. Recent investigations have shown that leg-spring stiffness differs between athletes in different sport categories [20, 31, 38]. On the basis of EMG analyses, Hobara *et al.* [20] concluded that the difference in leg-spring stiffness between endurance- and power-trained athletes may be largely attributed to differences in intrinsic stiffness of the muscle tendon complex, rather than to altered neural activity. These conclusions are however inconsistent with recent investigations that failed to observe any significant relationships between leg-spring stiffness during hopping and tendon [29], MT [38] or MA [34, 38] stiffness.

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Bibliography

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Correspondence

Giuseppe Rabita, PhD
National Institute of Sport
Expertise and Performance
Research Department
11 Av du Tremblay
75012 Paris
France
Tel.: +33/1/41 74 44 71
Fax: +33/1/41 74 45 35
giuseppe.rabita@insep.fr

Therefore, the aim of the present study was to characterize, in high level athletes belonging to sports categories requiring different MT mechanical solicitations, the relationships between ankle MT and MA stiffness and the overall MS stiffness.

Methods

Populations

27 subjects participated in this study. Their characteristics are presented in **Table 1**. Based on their sport category, they were divided into 3 groups: aerobic gymnasts (G; $n=8$), long-distance runners (R; $n=10$) and controls (C; moderate physical activity; $n=7$). Subjects in the G and R groups were recruited from among highly-trained sportsmen (7–9 sessions per week) belonging to the French National Institute of Sport and Physical Education. All of these athletes had competed at national or international level during the year. Control subjects were matched for age, height and body mass. Written informed consent was obtained from each of the subjects, and the study was conducted in accordance with the Declaration of Helsinki. The study protocol was approved by the local ethics committee prior to initiation and was performed in accordance with the ethical standards of the IJSM [18].

Experimental protocol

Ergometric tests

The protocol used in this study was nearly identical to that described previously [38]. Briefly, the subject was laid prone on an adjustable table with both knees and ankle joints bent at 90° . Trunk and thigh were physically restrained by straps. The subject was positioned so that the actuator rotation axis was placed at the level of the mean bi-malleolar axis. The plantarflexion maximal voluntary contraction (MVC) was first determined under isometric conditions. 3 trials were carried out and the best performance was taken as the MVC of that day. Secondly, quick-release (QR) and sinusoidal perturbation (SP) tests were imposed in random order. QR consisted of a sudden release of the actuator while the subject performed an isometric plantar flexion at the neutral ankle position. 3 measurements were collected at each imposed submaximal isometric torque (25, 50 and 75% of MVC). SP consisted of a 3° peak-to-peak harmonic angular displacement imposed on the ankle joint while the subject maintained a submaximal plantarflexion torque (25, 50 and 75% of MVC). Each sinusoidal perturbation was performed for 4 s at random imposed frequencies ranging from 4 to 16 Hz. Sinusoidal perturbations with no participation of subject (i.e., 0% of MVC) were also carried out.

Hopping tests

Subjects performed 2-legged vertical hopping. They were asked to hop as high as possible while minimizing the ground contact time in order to maximize the ankle influence on leg stiffness [12]. Subject's data were included in subsequent analyses only if they presented spring-mass behaviour during hopping, as evi-

denced by the linear force-displacement relationships (see below, *data processing section*). 2 out of 9 control subjects were ultimately discarded from the population. After a familiarization with the procedure, 2 trials of 5 jumps were required after a brief period of stability (3–5 s) on the platform. For control purposes, the subjects were instructed to keep their hands on their hips during the jumps.

Materials

Ergometric tests

The ankle ergometer consisted of 2 main units: i) a power unit which contained the actuator, power supply, position and torque transducers, and their associated electronics, and ii) a driving unit composed of a PC-type computer equipped with a specific 12-bit A/D converter and a timer board. Angular displacement was measured with an optical digital sensor and angular velocity was captured from a resolver bound to the rotor. A tachometer was used to measure velocities greater than $15.7 \text{ rad}\cdot\text{s}^{-1}$. Torque was obtained using a strain-gauge torque transducer. Specific menu-driven software controlled all procedures and digitally recorded the mechanical variables for subsequent analysis. An oscilloscope provided the subject with visual feedback in time with the procedure's progress.

Hopping tests

During the hopping test, the vertical component of the ground reaction force was measured by a force platform signal (Kistler, type 9281A11) sent to an acquisition card (ATMIO16; National Instrument, sampling rate=1000Hz) driven by commercially-available software (Daqware, National Instrument). Data was analysed with Origin 6.1 (OriginLab Corporation, Northampton, USA).

Data processing

A typical example of the recorded signals is presented in **Fig. 1**. For each QR trial, the parameters collected were: i) isometric torque before release (T_{iso}); ii) changes in angular position ($\Delta\theta$) and changes in angular acceleration ($\Delta\theta''$, as a derivative of the angular velocity signal θ') – these 2 parameters were characterized within the first 20 ms at the beginning of the quickw release movement when the series elastic component was expected to recoil; iii) inertia (I) as calculated by considering the transition

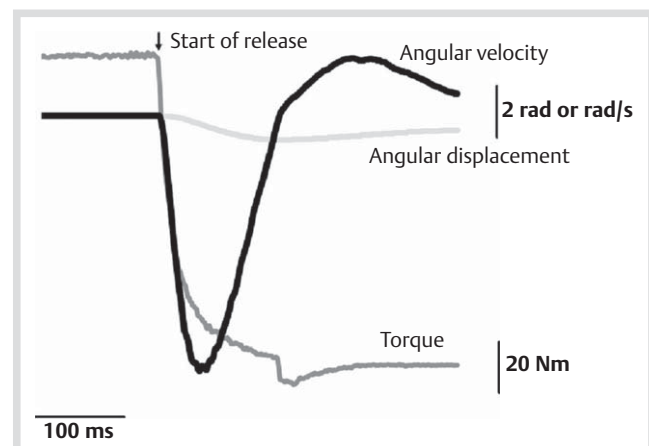


Fig. 1 Raw mechanical data from the quick-release experiment. Torque (dark grey curve), angular displacement (light grey curve) and angular velocity (black curve) are shown. Angular acceleration was calculated by the derivation of the spline-filtered angular velocity (not shown). The start of the quick-release movement is indicated.

Table 1 Subjects characteristics [mean (\pm SD)].

	height (m)	mass (kg)	age (years)
aerobic gymnasts (G; $n=8$)	1.77 (± 0.06)	69.3 (± 2.5)	27.5 (± 1.5)
runners (R; $n=10$)	1.76 (± 0.04)	63.2 (± 2.7)	30.0 (± 6.0)
controls (C; $n=7$)	1.77 (± 0.03)	66.9 (± 5.3)	29.3 (± 3.9)

between the static phase and the dynamic phase – at this point, acceleration was maximal (θ''_{\max}) and static torque equaled dynamic torque ($T_{iso} = I \cdot \theta''_{\max}$). The angular MT stiffness (K_{MT}) was calculated according to the formula:

$$K_{MT} = I \cdot \Delta\theta'' / \Delta\theta$$

K_{MT} was related to the corresponding isometric torque (T_{iso}) initially exerted by the subject. The slope of the linear stiffness-torque relationship was defined as a stiffness index of the MT stiffness (SI_{MT}). This methodology was previously shown to be reproducible [33].

The sinusoidal perturbation tests were used to construct Bode diagrams from i) the ratio between averaged θ changes and modulated torque (T_{mod}) changes (i.e., gain curve) and ii) the phase shift between θ and T_{mod} signals (phase curve); both parameters were plotted against the imposed frequencies. A typical example of the resultant Bode diagrams is presented in **Fig. 2**. A Fast Fourier transform algorithm was used to remove the non-linearities of the torque signal shown at the different angular displacement driving frequencies [23]. The gain diagram displayed the expected characteristic features. Namely,

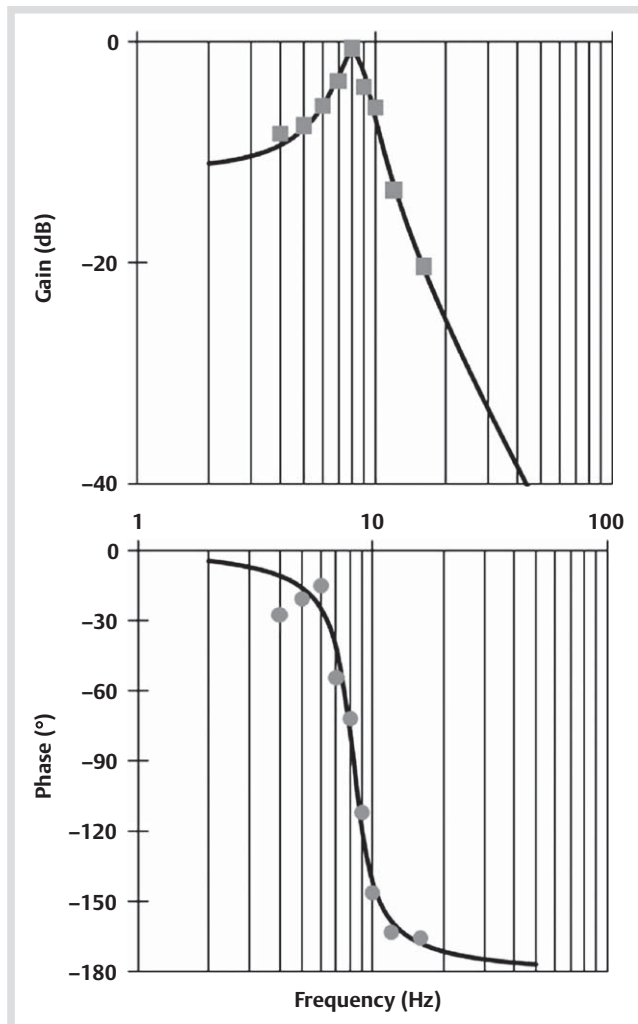


Fig. 2 Typical example of a Bode Diagram including Gain – frequency (\square) and Phase – frequency (\bullet) relationships from sinusoidal oscillation at 50% of maximal voluntary contraction. A second order model has been adjusted to the experimentally achieved data to facilitate the calculation of MA stiffness.

there was an increase at low frequencies, a resonant valley at intermediate frequencies and a decrease in gain with a slope of -40dB/decade at high frequencies. These frequency-dependent changes in gain and phase shifting reflected the classical features of a mixed mechanical contribution from elasticity (K), viscosity (B) and inertia (I) of the MA system [23]. Using identification techniques, a second order model was adjusted to the Bode diagrams as expressed by the formula:

$$T(t) = I \cdot [d^2\theta(t)/dt^2] + B \cdot [d\theta(t)/dt] + K \cdot [\theta(t)]$$

where T represented the external torque ($\text{N}\cdot\text{m}$), and θ represented the angular position (rad).

Thus, for each level of torque, the MA stiffness, K_{MA} ($\text{N}\cdot\text{m}\cdot\text{rad}^{-1}$) could be determined. These values were then related to the maintained torque. The slope of the linear K_{MA}/T relationship was defined as a stiffness index of the SI_{MA} . In addition, K_{MA} measurements obtained under passive conditions (designated as K_p) were analysed independently.

SI_{MT} , SI_{MA} and K_p were measured in pseudo-isolated conditions. Unlike the leg-spring stiffness obtained in hopping conditions, these parameters are referred as “intrinsic” stiffness as i) the load of the neuromuscular system is supposed to be constant within each contraction level and ii) this level was taken into account in the calculation.

A spring-mass model was used to calculate the stiffness of the leg-spring (K_{leg}) during the ground contact phase of hopping in place (**Fig. 3**). The combined stiffness of the 2 legs was calculated during the second-to-fourth ground contact phase from the ratio of the peak ground reaction force (F_{peak}) to the maximal displacement of the leg spring (ΔL) using the formula:

$$K_{leg} = F_{peak} / \Delta L$$

ΔL was equal to the negative vertical displacement of the center of mass (COM) during the ground contact phase and was calculated by double integration of the vertical acceleration with respect to time. This model was then applied after calculating the individual force-displacement relationships (**Fig. 4**) and verifying that the body behaved effectively like a simple spring-mass system. The maximal positive vertical displacement (i.e., the maximal jump height, H_{max}), the maximal velocity and the maximal power were also analysed (**Fig. 3**). For each parameter, the values obtained from both trials were averaged.

All parameters are expressed with respect to body mass by using allometric parameters listed in **Table 2** [5,22]. The following equation was used to obtain the normalized parameter:

$$P_n = P / BM^{ap}$$

where P represented the respective parameter, BM represented the Body Mass and ap the allometric parameter.

Statistical analysis

For each measured or calculated parameter, a one-way ANOVA was used to compare the populations. When a significant main effect for groups was observed, the post-hoc Sheffé test was applied to determine statistical significance. Furthermore, effect sizes (ES) were calculated using the Cohen's d coefficient [6]. ES of 0.8 or greater, around 0.5 and 0.2 or less were considered as large, moderate or small, respectively. Correlations between the different parameters were investigated using Pearson product-

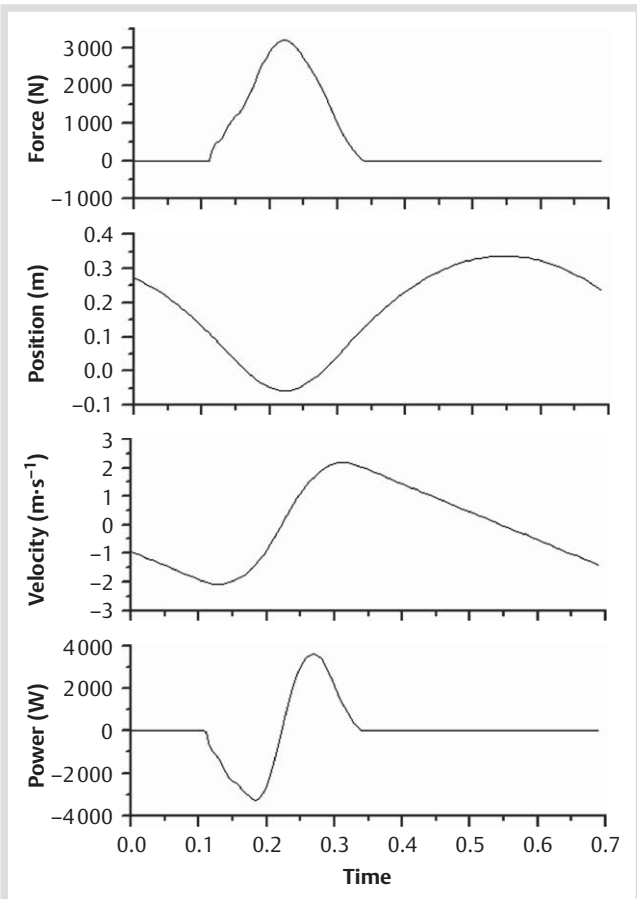


Fig. 3 Representative data from a single subject performing a hop. Bottom trace: The vertical ground reaction force (Force, N) allowed for the calculation of the temporal parameters (contact time, aerial time and frequency). The vertical velocity of the centre of mass (COM) was determined by integration over the time of the acceleration, which was calculated from the ground reaction force signal. Vertical power was calculated as the product of force and COM velocity.

Table 2 Correction to body size.

Variable	Unit	Allometric parameter
<i>Ankle-ergometer parameters</i>		
MVC	N · m	1
intrinsic stiffness	N · m · rad ⁻¹	1/3
<i>Hopping parameters</i>		
hopping force	N	2/3
hopping stiffness	kN · m ⁻¹	1/3
hopping power	W	2/3
hopping velocity	m · s ⁻¹	0
hopping height	m	0

Allometric parameters were used to express the present data relative to body mass; The following equation was used to obtain the normalized parameter : $P_n = P/BM^{ap}$, where P is the respective parameter, BM is Body Mass and ap the allometric parameter

moment correlation. Values have been presented as mean (\pm SD). Statistical significance was reached when $P < 0.05$.

Results

Mean normalized MVC values obtained during isometric plantar-flexion were significantly higher ($P < 0.05$; $ES = 0.72$) for the G group ($1.58 \pm 0.32 \text{ N} \cdot \text{m} \cdot \text{kg}^{-1}$) than for C ($1.34 \pm 0.23 \text{ N} \cdot \text{m} \cdot \text{kg}^{-1}$).

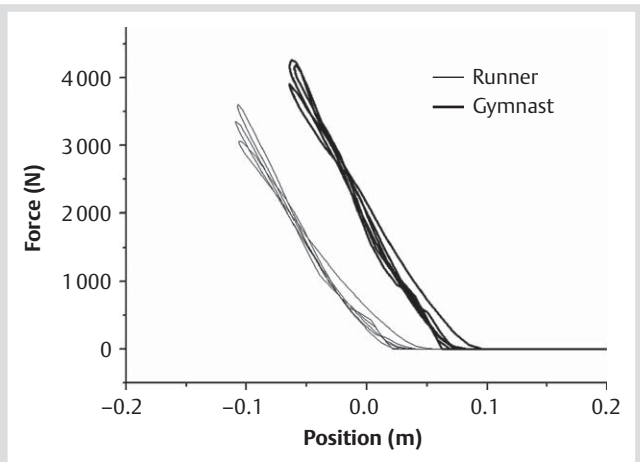


Fig. 4 Force-displacement relationships recorded during the second-to-fourth ground contact phases for a runner (thin line) and an aerobic gymnast (thick line) representative of their respective groups. The displacement (m) corresponds to the variation of the centre of mass position (0 is equal to the vertical COM position when the subject was standing upright prior to the test).

The runners ($1.42 \pm 0.26 \text{ N} \cdot \text{m} \cdot \text{kg}^{-1}$) were not significantly different from other groups.

Fig. 5 presents the mean values of normalized intrinsic stiffness for each group. Considering the quick-release results, mean coefficients of determination R^2 of the linear $K_{MT}-T_{iso}$ relationships were $0.85 (\pm 0.11)$ for G, $0.80 (\pm 0.13)$ for R and $0.88 (\pm 0.11)$ for C. Runners presented significantly higher SI_{MT} values ($72.7 \pm 23.8 \text{ rad}^{-1} \cdot \text{kg}^{2/3}$) than the control group ($38.8 \pm 6.5 \text{ rad}^{-1} \cdot \text{kg}^{2/3}$, $P < 0.001$, $ES = 0.92$). Gymnasts' SI_{MT} values ($60.4 \pm 14.1 \text{ rad}^{-1} \cdot \text{kg}^{2/3}$) were also higher than the control group but to a lower extent ($P < 0.01$, $ES = 0.92$) [**Fig. 5a**].

Regarding the sinusoidal perturbation tests, the mean coefficients of determination R^2 of the linear $K_{MA}-T$ relationships were $0.93 (\pm 0.11)$ for G, $0.94 (\pm 0.13)$ for R and $0.92 (\pm 0.11)$ for C. Mean SI_{MA} values normalized to the body size were $72.2 (\pm 7.4) \text{ rad}^{-1} \cdot \text{kg}^{2/3}$ for the aerobic gymnasts, $73.6 (\pm 17.6) \text{ rad}^{-1} \cdot \text{kg}^{2/3}$ for the runners and $70.7 (\pm 13.3) \text{ rad}^{-1} \cdot \text{kg}^{2/3}$ for the control subjects (**Fig. 5b**). The differences were not significant ($P > 0.05$). The normalized passive MA stiffness values (K_p) are presented in **Fig. 5c**. Mean values were calculated as $11.6 (\pm 1.8)$, $12.1 (\pm 2.3)$ and $9.9 (\pm 2.8) \text{ Nm} \cdot \text{rad}^{-1} \cdot \text{kg}^{-1/3}$ for G, R and C, respectively. The ANOVA revealed a significant effect of training background ($P < 0.05$). Post-hoc tests showed that while this parameter was greater in runners as compared to controls ($P < 0.05$; $ES = 0.73$), gymnasts did not differ from either group. K_p was found to be inversely correlated ($P < 0.05$) with SI_{MT} for R ($R^2 = 0.92$; $P < 0.0001$) and, to a lower extent for G ($R^2 = 0.41$; $P < 0.05$). Correlations were not significant neither for C ($R^2 = 0.34$; $P > 0.05$) nor for the whole population ($R^2 = 0.02$; $P > 0.05$).

Hopping frequency, contact and aerial times are presented in **Table 3**. Among these parameters, only the aerial time reached statistical significance, with post-hoc tests showing higher values in G compared to R ($P = 0.03$; $ES = 0.80$). This result in hopping performance attests that high level aerobic gymnasts presented intermediate lower limb explosive capacity compared to runners (**Table 3**) and long or triple jumpers [38]. A tendency to reach higher hopping frequencies was observed in runners (non significant; $P = 0.07$). This trend appeared to be linked to shorter aerial times rather than shorter contact times ($P = 0.71$).

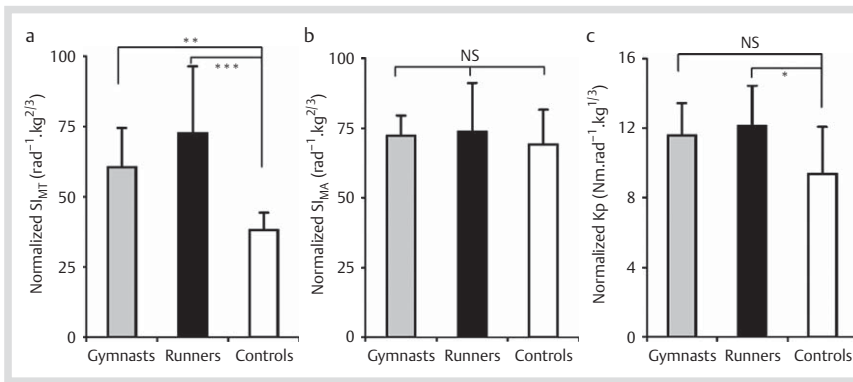


Fig. 5 Mean values (\pm SD) of the stiffness index of the musculotendinous system (S_{MT} , in $\text{rad}^{-1} \cdot \text{kg}^{2/3}$), stiffness index of the musculoarticular system (S_{MA} , in $\text{rad}^{-1} \cdot \text{kg}^{2/3}$), passive musculoarticular stiffness (K_p , in $\text{Nm} \cdot \text{rad}^{-1} \cdot \text{kg}^{-1/3}$) as measured during the ergometric tests for the aerobic gymnasts (G), the runners (R) and the controls (C). *, **, *** denote significant differences at $P < 0.05$, $P < 0.01$ or $P < 0.001$, respectively. NS: non-significant.

Hopping parameters	Gymnasts	Runners	Controls
hopping frequency (Hz)	1.45 (0.10)	1.57 (0.13)	1.45 (0.10)
contact time (s)	0.201 (0.037)	0.202 (0.017)	0.213 (0.035)
aerial time	0.49 (0.03) ^R	0.44 (0.05) ^G	0.48 (0.04)
peak reaction force ($\text{N} \cdot \text{m} \cdot \text{kg}^{-2/3}$)	275 (51)	244 (27)	252 (44)
COM displacement (m)	0.18 (0.04)	0.17 (0.02)	0.19 (0.03)
K_{leg} ($\text{kN} \cdot \text{m} \cdot \text{kg}^{-1/3}$)	6.64 (2.25)	5.99 (0.99)	5.70 (1.79)
maximal height (m)	0.39 (0.04) ^R	0.34 (0.06) ^G	0.37 (0.03)
maximal power ($\text{W} \cdot \text{kg}^{-1/3}$)	340 (51)	283 (41)	305 (58)
maximal velocity (m/s)	2.53 (0.17)	2.29 (0.21)	2.46 (0.19)
velocity at maximal power (m/s)	1.92 (0.1)	1.75 (0.2)	1.87 (0.1)
force at maximal power ($\text{N} \cdot \text{m} \cdot \text{kg}^{-2/3}$)	178 (24)	145 (52)	162 (25)

^{R, G}: significant difference at $P < 0.05$ with the runners or the gymnasts, respectively

Table 3 Comparison of temporal, kinetics and kinematics parameters between groups.

Table 4 Correlations between k_{leg} and intrinsic stiffness for gymnasts (G), runners (R) controls (C) and for the whole population (G + C + R).

	G			R			C			G+R+C		
	R	R ²	P	R	R ²	P	R	R ²	P	R	R ²	P
$k_{leg} - S_{MT}$	0.53	0.29	0.30	0.30	0.09	0.49	0.31	0.09	0.51	0.25	0.06	0.28
$k_{leg} - S_{MA}$	0.01	<0.01	0.98	-0.33	0.11	0.40	-0.68	0.47	0.09	-0.29	0.08	0.19

Table 3 shows the lack of differences between groups observed for F_{peak} ($P=0.36$) and ΔL parameters ($P=0.36$). Likewise, while greater mean values were observed for the high level sportsmen, K_{leg} did not reach statistical significance either ($P=0.59$; Table 3).

While identical tendencies were observed in maximal height, power and velocity, the ANOVA revealed that only the maximal height was significantly dependent on the training status ($P < 0.05$; Table 3).

To further understand the effect of intrinsic stiffness on whole leg-spring stiffness, relationships between K_{leg} and MT or MA stiffness were analyzed. Results are summarized in Table 4. None of the tested groups exhibited significant correlations between K_{leg} and intrinsic stiffness parameters. Moreover, when the results were analyzed for the whole population (G, R and C groups together), no significant relationships was observed (Table 4).

Discussion

In the present study, high level runners and aerobic gymnasts presented higher MT stiffness than controls. This result corroborates findings from previous investigations in which long-term training was associated with changes in the mechanical properties of MT complex [38]. Interestingly, the runner group exhib-

ited the highest S_{MT} values. As mentioned above, the MT stiffness represents both active and passive parts of the series elastic component. Previous studies have shown that the mechanical load induced as a cyclic strain can influence the regulation of connective tissue biosynthesis and lead to modification of the mechanical properties of collagen fascicles [43,44]. Thus, it is likely that the cyclic strain imposed on the Achilles tendon by habitual SSC training during running could alter its elastic properties. This assumption is supported by the findings of Kubo *et al.* [27]. Using ultrasound images, the authors showed that long distance runners experienced higher tendon stiffness than sedentary subjects. Nevertheless, these findings have been discussed more recently by Arampatzis *et al.* [2] and Rosager *et al.* [39]. In runner populations, these authors found that the Achilles tendon has been shown to differ from controls in morphological aspects (hypertrophy) but not elastic properties (stiffness) [2,39]. With the methodology used in the present study, it was not possible to determine specifically whether the Achilles tendon was stiffer in runners than controls or not. However, the great differences in MT stiffness found between runners and controls, when considered together with the previously published tendon studies, suggest that an adaptation process was located in the active part of the series elastic component. Indeed, numerous studies have described the plastic nature of muscle fibres elastic properties [1,15,41]. These investigations have demonstrated that type I fibres exhibit a higher stiffness than

type II fibres. Although the plantarflexor fibre typology was not experimentally characterized in the present study, it is likely that long distance runners present the highest amount of type I fibres [17]. Consequently, the higher SI_{MT} values observed in our runner group could mainly be related to active cross-bridges adaptation. Such a differential adaptation between both fractions of the series elastic component was recently reported after a plyometric training by Fouré *et al.* [14]. However, these authors observed a decrease in the active part stiffness and an increase in the passive part. The reverse adaptations observed in their study and in the present one show that both fractions adapted differently to endurance and plyometric trainings, confirming the study of Grosset *et al.* [16]. Furthermore, they highlight the fact that, the gymnasts, who realized these types of relatively high intensity plyometric exercises in their daily practice, exhibited a lower increase in MT stiffness than the runners.

Recent results of ultrasound measurements have suggested that a threshold exists for the mechanical load intensity necessary for the adaptations of the tendon mechanical properties [2]. The authors measured higher tendon stiffness in sprinters compared to runners who did not differ from controls. They concluded that the stimulus exerted at the Achilles tendon during endurance running was not sufficient to provide any further adaptational effects on the tendon mechanical properties as compared to the stimulus provided by normal daily activities. The results of the study do not support this type of adaptation when the global MT structures are implied. When MT stiffness values obtained for high level sportsmen were compared to those obtained in similar conditions for long and triple jumpers [38], it appeared that the greater MT adaptation to training occurred in the runners; the changes in gymnasts and jumpers were quite similar. Overall, these data indirectly imply that the training adaptation of the whole series elastic component differs from the specific tendon changes and that factors other than the mechanical load intensity are likely to explain these differences. The number of stretch-shortening cycles, rather than their intensity, appears to exert the most influence on the adaptation of the active part of the MT mechanical properties, in agreement with recent findings [16]. By using sinusoidal perturbations, the present study reported that ankle MA stiffness was not affected by training status. These results are not in line with the previous investigation reported by Cornu *et al.* [7] which showed that short-term plyometric training led to a decrease in SI_{MA} values. These authors interpreted this result in terms of fibre type transition (toward type II fibres phenomenon) as a result of training. Nevertheless, the reasons underlying these discrepancies between the elastic MA adaptations as a result of short- and long-term training are unclear. It is possible that i) the aerobic gymnasts regularly use intensive plyometric exercises consisting of various hops in the vertical plane and this may lead to the same type of MA changes as those resulting from short term plyometric training; ii) the runners likely present a higher type I fibre proportion than controls and they could be expected to present higher SI_{MA} mean values. This result is difficult to interpret, especially because SI_{MA} values are assumed to reflect the combined effect of changes in SI_{MT} and the passive MA stiffness K_p . In previous studies, adaptations of the mechanical properties were observed as a result of hypoactivity (long-term spaceflight [32]) or ageing [37]. In both cases, SI_{MT} and K_p were altered by the same amount, but in opposite direction. It was hypothesized that the modifications in passive ankle joint structures resulted from an adaptation to alterations in MT elastic properties in order to minimize the

changes in the global MA system. This result is partly supported here by the correlations observed between these intrinsic parameters. It is noteworthy that significant negative correlations were observed between both parameters for the runners and, to a lesser extent, for the gymnasts. However, in the present study, runners presented higher values in both SI_{MT} and K_p compared to controls while SI_{MA} did not differ significantly between populations. Thus, the discrepancies between our study and the previous one indicate that regular hyper-solicitations of MA structures may be adaptations which are different from hypo-solicitation or short-term hyper-solicitations. We are unaware of any physiological data to support this hypothesis and further investigations are required to define the mechanisms underlying such MA adaptations in persons highly engaged in daily practice sessions.

The parameter K_p reflects the combined effects of passive elastic structures, including skin, tendon, ligament, articular surfaces and the giant protein titin. The increased diameter and packing density of collagen fibrils [36], together with the changes in collagen crimp structure [42], are likely to influence the stiffness of tendons and ligaments as a result of training. Moreover, titin has been shown to be involved in running economy in middle distance runners [30] and it may, therefore, participate in the higher passive MA observed in gymnasts and runners.

Considering the hopping exercise, the G group presented intermediate lower limb explosive capacity compared to elite long/triple jumpers and runners, which can be explained by the nature of their daily activities. The values were in agreement with those reported previously. For example, Di Cagno *et al.* [10] tested gymnasts in hopping conditions close to those of the present study. The comparison between their results and ours was consistent considering that their population was composed of well-trained but non-elite gymnasts. Indeed, the mean hopping height (0.36 m) was slightly lower than in the present study (0.39 m) although the mean contact time was higher than those observed here (201 vs. 270 ms). The fact that the control group did not show significant differences in hopping height could be attributed to the fact that these subjects were not strictly sedentary but engaged in occasional sport activities.

The other purpose of the present study was to characterize the influence of training background on the relationships between intrinsic ankle stiffness and the overall leg-spring stiffness. Contrary to the significant influence of the training status on the intrinsic stiffness (● Fig. 5), we failed to observe any inter-group differences concerning the hopping leg-spring stiffness (● Table 3). Moreover, we found no significant correlation between intrinsic (SI_{MT} or SI_{MA}) and K_{leg} stiffness for any of the 3 groups, either individually or for the whole population (● Table 4). These results confirm the recent studies that failed to observe any significant relationship between hopping stiffness and tendon [29], MT [38] or MA [34, 38] stiffness. Kubo *et al.* [29] showed that the Achilles tendon stiffness does not influence either the global leg-spring stiffness or the ankle joint stiffness during hopping. They concluded that the stiffness measured in hopping conditions was more related to muscle (active cross-bridge) than to tendon properties. Our results, which take into account both parts of the series elastic component (active and passive), suggest that other factors mainly contribute to the leg-spring stiffness. Some such factors have already been reported, including adequate coordination and modulation of activation amplitude, efficient timing sequence of muscle pre-activation and amplitude of stretch reflex activities.

In conclusion, the study presented here on the leg-spring stiffness in runners and gymnasts suggests that adaptations of the intrinsic stiffness are principally associated with runners and mainly involve the active fraction of the series elastic component. The adaptation of this active fraction seems mainly determined by the number of stretch stretch-shortening cycles during the daily practice sessions rather than their intensity. Moreover, the lack of a significant influence of intrinsic mechanical properties on the whole leg-spring stiffness confirms the importance of other factors such as neuromuscular factors. Further works are needed to specify the relative contributions of neuromuscular and mechanical properties in the hopping spring-leg behaviour.

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