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Hamstring muscle elasticity differs in specialized high-performance athletes

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ABSTRACT (250 Words)

The effect of training on hamstring flexibility has been widely assessed through the measurement of the maximal range of motion or passive torque. However, these global measures do not provide direct information on the passive muscle mechanical properties of individual muscle. This characterization is crucial to better understand the effect of interventions as selective adaptations may occur among synergist muscles.

Taking advantage of shear wave elastography, we aimed to determine whether elite sport athletes exhibit different passive shear modulus of hamstring heads compared to controls. Passive shear modulus was measured on semitendinosus (ST), semimembranosus (SM) and biceps femoris (BF) using shear wave elastography with the knee flexed at 60° and 90°, and 90° of hip flexion. A total of 97 elite athletes from various sports including running sprint, figure skating, fencing, field hockey, taekwondo, basket-ball and soccer, and 12 controls were evaluated.

The shear modulus measured at 60° of knee flexion was lower in SM for figure skating ($P<0.001; d=1.8$), taekwondo ($P<0.001; d=2.1$), fencing ($P=0.024; d=1.0$) and soccer ($P=0.011; d=0.9$) compared to controls, while no difference were found for athletic sprinters, field hockey and basket-ball players. Shear modulus of the BF and ST muscle was not significantly different between controls and elite athletes, regardless of the sport specialization (all $P$ values=1).

We provide evidence that the shear modulus of the SM is altered in athletes involved in elite sport practice performed over large range of motion and/or including substantial stretching program in training content (taekwondo, figure skating, fencing and soccer).
23 **Keywords:** Stiffness - shear wave elastography - elite athletes
INTRODUCTION

Hamstring muscle complex consists of three main heads [biceps femoris long head (BF), semimembranosus (SM), and semitendinosus (ST)] acting on both hip and knee joint \(^1,^2\). These bi-articular muscles are therefore significantly involved in numerous dynamic tasks (i.e., jumping, landing, running, kicking). The substantial loading applied on large range of motions during such movements expose hamstring muscles to a high risk of strain injury, particularly in high-velocity running during which they are actively stretched and withstand a maximum peak force at long muscle lengths \(^3,^4\). Because flexibility may influence the ability of hamstring muscles to resist such stress, it has been proposed as a predisposing factor for developing muscle injury \(^5,^6\).

Hamstring flexibility has been widely assessed through the maximal range of motion achieved during passive straight-leg-raise and sit-and-reach tests to determine the effects of training, to orient training contents, to determine the risk of injury or to evaluate the impact of previous injury \(^7\). Although reliable and easy-to-use, these evaluations are influenced by examiners’ or subjects’ subjectivity, lumbar and thoracic flexibility (for the sit-and-reach test), as well as stretch tolerance \(^8,^9\). As a consequence, this global measure does not provide a direct estimation of the mechanical properties of each individual muscle \(^8\), and, in turn, do not inform about putative between-muscles differences due to intrinsic morphological properties (composition and architecture), various training contents (e.g., stretching \(^10\)) or previous injury events \(^11\). It is therefore crucial to use appropriate methods allowing for reliable assessment of individual muscle mechanical properties in order to determine their specific training requirements.

Ultrasound shear wave elastography (SWE) can be used as a reliable \(^12\) and valid \(^13\) method to assess regional shear modulus. This parameter reflects intrinsic muscle mechanical properties, regardless of its size. More precisely, it represents an index of tissue stiffness. For
a muscle of a given size, the higher the shear modulus, the higher the stiffness. Using SWE, it has been recently shown that passive muscle shear modulus increased after repeated eccentric contractions \(^{14}\) or inversely decreased after a stretching protocol \(^{15}\). Interestingly, the magnitude of these changes may differ among the synergist muscles \(^{15}\). More precisely, a recent study has shown that a 4-week static stretching program induces a decrease in shear modulus in hamstring muscles (i.e., increase in hamstring shear modulus), with a higher effect on the SM compared to the BF and ST \(^{10}\). However, the impact of chronic sport practice on individual muscle shear modulus has not been described. It is well known that most of sports activities involve bouncing and jumping with high-intensity stretch-shortening cycles (e.g., soccer, basketball, athletic sprinting). Such motor tasks stimulate muscle-tendon units of the lower limb to store and release high amounts of elastic energy and in turn amplify power \(^{16}\). In these sports and others, the hamstring muscles are also involved over moderate to large ranges of motion. For instance, Preuschl et al. \(^{17}\) reported that specific movements regularly executed in taekwondo involved hip flexed angles about 65° (180° = full hip extension) and knee angles close to full extension (178°, 180° = full extension). Similarly, elite fencers regularly execute lunges with hip almost fully flexed (49°) combined with moderated knee extension angles (116°) \(^{18}\). A recent cross-sectional study reported that highly flexible ballet dancers display different morphological, mechanical, and functional properties of the triceps surae muscle-tendon unit, compared to control individuals with no history of stretching training \(^{19}\). Therefore, it is reasonable to assume that daily exposure to elite sport practice may lead to adaptations in hamstring muscle shear modulus. The description of the shear modulus of each individual hamstring head in elite athletes specialized in various activities (e.g., soccer, athletic sprinting, fencing, taekwondo) would provide the impetus to explore its putative importance in motor performance.
Taking advantage of shear wave elastography, we aimed to determine whether the shear modulus of hamstring heads (ST, SM, BF) differs between elite athletes (i.e., basketball, field-hockey, soccer, track and field, fencing, taekwondo, figure skating) and controls. We hypothesized that, compared to controls, elite athletes exhibit lower hamstring shear modulus due to high intensity stretch-shortening cycles and/or moderate to large range of motion movements at the hip and knee (e.g., Preuschl et al.), performed daily in their sport activities. We also hypothesized that sport specialization (i.e., taekwondo, figure skating, fencing, athletic sprinting, basketball, soccer, and field-hockey) would induce specific alterations of the shear modulus among hamstring muscle heads depending on the specific mechanical constraints associated with each sport activity.

METHODS

Participants

A total of 109 participants: 97 elite athletes (61 males) who trained once-to-twice a day on 25 to 40 h/wk regular basis, from soccer, track and field sprinting, fencing, taekwondo, figure skating, field hockey and basketball, and 12 healthy moderately active participants without sport specialization (6 males, 6 females) participated in this study (Table 1). Training programs of elite athletes included about ~150±110 min of hamstring stretching routines per week. Note that this volume varied greatly between athletes, as some of them are doing additional individual specific stretching workout with physiotherapists. All of them had competed at the international level during the year of the experiment. 29 participants had an history of unilateral hamstring injury. Only the uninjured side of these athletes was included in the study to evaluate the effect of sport to avoid any putative effect of injury on shear modulus values. One participant who had a hamstring injury history for both sides was excluded from the analyses. All athletes did not perform any vigorous strength training of the
lower limb 48 hours before the experiment. They were informed regarding the nature, aims and risks associated with the experimental procedure before they gave their written consent to participate. This study was approved by the ethics committee of Île de France III (agreement no 3418) and conformed to the standards of the Declaration of Helsinki.

**Experimental set-up**

Participants laid supine on a bench positioned next to the motor of an isokinetic dynamometer (Con-trex, CMV AG, Dübendorf, Switzerland), with their hip flexed at 90° (0° = full extension; Fig. 1) \(^{20}\). The leg and the thigh were firmly fixed to the dynamometer arm with non-compliant straps to avoid any antero-posterior shift.

**Shear-wave elastography**

An ultrasound scanner (Aixplorer v6, Supersonic Imagine, Aix-en-Provence, France) coupled with a linear transducer (4-15 MHz, SuperLinear 15-4, Vermon, Tours, France) was used in SWE mode (custom musculoskeletal preset, penetration mode, smoothing level 5, persistence off). This technique provides a 2-dimensional map of the shear modulus (for review see Hug et al. \(^{21}\)) of the targeted tissue at 1 Hz with a spatial resolution of 1×1 mm (Fig. 1).

The examiner was trained three months on the ultrasound scanner to adequately measure the shear modulus in hamstring muscles with minimal transducer pressure on the skin. Muscles were scanned using a handheld technique based on previous studies from our group that allowed reliable assessment of the shear modulus in hamstring muscles \(^{20}\). The probe was placed over the posterior face of the thigh, proximally to the tendinous inscription dividing this muscle into two portions to image ST. For SM and BF, the probe was placed
proximal to the musculotendinous junction, close to mid-thigh. Once the site of measurement was determined, the probe was orientated to measure the shear modulus along the fascicle’s line of action. The probe location was considered appropriate when fascicles were clearly visible across the image and the obtained shear modulus map included no aponeurosis, and little amount of missing or non-physiological values. The locations were marked on the skin using a waterproof marker so that the transducer location remained constant throughout measurements.

**Protocol**

Participants first performed four slow (10°.s⁻¹) passive loading/unloading cycles between 90° and 30° of knee flexion (0° = full extension) to account for the possible effect of conditioning. The resting shear modulus was then measured in each hamstring muscle during 10 s at two knee angles (90° and 60°). Before each acquisition, a 10-s period was kept between knee positioning and the onset of the elastography acquisition to further account for any potential stretch–relaxation effect. The participants were instructed to remain as relaxed as possible throughout the measurements. The shear modulus was assessed in hamstring muscles of both legs to compare the dominant and non-dominant leg. These measures were performed in a randomized order on 79 participants with no injury in both lower limbs. The dominant leg was defined as the leg preferentially used to kick a ball.

**Data analysis**

All data were processed using Matlab custom-written scripts (R2017a, The MathWorks Inc., Natick, USA) and Origin 2018 software (OriginLab Corporation, Northampton, USA). Mean shear modulus values were obtained over the largest possible region of interest. The unexpected presence of vein and intramuscular fascia may punctually
induce small-size artifacts. Particular care was taken to not include artefacts and aponeurosis in the region of interest. Data were exported in ‘mp4’ format and transformed to a sequence of ‘jpeg’ images. Image processing then converted the resulting colored map into shear modulus values. The average Young’s modulus was divided by 3, to obtain the muscle shear modulus. The five successive images that resulted in the lowest standard deviation were considered to calculate an average value of the shear modulus (μ).

**Statistics**

All statistical analyses were conducted using Statistica version 7.1 software (StatSoft, Tulsa, OK). Data were screened for normal distribution using the Shapiro–Wilk test. The inter-day reliability of shear modulus measurements was evaluated on control participants (n = 12) using the intraclass correlation coefficient (ICC), typical error (TE) and coefficient of variation (CV). Ages were compared between sports by using a one-way ANOVA (between subject factor: sport). The effect of laterality on muscle shear modulus was tested through a three-way ANOVA [side (dominant, non-dominant) × muscle (BF, ST, SM) × angle (90°, 60°)] on participants with no injury on both lower limbs (n = 79). As the proportion of males and females differs between sports (cf. Table 1), the effect of sex was tested using a two-way ANOVA [within-subject variable: muscle (BF, ST, SM) × angle (90°, 60°); categorical factor: sex (male, female)] on participants with no injury on both lower limbs (n = 79). For controls and uninjured athletes, the muscle shear modulus of the two limbs was averaged.

A three-way ANOVA was performed to determine whether elite athletes exhibit altered muscle shear modulus compared to controls [within-subject variable: muscle (BF, ST, SM), angle (90°, 60°), categorical factor: group (athlete (all sports pooled), control)]. Then, the effect of elite sport specialization on the shear modulus of each head of the hamstring was assessed using a three-way ANOVA [within-subject variable: muscle (BF, ST, SM), angle...
(90°, 60°); categorical factor: group (soccer, track and field, fencing, taekwondo, figure skating, field hockey, basketball, control)]. When the sphericity assumption in repeated measures ANOVAs was violated (Mauchly’s test), a Geisser-Greenhouse correction was used. Post-hoc analyses were performed using Bonferroni tests. The effect size was calculated using Cohen's $d$ for between-sport comparisons considering $<0.15, 0.15, 0.4, 0.75, 1.1, 1.45,$ $>1.45$ as negligible, small, medium, large, very large, and huge effect, respectively. The mean difference was calculated for between-sport comparisons and presented with 95% confidence intervals. For all tests, the significance level was set at $P < 0.05$. Data are presented as mean ± SD.
RESULTS

The resting shear modulus values showed a good inter-day reliability for each hamstring head (ICC: 0.80-0.98, TE: 0.6-3.4 kPa, CV: 8.2-13.0%; Table 2). Considering this result, data were averaged between days for controls. We found a significant main effect of sport (P < 0.001) on age. Specifically, control participants were significantly older than basketball players (+ 9.7 years; P < 0.001), while no difference were found with other sports (P > 0.063). The comparison between dominant and non-dominant limb in uninjured participants showed no main effect of laterality (P = 0.65; Fig. 2). We found no main effect of sex (14.3±8.4 vs. 13.8±7.8 kPa, for females and males, respectively; P = 0.46) on shear modulus values. A significant effect of muscle (P < 0.0001), angle (P < 0.0001) and a significant muscle × angle interaction was found (P < 0.0001). Shear modulus was higher in BF (+41.8±28.8%) and SM (+38.3±37.8%) on average compared to ST (P values < 0.0001), while no significant difference was observed between BF and SM (P = 1.00).

The comparison between controls and athletes revealed a significant main effect of group (P = 0.005), muscle (P < 0.0001), angle (P < 0.0001), muscle × group interaction (P < 0.0001), muscle × angle interaction (P < 0.0001), group × angle (P = 0.013) and muscle × group × angle interaction (P < 0.0001) on shear modulus values of hamstring muscles. Post-hoc analysis showed that SM shear modulus measured at 60° was lower for athletes (21.9±6.5 kPa) than for control participants (32.1±11.9 kPa) (P < 0.0001). No significant between-group differences were found for ST and BF.

When comparing control and each sport specialization group, we found a significant main effect of group (P ≤ 0.0001), muscle (P < 0.0001) and muscle × group interaction (P < 0.001) and muscle × group × angle interaction (P < 0.03) on shear modulus values of hamstring muscles (Fig. 3). Muscle × group × angle interaction showed that, compared to control, shear modulus at 60° was lower in SM for figure skating (-17.2 kPa [-26.0,-8.5]; P <
0.001; d = 1.8), taekwondo (-18.0 kPa [-26.0;-10.1]; P < 0.001; d = 2.1), soccer (-9.0 kPa [-
17.3;-0.8]; P = 0.011; d = 0.9), and fencing (-10.3 kPa [-19.7;-0.9]; P = 0.024; d = 1.0) (Fig.
3). No significant differences were found between controls and basketball, athletics, and field
hockey (all P values > 0.14). Shear modulus of the BF and ST muscle was not significantly
different between controls and elite athletes, regardless of the sport specialization (all P values
= 1; Fig. 3).
DISCUSSION

To our knowledge, this the first study to report a variable distribution of shear modulus among hamstring muscle heads between sports in a large cohort of elite athletes.

Two major findings can be highlighted from this investigation: (i) the shear modulus of the SM is lower in athletes involved in taekwondo, figure skating, soccer and fencing compared to controls while no significant difference were found for basketball, athletics and field hockey, (ii) the shear modulus of the BF and ST is not different from controls in elite athletes, regardless of the sport specialization. Prospective work is needed to determine whether the selective lower SM shear modulus relates to the mechanical constraints imposed by sport activities and its putative role in motor performance.

The shear modulus values obtained for control participants in relaxed condition were close to those previously obtained from hamstring heads during passive stretching cycle at the same hip (90°) and knee configuration (90°) [ST = 9.7 vs. 6.8 kPa, SM = 10.4 vs. 10.9 kPa, BF = 13.2 vs. 11.8 kPa for 20 and the current study, respectively]. In agreement with most of the studies dealing with the effect of sex on muscle shear modulus 26,27, no significant differences in hamstring muscles shear modulus were found between male and female athletes. This allowed us to compare muscle shear modulus between sports, regardless of the distribution between males and females. In addition, laterality did not affect muscle shear modulus (Fig. 2), even when only considering asymmetric sport activities (i.e. field hockey, taekwondo, fencing; leg effect: \( P = 0.53 \)). In line with the current body of literature using shear wave elastography 15,28, we observed a high variability of hamstring shear modulus between individuals among both healthy controls and elite athletes, especially in extended knee position (i.e. 60°) with SD comprised between 4.3 kPa (27% of the mean value) and 10.0 kPa (44%) (cf. Fig. 2). The hip and knee joint angles used in the current study placed the
participants at a different percentage of their maximal range of motion which may partly explain the variability in muscle shear modulus observed between individuals. However, both passive tension developed by muscle-tendon units and the sensation of this tension (i.e., discomfort) limit the maximal tolerable range of motion (for review, see Wepppler & Magnusson 9). Therefore, a similar relative joint angle (i.e., normalized to the maximal range of motion) would have not necessarily reduced the inter-individual variability in muscle shear modulus. This could also reflect the effect of innate properties and/or functionally driven adaptations elicited by elite sport practice.

Of note, our findings showed that SM and BF muscles were 38% and 42% stiffer than ST, respectively. This finding is similar to previous reports, which demonstrated that ST muscle exhibits the lowest resting shear modulus values among hamstring heads 20,29. Hamstring muscles present distinct architecture, SM and BF being pennate muscles while ST is fusiform or with a small pennation angle depending on the studies 2. Due to this muscle architecture, the assessment of shear modulus in hamstring remains limited to some specific regions 20. Hence, the regions of interest were chosen to ensure reliable measurements as reflected by the high to very-high inter-day reliability reported in the results section. One could note that the alignment between the ultrasound probe and the fascicle’s path may increase the shear modulus values 21. Importantly, this methodological issue does not explain the higher shear modulus values obtained for BF and SM compared to ST, as the maximal shear wave velocity is reached when the probe is along the fibres 30. Therefore, this influence is likely marginal between SM and BF which present close pennation angle 31. Thus, the lower shear modulus values for ST compared to SM and BF could result from the variance in biomechanical loads for each hamstring muscle. During running, Schache et al. 32 showed that BF exhibits the largest peak strain while SM produced the highest peak force and performed
the largest amount of work. When repeated, these actions elicited by sport activity may induce specific mechanical adaptations on each head. This could in turn contribute to the lower passive muscle shear modulus observed in BF and SM comparatively to ST.

In line with our hypothesis, the present study reports that the shear modulus of the SM is lower in athletes than in controls. Specifically, taekwondo practitioners, figure skaters, fencers and soccer players had a lower shear modulus than controls when considering SM (Fig. 3). Even though we cannot rule out that muscle shear modulus is related to initial (innate) properties, we assume that the resting shear modulus may reflect localized mechanical adaptations resulting from joints movements and repeated solicitations encountered during elite sport practice. Indeed, these activities demand high flexibility of the lower limbs to execute complex movements over large joint amplitude. For instance, Preuschl et al. reported that specific movements regularly executed in taekwondo involved hip flexed angles (65°, 180° = full hip extension) and knee angles close to full extension (178°, 180° = full extension). Similarly, elite fencers regularly execute lunge with hip flexed (49°) combined with moderated knee extension angles (116°). Interestingly, during these fencing and taekwondo movements, the activation of the stretched hamstrings remains low (10% of the EMG max) towards the ending phase of the motion. The selective lower shear modulus of the SM in sports that elicit stretching of the hamstrings over large range of motion activities (taekwondo, figure skating and fencing) is in accordance with the greater association between maximal hip flexion angle (straight-leg-raises test) and SM shear modulus (r = -0.75) compared to ST (r = -0.67) and BF (r = -0.61). The inclusion of substantial stretching routines in the training volume may also explain this result as two recent studies showing a larger decrease in shear modulus of the SM compared to ST and BF after an acute and chronic stretching program. It is likely that stretching usually performed to
increase flexibility in taekwondo and figure skating contributes to the selective lower stiffness in the SM (large effect for both sports; \(d > 1.8\)). Although the volume of the stretching routines has not been quantified in the current study, it is also reasonable to assume that the lower shear modulus in SM (large effect; \(d = 0.9\)) exhibited by soccer players compared to controls relates to their high amount of stretch training, as it represents one of the main strategy used to prevent muscle strain injury.\(^{37}\) Contrarily to our hypothesis, we did not find any difference in hamstring shear modulus (SM, ST, and BF) in basketball, athletics, and field hockey compared to controls while these activities elicit movement over moderate amplitudes (e.g., drag flick in field hockey) and stretch shortening cycles. This result is strengthened by the negligible to moderate differences observed with controls, depending on the muscle and the sport activity. Note that we found that basketball players were younger than control participants. However, it is unlikely that this difference in age between basketball players and controls (9.7 years) explain the absence of difference in shear modulus, as previous works reported a negligible impact of age on muscle shear modulus below 60 years old.\(^{27}\) Both the duration and intensity of the stretching play an important role on muscle mechanical and architectural adaptations (e.g., Freitas et al.\(^{38}\)). Therefore, we can speculate that the absence of differences in shear modulus in these activities may be related to the relative small time spent at moderate amplitudes compared to other actions performed at short muscle length (e.g., jogging, walking, strength and conditioning;\(^{39,40}\)). More importantly, these sports elicit high intensity eccentric contractions of the hamstring muscles\(^{41,42}\) which may lead to potential adaptations in muscle shear modulus. A recent study has shown a prolonged increase in muscle shear modulus (i.e., 21 days) after a protocol including a high amount of high intensity negative work (i.e., maximal eccentric actions)\(^{14}\). In contrast, taekwondo, figure skating and fencing result in lower hamstring activation during stretching-oriented
movements. Further investigations are required to determine how muscle state (high or low eccentric force) modulates long-term muscle mechanical adaptations.

PERSPECTIVES

Askling et al. \(^3\) reported the existence of two specific type of acute hamstring injury. The first occurring in extreme positions during stretching exercise affects the SM, while the second, occurring during maximal speed running affects the BF. Despite the preventive strategies adopted by elite sports stakeholders involved in sprinting activities (e.g., eccentric strengthening of the hamstring), their shear modulus values were similar to that of moderately active individuals. The absence of difference in BF is surprising as this muscle exhibits the greater muscle-tendon unit strain among the hamstrings during sprinting \(^32\). Taken together with the high injury rate of the BF among hamstring muscle \(^11\), findings suggest further research to determine whether selective stretching exercises (e.g., foot external rotation during prone leg curl; Beuchat & Maffiuletti \(^43\)) is an effective strategy to reduce the occurrence of BF muscle injury \(^44\). One should note that the way muscle shear modulus interacts with force-generating potential (activation, force-length relationship) is still unclear (for review see Holt & Williams \(^45\)), especially during dynamic tasks. Therefore, an increase in muscle shear modulus may not be relevant when muscles have to produce a substantial amount of negative work at long muscle length. The recent advances in musculo-skeletal models implementing individual muscle geometry and mechanical properties (e.g., Martin & Nichols \(^46\)) may provide new insights of the optimal biomechanical muscle properties for human performance while minimizing injury risk.

CONCLUSION
Hamstring shear modulus varied between individuals, muscles and sports, reflective of mechanical adaptations elicited by high-level sport practice. We provide evidence that the shear modulus of the SM is increased in athletes involved in elite sport practice performed over large range of motion (taekwondo, figure skating and fencing). Despite the execution of movement over moderate to large range of motion and/or preventive strategies adopted by elite sports stakeholders, they exhibit similar BF and ST shear modulus than moderately active individuals. Prospective work is needed to determine whether the selective lower SM shear modulus relates to the mechanical constraints of the sport activities and its putative role in motor performance.
We are grateful to the athletes of the French Federations for their thorough implication in this project. As a member of the French-speaking Research Centre for the Prevention of Injury and Illness and the Protection of Athletes, the Laboratory Sport, Expertise and Performance has received funding from the International Olympic Committee to establish long-term research program on the prevention of injuries and illnesses in sport for the protection of athlete health. This project was funded by the French Ministry of Sport (BLESSI research project; contract n°15-r-19). S. Avrillon was supported by a scholarship funded by the French Ministry of Research. G. Le Sant was supported by a scholarship co-funded by the French National Association Research Technology and the School of Physiotherapy (IFM3R), Nantes, France. F. Hug was supported by a fellowship from the Institut Universitaire de France (IUF). This study was partly supported by a grant from the Région Pays de la Loire (QUETE project, no. 2015-09035).

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


FIGURES

**Figure 1.** Typical example of shear modulus measurements in *semitendinosus* (A), *semimembranosus* (B) and *biceps femoris* (C) muscle. Participants were lying supine with the hip angle fixed at 90° (0° = hip fully extended), and knee at 90° and 60° using an isokinetic dynamometer (0° = full knee extension). Shear modulus was measured over the region of interest outlined by white dashed lines (the images display shear modulus maps obtained at 60° of knee angle). The ultrasound probe was held manually by the investigator over the posterior face of the thigh.

**Figure 2.** Individual (dots) and mean (black lines) shear modulus values measured at 90° (A, left panel) and 60° (B, right panel; 0° = full leg extension) in *semitendinosus* (ST, black), *semimembranosus* (SM, dark grey) and *biceps femoris* long head (BF, light grey) for dominant and non-dominant limb of uninjured participants. n = 79 (67 athletes + 12 controls). *, significant difference with ST muscle (*P* < 0.05).

**Figure 3.** Individual (colored dots) and mean (vertical solid line) shear modulus values in *semitendinosus* (A, top panel), *semimembranosus* (B, middle panel) and *biceps femoris* long head (C, bottom panel) of elite athletes in each sport and control participants, grey dots and dashed line, respectively. Data correspond to values of the measurements performed at 60° of knee angle and are pooled between limbs for non-injured participants (n = 79; no effect of laterality), for the sake of clarity.