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► **To cite this version:**

Simon Avrillon, Lilian Lacourpaille, François Hug, Guillaume Le Sant, Alain Frey, et al.. Hamstring muscle elasticity differs in specialized high-performance athletes. *Scandinavian Journal of Medicine and Science in Sports*, 2019, 30 (1), pp.83-91. 10.1111/sms.13564 . hal-03325056

HAL Id: hal-03325056

<https://nantes-universite.hal.science/hal-03325056>

Submitted on 1 Sep 2021

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Hamstring muscle elasticity differs in specialized high-performance athletes

Type of Article: ORIGINAL ARTICLE

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Running title: Impact of sport on hamstring shear modulus

Grant support:

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).

1 **ABSTRACT (250 Words)**

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

7 Taking advantage of shear wave elastography, we aimed to determine whether elite sport
8 athletes exhibit different passive shear modulus of hamstring heads compared to controls.

9 Passive shear modulus was measured on *semitendinosus* (ST), *semimembranosus* (SM) and
10 *biceps femoris* (BF) using shear wave elastography with the knee flexed at 60° and 90°, and
11 90° of hip flexion. A total of 97 elite athletes from various sports including running sprint,
12 figure skating, fencing, field hockey, taekwondo, basket-ball and soccer, and 12 controls were
13 evaluated.

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

20 We provide evidence that the shear modulus of the SM is altered in athletes involved in elite
21 sport practice performed over large range of motion and/or including substantial stretching
22 program in training content (taekwondo, figure skating, fencing and soccer).

23 **Keywords:** Stiffness - shear wave elastography - elite athletes

24 INTRODUCTION

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

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

46 Ultrasound shear wave elastography (SWE) can be used as a reliable ¹² and valid ¹³
47 method to assess regional shear modulus. This parameter reflects intrinsic muscle mechanical
48 properties, regardless of its size. More precisely, it represents an index of tissue stiffness. For

49 a muscle of a given size, the higher the shear modulus, the higher the stiffness. Using SWE, it
50 has been recently shown that passive muscle shear modulus increased after repeated eccentric
51 contractions ¹⁴ or inversely decreased after a stretching protocol ¹⁵. Interestingly, the
52 magnitude of these changes may differ among the synergist muscles ¹⁵. More precisely, a
53 recent study has shown that a 4-week static stretching program induces a decrease in shear
54 modulus in hamstring muscles (i.e., increase in hamstring shear modulus), with a higher effect
55 on the SM compared to the BF and ST ¹⁰. However, the impact of chronic sport practice on
56 individual muscle shear modulus has not been described. It is well known that most of sports
57 activities involve bouncing and jumping with high-intensity stretch-shortening cycles (e.g.,
58 soccer, basketball, athletic sprinting). Such motor tasks stimulate muscle-tendon units of the
59 lower limb to store and release high amounts of elastic energy and in turn amplify power ¹⁶. In
60 these sports and others, the hamstring muscles are also involved over moderate to large ranges
61 of motion. For instance, Preuschl et al. ¹⁷ reported that specific movements regularly executed
62 in taekwondo involved hip flexed angles about 65° (180° = full hip extension) and knee
63 angles close to full extension (178°, 180° = full extension). Similarly, elite fencers regularly
64 execute lunges with hip almost fully flexed (49°) combined with moderated knee extension
65 angles (116°) ¹⁸. A recent cross-sectional study reported that highly flexible ballet dancers
66 display different morphological, mechanical, and functional properties of the triceps surae
67 muscle-tendon unit, compared to control individuals with no history of stretching training ¹⁹.
68 Therefore, it is reasonable to assume that daily exposure to elite sport practice may lead to
69 adaptations in hamstring muscle shear modulus. The description of the shear modulus of each
70 individual hamstring head in elite athletes specialized in various activities (e.g., soccer,
71 athletic sprinting, fencing, taekwondo) would provide the impetus to explore its putative
72 importance in motor performance.

73 Taking advantage of shear wave elastography, we aimed to determine whether the
74 shear modulus of hamstring heads (ST, SM, BF) differs between elite athletes (i.e., basketball,
75 field-hockey, soccer, track and field, fencing, taekwondo, figure skating) and controls. We
76 hypothesized that, compared to controls, elite athletes exhibit lower hamstring shear modulus
77 due to high intensity stretch-shortening cycles ¹⁶ and/or moderate to large range of motion
78 movements at the hip and knee (e.g., Preuschl et al. ¹⁷), performed daily in their sport
79 activities. We also hypothesized that sport specialization (i.e., taekwondo, figure skating,
80 fencing, athletic sprinting, basketball, soccer, and field-hockey) would induce specific
81 alterations of the shear modulus among hamstring muscle heads depending on the specific
82 mechanical constraints associated with each sport activity.

83

84 **METHODS**

85 **Participants**

86 A total of 109 participants: 97 elite athletes (61 males) who trained once-to-twice a
87 day on 25 to 40 h/wk regular basis, from soccer, track and field sprinting, fencing, taekwondo,
88 figure skating, field hockey and basket-ball, and 12 healthy moderately active participants
89 without sport specialization (6 males, 6 females) participated in this study (Table 1). Training
90 programs of elite athletes included about $\sim 150 \pm 110$ min of hamstring stretching routines per
91 week. Note that this volume varied greatly between athletes, as some of them are doing
92 additional individual specific stretching workout with physiotherapists. All of them had
93 competed at the international level during the year of the experiment. 29 participants had an
94 history of unilateral hamstring injury. Only the uninjured side of these athletes was included
95 in the study to evaluate the effect of sport to avoid any putative effect of injury on shear
96 modulus values. One participant who had a hamstring injury history for both sides was
97 excluded from the analyses. All athletes did not perform any vigorous strength training of the

98 lower limb 48 hours before the experiment. They were informed regarding the nature, aims
99 and risks associated with the experimental procedure before they gave their written consent to
100 participate. This study was approved by the ethics committee of Île de France III (agreement
101 no 3418) and conformed to the standards of the Declaration of Helsinki.

102

103 **Experimental set-up**

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

108

109 **Shear-wave elastography**

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

116

117 The examiner was trained three months on the ultrasound scanner to adequately
118 measure the shear modulus in hamstring muscles with minimal transducer pressure on the
119 skin. Muscles were scanned using a handheld technique based on previous studies from our
120 group that allowed reliable assessment of the shear modulus in hamstring muscles²⁰. The
121 probe was placed over the posterior face of the thigh, proximally to the tendinous inscription
122 dividing this muscle into two portions to image ST. For SM and BF, the probe was placed

123 proximal to the musculotendinous junction, close to mid-thigh. Once the site of measurement
124 was determined, the probe was orientated to measure the shear modulus along the fascicle's
125 line of action. The probe location was considered appropriate when fascicles were clearly
126 visible across the image and the obtained shear modulus map included no aponeurosis, and
127 little amount of missing or non-physiological values. The locations were marked on the skin
128 using a waterproof marker so that the transducer location remained constant throughout
129 measurements.

130

131 **Protocol**

132 Participants first performed four slow ($10^{\circ} \cdot s^{-1}$) passive loading/unloading cycles
133 between 90° and 30° of knee flexion (0° = full extension) to account for the possible effect of
134 conditioning ²². The resting shear modulus was then measured in each hamstring muscle
135 during 10 s at two knee angles (90° and 60°). Before each acquisition, a 10-s period was kept
136 between knee positioning and the onset of the elastography acquisition to further account for
137 any potential stretch–relaxation effect ²³. The participants were instructed to remain as relaxed
138 as possible throughout the measurements. The shear modulus was assessed in hamstring
139 muscles of both legs to compare the dominant and non-dominant leg. These measures were
140 performed in a randomized order on 79 participants with no injury in both lower limbs. The
141 dominant leg was defined as the leg preferentially used to kick a ball.

142

143 **Data analysis**

144 All data were processed using Matlab custom-written scripts (R2017a, The
145 MathWorks Inc., Natick, USA) and Origin 2018 software (OriginLab Corporation,
146 Northampton, USA). Mean shear modulus values were obtained over the largest possible
147 region of interest. The unexpected presence of vein and intramuscular fascia may punctually

148 induce small-size artifacts ²⁴. Particular care was taken to not include artefacts and
149 aponeurosis in the region of interest. Data were exported in ‘mp4’ format and transformed to
150 a sequence of ‘jpeg’ images. Image processing then converted the resulting colored map into
151 shear modulus values. The average Young’s modulus was divided by 3, to obtain the muscle
152 shear modulus ²¹. The five successive images that resulted in the lowest standard deviation
153 were considered to calculate an average value of the shear modulus (μ).

154

155 **Statistics**

156 All statistical analyses were conducted using Statistica version 7.1 software (StatSoft,
157 Tulsa, OK). Data were screened for normal distribution using the Shapiro–Wilk test. The
158 inter-day reliability of shear modulus measurements was evaluated on control participants (n
159 = 12) using the intraclass correlation coefficient (ICC), typical error (TE) and coefficient of
160 variation (CV). Ages were compared between sports by using a one-way ANOVA (between
161 subject factor: sport). The effect of laterality on muscle shear modulus was tested through a
162 three-way ANOVA [side (dominant, non-dominant) \times muscle (BF, ST, SM) \times angle (90°,
163 60°)] on participants with no injury on both lower limbs (n = 79). As the proportion of males
164 and females differs between sports (cf. Table 1), the effect of sex was tested using a two-way
165 ANOVA [within-subject variable: muscle (BF, ST, SM) \times angle (90°, 60°); categorical factor:
166 sex (male, female)] on participants with no injury on both lower limbs (n = 79). For controls
167 and uninjured athletes, the muscle shear modulus of the two limbs was averaged.

168 A three-way ANOVA was performed to determine whether elite athletes exhibit
169 altered muscle shear modulus compared to controls [within-subject variable: muscle (BF, ST,
170 SM), angle (90°, 60°), categorical factor: group (athlete (all sports pooled), control)]. Then,
171 the effect of elite sport specialization on the shear modulus of each head of the hamstring was
172 assessed using a three-way ANOVA [within-subject variable: muscle (BF, ST, SM), angle

173 (90°, 60°); categorical factor: group (soccer, track and field, fencing, taekwondo, figure
174 skating, field hockey, basket-ball, control)]. When the sphericity assumption in repeated
175 measures ANOVAs was violated (Mauchly's test), a Geisser-Greenhouse correction was
176 used. Post-hoc analyses were performed using Bonferroni tests. The effect size was calculated
177 using Cohen's d for between-sport comparisons considering <0.15, 0.15, 0.4, 0.75, 1.1, 1.45,
178 >1.45 as *negligible*, *small*, *medium*, *large*, *very large*, and *huge* effect, respectively ²⁵. The
179 mean difference was calculated for between-sport comparisons and presented with 95%
180 confidence intervals. For all tests, the significance level was set at $P < 0.05$. Data are
181 presented as mean \pm SD.

182 RESULTS

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

195 The comparison between controls and athletes revealed a significant main effect of
196 group ($P = 0.005$), muscle ($P < 0.0001$), angle ($P < 0.0001$), muscle \times group interaction ($P <$
197 0.0001), muscle \times angle interaction ($P < 0.0001$), group \times angle ($P = 0.013$) and muscle \times
198 group \times angle interaction ($P < 0.0001$) on shear modulus values of hamstring muscles. Post-
199 hoc analysis showed that SM shear modulus measured at 60° was lower for athletes (21.9 ± 6.5
200 kPa) than for control participants (32.1 ± 11.9 kPa) ($P < 0.0001$). No significant between-group
201 differences were found for ST and BF.

202 When comparing control and each sport specialization group, we found a significant
203 main effect of group ($P \leq 0.0001$), muscle ($P < 0.0001$) and muscle \times group interaction ($P <$
204 0.001) and muscle \times group \times angle interaction ($P < 0.03$) on shear modulus values of
205 hamstring muscles (Fig. 3). Muscle \times group \times angle interaction showed that, compared to
206 control, shear modulus at 60° was lower in SM for figure skating (-17.2 kPa [-26.0 ; -8.5]; $P <$

207 0.001; $d = 1.8$), taekwondo (-18.0 kPa [-26.0;-10.1]; $P < 0.001$; $d = 2.1$), soccer (-9.0 kPa [-
208 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.
209 3). No significant differences were found between controls and basketball, athletics, and field
210 hockey (all P values > 0.14). Shear modulus of the BF and ST muscle was not significantly
211 different between controls and elite athletes, regardless of the sport specialization (all P values
212 = 1; Fig. 3).

213 **DISCUSSION**

214 To our knowledge, this the first study to report a variable distribution of shear
215 modulus among hamstring muscle heads between sports in a large cohort of elite athletes.
216 Two major findings can be highlighted from this investigation: (i) the shear modulus of the
217 SM is lower in athletes involved in taekwondo, figure skating, soccer and fencing compared
218 to controls while no significant difference were found for basketball, athletics and field
219 hockey, (ii) the shear modulus of the BF and ST is not different from controls in elite athletes,
220 regardless of the sport specialization. Prospective work is needed to determine whether the
221 selective lower SM shear modulus relates to the mechanical constraints imposed by sport
222 activities and its putative role in motor performance.

223

224 The shear modulus values obtained for control participants in relaxed condition were
225 close to those previously obtained from hamstring heads during passive stretching cycle at the
226 same hip (90°) and knee configuration (90°) [ST = 9.7 vs. 6.8 kPa, SM = 10.4 vs. 10.9 kPa,
227 BF = 13.2 vs. 11.8 kPa for ²⁰ and the current study, respectively]. In agreement with most of
228 the studies dealing with the effect of sex on muscle shear modulus ^{26,27}, no significant
229 differences in hamstring muscles shear modulus were found between male and female
230 athletes. This allowed us to compare muscle shear modulus between sports, regardless of the
231 distribution between males and females. In addition, laterality did not affect muscle shear
232 modulus (Fig. 2), even when only considering asymmetric sport activities (i.e. field hockey,
233 taekwondo, fencing; leg effect: $P = 0.53$). In line with the current body of literature using
234 shear wave elastography ^{15,28}, we observed a high variability of hamstring shear modulus
235 between individuals among both healthy controls and elite athletes, especially in extended
236 knee position (i.e. 60°) with SD comprised between 4.3 kPa (27% of the mean value) and 10.0
237 kPa (44%) (cf. Fig. 2). The hip and knee joint angles used in the current study placed the

238 participants at a different percentage of their maximal range of motion which may partly
239 explain the variability in muscle shear modulus observed between individuals. However, both
240 passive tension developed by muscle-tendon units and the sensation of this tension (i.e.,
241 discomfort) limit the maximal tolerable range of motion (for review, see Weppeler &
242 Magnusson ⁹). Therefore, a similar relative joint angle (i.e., normalized to the maximal range
243 of motion) would have not necessarily reduced the inter-individual variability in muscle shear
244 modulus. This could also reflect the effect of innate properties and/or functionally driven
245 adaptations elicited by elite sport practice.

246

247 Of note, our findings showed that SM and BF muscles were 38% and 42% stiffer than
248 ST, respectively. This finding is similar to previous reports, which demonstrated that ST
249 muscle exhibits the lowest resting shear modulus values among hamstring heads ^{20,29}.
250 Hamstring muscles present distinct architecture, SM and BF being pennate muscles while ST
251 is fusiform or with a small pennation angle depending on the studies ². Due to this muscle
252 architecture, the assessment of shear modulus in hamstring remains limited to some specific
253 regions ²⁰. Hence, the regions of interest were chosen to ensure reliable measurements as
254 reflected by the high to very-high inter-day reliability reported in the results section. One
255 could note that the alignment between the ultrasound probe and the fascicle's path may
256 increase the shear modulus values ²¹. Importantly, this methodological issue does not explain
257 the higher shear modulus values obtained for BF and SM compared to ST, as the maximal
258 shear wave velocity is reached when the probe is along the fibres ³⁰. Therefore, this influence
259 is likely marginal between SM and BF which present close pennation angle ³¹. Thus, the
260 lower shear modulus values for ST compared to SM and BF could result from the variance in
261 biomechanical loads for each hamstring muscle. During running, Schache et al. ³² showed that
262 BF exhibits the largest peak strain while SM produced the highest peak force and performed

263 the largest amount of work. When repeated, these actions elicited by sport activity may induce
264 specific mechanical adaptations on each head. This could in turn contribute to the lower
265 passive muscle shear modulus observed in BF and SM comparatively to ST³³.

266

267 In line with our hypothesis, the present study reports that the shear modulus of the SM
268 is lower in athletes than in controls. Specifically, taekwondo practitioners, figure skaters,
269 fencers and soccer players had a lower shear modulus than controls when considering SM
270 (Fig. 3). Even though we cannot rule out that muscle shear modulus is related to initial
271 (innate) properties, we assume that the resting shear modulus may reflect localized
272 mechanical adaptations resulting from joints movements and repeated solicitations
273 encountered during elite sport practice. Indeed, these activities demand high flexibility of the
274 lower limbs to execute complex movements over large joint amplitude^{17,34}. For instance,
275 Preuschl et al.¹⁷ reported that specific movements regularly executed in taekwondo involved
276 hip flexed angles (65°, 180° = full hip extension) and knee angles close to full extension
277 (178°, 180° = full extension). Similarly, elite fencers regularly execute lunge with hip flexed
278 (49°) combined with moderated knee extension angles (116°). Interestingly, during these
279 fencing and taekwondo movements, the activation of the stretched hamstrings remains low
280 (10% of the EMG max) towards the ending phase of the motion^{18,35,36}. The selective lower
281 shear modulus of the SM in sports that elicit stretching of the hamstrings over large range of
282 motion activities (taekwondo, figure skating and fencing) is in accordance with the greater
283 association between maximal hip flexion angle (straight-leg-raises test) and SM shear
284 modulus ($r = -0.75$) compared to ST ($r = -0.67$) and BF ($r = -0.61$)³⁷. The inclusion of
285 substantial stretching routines in the training volume may also explain this result as two recent
286 studies showing a larger decrease in shear modulus of the SM compared to ST and BF after an
287 acute³⁶ and chronic¹⁰ stretching program. It is likely that stretching usually performed to

288 increase flexibility in taekwondo and figure skating contributes to the selective lower stiffness
289 in the SM (large effect for both sports; $d > 1.8$). Although the volume of the stretching
290 routines has not been quantified in the current study, it is also reasonable to assume that the
291 lower shear modulus in SM (large effect; $d = 0.9$) exhibited by soccer players compared to
292 controls relates to their high amount of stretch training, as it represents one of the main
293 strategy used to prevent muscle strain injury³⁷. Contrarily to our hypothesis, we did not find
294 any difference in hamstring shear modulus (SM, ST, and BF) in basketball, athletics, and field
295 hockey compared to controls while these activities elicit movement over moderate amplitudes
296 (e.g. drag flick in field hockey) and stretch shortening cycles. This result is strengthened by
297 the *negligible to moderate* differences observed with controls, depending on the muscle and
298 the sport activity. Note that we found that basketball players were younger than control
299 participants. However, it is unlikely that this difference in age between basketball players and
300 controls (9.7 years) explain the absence of difference in shear modulus, as previous works
301 reported a negligible impact of age on muscle shear modulus below 60 years old²⁷. Both the
302 duration and intensity of the stretching play an important role on muscle mechanical and
303 architectural adaptations (e.g., Freitas et al.³⁸). Therefore, we can speculate that the absence
304 of differences in shear modulus in these activities may be related to the relative small time
305 spent at moderate amplitudes compared to other actions performed at short muscle length
306 (e.g., jogging, walking, strength and conditioning;^{39,40}). More importantly, these sports elicit
307 high intensity eccentric contractions of the hamstring muscles^{41,42} which may lead to
308 potential adaptations in muscle shear modulus. A recent study has shown a prolonged increase
309 in muscle shear modulus (i.e. 21 days) after a protocol including a high amount of high
310 intensity negative work (i.e., maximal eccentric actions)¹⁴. In contrast, taekwondo, figure
311 skating and fencing result in lower hamstring activation during stretching-oriented

312 movements. Further investigations are required to determine how muscle state (high or low
313 eccentric force) modulates long-term muscle mechanical adaptations.

314

315 **PERSPECTIVES**

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

334

335 **CONCLUSION**

336 Hamstring shear modulus varied between individuals, muscles and sports, reflective of
337 mechanical adaptations elicited by high-level sport practice. We provide evidence that the
338 shear modulus of the SM is increased in athletes involved in elite sport practice performed
339 over large range of motion (taekwondo, figure skating and fencing). Despite the execution of
340 movement over moderate to large range of motion and/or preventive strategies adopted by
341 elite sports stakeholders, they exhibit similar BF and ST shear modulus than moderately
342 active individuals. Prospective work is needed to determine whether the selective lower SM
343 shear modulus relates to the mechanical constraints of the sport activities and its putative role
344 in motor performance

345

346 **ACKNOWLEDGMENTS**

347 We are grateful to the athletes of the French Federations for their thorough implication in this
348 project. As a member of the French-speaking Research Centre for the Prevention of Injury
349 and Illness and the Protection of Athletes, the Laboratory Sport, Expertise and Performance
350 has received funding from the International Olympic Committee to establish long-term
351 research program on the prevention of injuries and illnesses in sport for the protection of
352 athlete health. This project was funded by the French Ministry of Sport (BLESSI research
353 project; contract n°15-r-19). S. Avrillon was supported by a scholarship funded by the French
354 Ministry of Research. G. Le Sant was supported by a scholarship co-funded by the French
355 National Association Research Technology and the School of Physiotherapy (IFM3R),
356 Nantes, France. F. Hug was supported by a fellowship from the Institut Universitaire de
357 France (IUF). This study was partly supported by a grant from the Région Pays de la Loire
358 (QUETE project, no. 2015-09035).

359

360 **CONFLICT OF INTEREST**

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

362

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- 480

481 **FIGURES**

482 **Figure 1.** Typical example of shear modulus measurements in *semitendinosus* (A),
483 *semimembranosus* (B) and *biceps femoris* (C) muscle. Participants were lying supine with the
484 hip angle fixed at 90° (0° = hip fully extended), and knee at 90° and 60° using an isokinetic
485 dynamometer (0° = full knee extension). Shear modulus was measured over the region of
486 interest outlined by white dashed lines (the images display shear modulus maps obtained at
487 60° of knee angle). The ultrasound probe was held manually by the investigator over the
488 posterior face of the thigh.

489

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

495

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