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1 **Faster early rate of force development in warmer muscle: an *in vivo***
2 **exploration of fascicle dynamics and muscle-tendon mechanical properties**

3
4 **Running title: Muscle-tendon interactions and explosive strength under heat exposure**

5
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26
27 **Keywords:** muscle temperature; explosive strength; muscle-tendon interactions; force-
28 velocity properties; stiffness; ultrafast ultrasound

29 **ABSTRACT**

30 While heat exposure has been shown to increase the skeletal rate of force development (RFD),
31 the underlying processes remain unknown. This study investigated the effect of heat on
32 *gastrocnemius medialis* (GM) muscle-tendon properties and interactions. Sixteen subjects
33 performed electrically-evoked and voluntary contractions combined with ultrafast ultrasound
34 under thermoneutral (CON: 25.8±1.8°C, core temperature 37.0±0.3°C, muscle temperature
35 34.0±1.1°C) and passive heat exposure (HOT: 47.4±1.8°C, core temperature 38.4±0.3°C,
36 muscle temperature 37.0±0.8°C) conditions. Maximal voluntary force changes did not reach
37 statistical significance (-5.0±11.3%, $P = 0.052$) while voluntary activation significantly
38 decreased (-4.6±8.7%, $P = 0.038$) in HOT. Heat exposure significantly increased voluntary
39 RFD before 100 ms from contraction onset (+48.2±62.7%; $P = 0.013$), without further
40 changes after 100 ms. GM fascicle dynamics during electrically-evoked and voluntary
41 contractions remained unchanged between conditions. Joint velocity at a given force was
42 higher in HOT (+7.1±6.6%; $P = 0.004$) but the fascicle force-velocity relationship remained
43 unchanged. Passive muscle stiffness and active tendon stiffness were lower in HOT than CON
44 ($P \leq 0.030$). This study showed that heat-induced increases in early voluntary RFD may not
45 be attributed to changes in contractile properties. Late voluntary RFD was unaltered, possibly
46 due to decreased soft tissues' stiffness in heat. Further investigations are required to explore
47 the influence of neural drive and motor unit recruitment in the enhancement of explosive
48 strength elicited by heat exposure.

49 INTRODUCTION

50

51 Explosive force, referred to as the ability of the human skeletal muscle to generate force as
52 fast as possible, is paramount in motor performance and daily functional tasks (1, 2). This
53 muscle capacity is classically evaluated through the rate of force development (RFD) during
54 the first 200 ms (or less) of an electrically-evoked or maximal voluntary isometric contraction
55 (2, 3). Explosive force production is largely explained by neural and contractile properties
56 which change during muscle contraction. Neural activation is an important determinant in the
57 initials 50 ms of explosive contraction, while the subsequent 50-ms period is correlated to
58 contractile capacity (4). More recently, some studies investigated the various determinants of
59 explosive force depending on time period from the onset of explosive contraction (2, 5, 6). At
60 the onset of the motor impulse (*i.e.*, 0-100 ms), explosive movement is strongly influenced by
61 recruitment velocity and the firing rate of the activated motor unit (5). From 100 to 200 ms,
62 voluntary RFD amplitude will thereafter be submitted to muscle mechanical constraints, as
63 reflected by muscle fascicle dynamics which fit to the fascicle force-velocity relationship (6).
64 RFD may also be influenced by the elastic properties of the muscle-tendon unit and the
65 muscle-tendon interactions (2, 7, 8).

66 It is well established that an increase in core temperature (T_{core}), with its repercussion on
67 muscle temperature (T_{muscle}), contributes to a reduction in voluntary force production (9-11),
68 while increasing maximum muscle shortening velocity in animals (12) and humans (13).
69 Furthermore, a rise in T_{core} or T_{muscle} increases electrically-evoked RFD (14-16). Some studies
70 reported an increase in voluntary RFD (17, 18), while a recent experiment demonstrated no
71 changes in early and middle RFD (19), reflecting that the effects of hyperthermia on voluntary
72 RFD remains to be elucidated. An increase in T_{muscle} has been shown to enhance the rate of
73 ATPase activity, *in vitro* in animals (20, 21), suggesting an increase in the rate of cross-bridge
74 cycling (21). Although increasing T_{muscle} has been reported to alter calcium ions (Ca^{2+})
75 sensitivity (22), an increase in T_{muscle} tends to improve muscle function, which has not been
76 attributed to its putative influence on Ca^{2+} sensitivity of the acto-myosin complex (23). This
77 could contribute to the improvement in maximal muscle shortening velocity (24-26) with
78 concomitant changes in the force-velocity relationship, shifted rightward (13, 27). Although
79 the aforementioned studies mainly focused on the effect of temperature on RFD and
80 contractile properties, there is to date no report investigating the effect of temperature on joint

81 and fascicle force-velocity relationship *in vivo*. Given that muscle fascicles and tendinous
82 tissues contribute to muscle-tendon shortening velocity [*i.e.*, 60 and 40%, respectively (28)],
83 their mechanical properties could both influence the joint and fascicle force-velocity
84 relationship. Yet, it is unclear whether passive heat exposure impacts muscle-tendon
85 interactions and could explain improved electrically-evoked and voluntary RFD together with
86 decreased voluntary force production. Using high-frame-rate ultrasound, our group recently
87 demonstrated a reduction in the electromechanical delay of plantar flexors under heat
88 exposure via accelerated electrochemical processes, while mechanical processes involved in
89 force transmission were unchanged (15). These findings suggest a major effect of increasing
90 T_{core} and T_{muscle} on the electrochemical and contractile component properties of the
91 *gastrocnemius medialis* (GM) muscle, without completely excluding an opposite effect at the
92 level of the series elastic component.

93 The present study aimed to examine the effect of passive heat exposure on GM muscle-tendon
94 complex properties in order to characterise the role of the muscle-tendon interaction in the
95 heat-induced changes in RFD. We hypothesised that fascicle shortening velocity might
96 increase, translating into a rightward shift of the force-velocity relationship for a given
97 fascicle force. We also expected an unchanged or even a potential decrease in soft tissues
98 stiffness. To test these assumptions, muscle fascicle dynamics were explored using high-
99 frame-rate ultrasound during electrically-evoked and voluntary isometric RFD, together with
100 an assessment of dynamic joint and fascicle force-velocity relationships, passive muscle
101 stiffness and active tendon stiffness.

102

103 **MATERIALS AND METHODS**

104

105 ***Ethical approval***

106 Subjects were informed about the nature, aims and risks associated with the experimental
107 procedure before giving their written consent. This study was approved by the Sud-Ouest et
108 Outre-mer III ethics committee (reference: 3849) and conformed to the standards of the
109 Declaration of Helsinki.

110

111 ***Subjects***

112 A non-inferiority sample size calculation was used to determine the sample size required,
113 using GPower (software version 3.1.9.7), based on contraction time, half-relaxation time and
114 electrically-evoked RFD from a previous study (16). With significance and power criteria set
115 at 5% and 80%, respectively, 6 subjects were initially required. We choose to increase the
116 number to 16, since we had men and women and measured other parameters. Sixteen healthy,
117 recreationally active subjects (9 men, 7 women, age: 24.9 ± 5.7 yrs, height: 174.8 ± 7.5 cm,
118 body mass: 69.8 ± 9.9 kg, practicing 5.5 ± 3.2 hrs of sport per week) volunteered to participate
119 in the study after completing a pre-inclusion medical visit. The exclusion criteria were illness,
120 musculoskeletal injuries, pregnancy and be a minor or over 45 years old.

121

122 ***Experimental design***

123 Two to four days after a familiarisation session, subjects underwent two identical testing
124 sequences in a single session: the first sequence was in thermoneutral condition (CON;
125 $25.8 \pm 1.8^\circ\text{C}$, $33.6 \pm 8.6\%$ relative humidity [RH]); the second in a hot ambient condition (HOT;
126 $47.4 \pm 1.8^\circ\text{C}$, $18.5 \pm 4.7\%$ RH, after 127 ± 33 min of heat exposure). The effect of heat was
127 assessed on GM muscle-tendon properties and interactions (muscle fascicle dynamics during
128 electrically-evoked and voluntary isometric RFD, joint and fascicle force-velocity
129 relationships, muscle and tendon stiffness).

130

131 ***Equipment and procedure***

132 Subjects lied prone with extended knees (0°), their right ankle flexed at 90° (foot
133 perpendicular to the tibia) with their right foot firmly fixed on the footplate of a customised
134 ergometer (Bio2M, Compiègne, France; Fig. 1A). The footplate rotated between 110° and 60°
135 for dynamic contractions (*i.e.*, ballistic contractions) or was firmly immobilized at 90° for
136 isometric contractions. The footplate was connected to a force sensor fixed below the plate at
137 the level of the 3rd metatarsal, and the steel rigid structure of the ergometer (2712-100 daN-
138 0.02-B; Sensy, Charleroi, Belgium) for isometric contractions (*i.e.*, electrically-evoked
139 contractions, voluntary isometric explosive and ramp contractions). The force and ankle angle
140 signals were digitised at 2000 Hz. During contractions, GM images were collected using an
141 ultrafast ultrasound scanner (v. 6, Aixplorer, Supersonic Imagine, Aix en Provence, France)
142 coupled with a linear transducer array (4-15 MHz, SuperLinear 15-4, Vermon, Tours, France),
143 encapsulated into a custom cast over the right GM muscle belly, at 30% of the distance

144 between the popliteal fossa and the centre of the lateral malleolus. The probe location was
145 considered appropriate when fascicles and aponeuroses were clearly visible across the image
146 (Fig. 1A).

147 *Electrically-evoked contractions.* The tibial nerve was electrically stimulated using a constant
148 current stimulator (DS7AH, Digitimer, Letchworth Garden City, UK), delivering a single
149 electrical pulse (200 μ s, 400 V) through a cathode placed in the popliteal cavity and an anode
150 placed distally to the patella (Fig. 1A). The intensity was adjusted for each subject by a
151 progressive increase in amperage until plantar flexor force reached a plateau. Five
152 stimulations were delivered at 150% of the electrical intensity required to elicit peak force
153 (29).

154 *Voluntary isometric explosive contractions.* Subjects performed three 5-s isometric MVC
155 (Fig. 1B) interspaced by a 2 min rest period. They were instructed to contract “*as fast and*
156 *hard as possible*” to reach maximal force from a relaxed condition (2). RFD and MVC peak
157 force were assessed on the same repetition to avoid fatigue occurrence (6). In the case of pre-
158 tension or countermovement (change of baseline force of < 1 N during the 100 ms prior to
159 contraction onset), the trial was not considered for further analysis. Voluntary activation (VA)
160 was assessed during two additional MVC using potentiated twitch, evoked during the force
161 plateau and 4 s after the end of the contraction (Fig. 1C), using doublet stimulations (100 Hz).

162 *Ballistic contractions.* Subjects performed maximal plantar flexions from 110° to 60° of ankle
163 flexion on the Bio2M ergometer, equipped with an angle sensor to provide ankle angle
164 measurements (30), as previously described [Fig. 1A (6, 28)]. Three conditions (1 min rest)
165 were tested in a randomised order: with 0 (five trials), 1.2 and 2.6 kg (three trials) attached to
166 the pedal.

167 *Resting shear modulus.* The ultrasound scanner was used in shear wave elastography mode
168 (musculoskeletal preset) to measure (3 measurements per condition) the shear modulus (*i.e.*,
169 index of muscle stiffness) of the GM at rest (Fig. 1D) (31).

170 *Isometric ramp contraction.* Subjects linearly increased in 9-s isometric plantar flexor force
171 from 0 to 90% of the MVC peak force, determined in CON, using a force visual feedback
172 (Fig. 1E). The task was performed twice (3 min rest).

173 *Temperature monitoring.* T_{core} was monitored rectally using an electronic capsule (e-Celsius,
174 BodyCap, Caen, France) (32). Subjects were also instrumented with four data loggers
175 (iButtons, Maxim Integrated, USE), attached to the skin with specific tape, to calculate the

176 average skin temperature (T_{skin}) as: $0.3 \times \text{arm} + 0.3 \times \text{chest} + 0.2 \times \text{thigh} + 0.2 \times \text{shin}$
177 temperature (33). T_{musc} of the contralateral GM was measured immediately before each
178 testing sequence, in a subsample of six subjects. T_{musc} was measured in the middle of GM
179 belly at his thickest place, previously determined with the ultrasound probe, using a needle
180 intramuscular thermistor (MKA08050-A, Ellab, Roedovre, Denmark) inserted at ~ 1.5 cm
181 from below the skin under local anesthesia (Xylocaine, 3mL). During the experimental
182 procedure, subjects could drink *ad libitum* and body mass was measured before and after heat
183 exposure.

184

185 ***Data collection and processing***

186 Mechanical data were recorded synchronously by a 12-bit analog to digital converter
187 (DT9800, Data Translation, Marlboro, USA), and were analysed using custom scripts (Origin
188 2020, OriginLab Corporation, Northampton, USA and Matlab 2017b, The Mathworks,
189 Natick, USA).

190 *Isometric contraction.* The mechanical response to the five electrically-evoked stimulations
191 was low-pass filtered (20 Hz, zero lag 3rd order Butterworth), analysed and averaged to
192 determine peak twitch amplitude (PT) and contraction time (CT). The average electrically-
193 evoked RFD was calculated as PT/CT. The onset of MVC was determined manually (6, 34).
194 Briefly, force signal was viewed with a constant y-axis scale of ~ 1 N and an x-axis scale of
195 500 ms. Then, a vertical cursor was placed on force onset displayed with a higher resolution
196 to verify the position of the vertical cursor (34). The force signal was low-pass filtered (150
197 Hz, zero-lag 4th order Butterworth). The two trials resulting in the highest RFD from
198 contraction onset to 200 ms (RFD_{0-200}) were averaged for analysis. RFD was calculated for
199 specific time periods as the change in force divided by the time windows from 0 to 100 ms
200 (RFD_{0-100}), 0 to 200 ms (RFD_{0-200}) and 100 to 200 ms ($\text{RFD}_{100-200}$, [Fig. 1B]). For each
201 overlapping time interval from force onset, force was divided by the time to calculate RFD_0
202 ‘X’ ms, to identify the maximal RFD ($\text{RFD}_{0-X_{\text{max}}}$; Fig. 1B). $\text{RFD}_{0-X_{\text{max}}}$ thus corresponding to
203 the average RFD between force onset and ‘X’ [‘X’ varied in the range 1-250 ms (5)]. The
204 MVC force corresponded to the maximal force value over a 500 ms moving window (Fig.
205 1B).

206 *Voluntary activation.* VA was determined as (%) as $(1 - \text{superimposed twitch} / \text{potentiated}$
207 $\text{twitch}) \times 100$. The highest VA value obtained was selected.

208 *Fascicle dynamics.* GM ultrasound images were acquired at 1000 Hz. Changes in GM
209 fascicles length (L_F) and pennation angle were assessed on three fascicles (Fig. 1A) using the
210 UltraTrack method (6, 35). Fascicle shortening velocity (V_F) was computed as the first-time
211 derivative of L_F (Fig. 1F).

212 *Joint and fascicle force-velocity relationship.* Angular velocity was computed as the
213 derivative of low-pass filtered (150 Hz, zero lag 3rd order Butterworth) ankle angle over time
214 and total plantar flexion force was calculated from the torque divided by the Achilles tendon
215 lever arm (36). GM ultrasound images were acquired at 2000 Hz. Fascicle force was
216 calculated from the GM muscle force [*i.e.*, 20.9% of total plantar flexion force (37)], divided
217 by the cosine of the pennation angle. Joint velocity, fascicle shortening velocity, force and
218 fascicle force were averaged from 100 to 70° to obtain the joint and fascicle force-velocity
219 relationship [Fig. 1G, H; (28)]. The two trials resulting in the highest mean joint velocity were
220 averaged. Peak force and fascicle force elicited during MVC performed were used as the
221 maximal theoretical force for each individual (F_0). Joint and fascicle force-velocity
222 relationships were determined using the hyperbolic equation proposed by Hill (38):

$$V = b \times (F_0 - F)/(F + a)$$

223 where F is force, V is velocity, a and b are coefficients, determined for each subject, using a
224 fit with F_0 , force and velocity values obtained at 0, 1.2 and 2.6 kg. The maximal theoretical
225 velocity (V_0) was considered as the x-intercept of the force-velocity curve.

226 *Muscle stiffness.* Shear wave elastography image processing converted the coloured map into
227 shear elastic modulus (μ) values (Fig. 1D). The region of interest was inspected to exclude
228 non-muscular structures and artefacts. The five successive maps that resulted in the lowest
229 standard deviation (SD) of the shear modulus were averaged across trials.

230 *Tendon stiffness.* The trial resulting in the lowest dispersion of force signal according to the
231 targeted force during ramp contraction was considered for analysis (Fig. 1E). Displacement of
232 the insertion of GM fascicle on the deep aponeurosis was manually measured (Image J,
233 National Institutes of Health, Bethesda, USA), every 5% of MVC force, on the image
234 (sampling frequency: 100 Hz) corresponding to targeted force level. The active stiffness of
235 tendon corresponded to the ratio between the change in force and the displacement of the
236 aponeurosis between 50 and 80% of MVC force [Fig. 5A; (28, 39)].

237

238 *Statistical analysis*

239 Statistical analyses were performed with Statistica (v. 13.0, StatSoft, Tulsa, USA). The
240 assumptions of normality of the data were verified using a Shapiro-Wilk's test. Values were
241 reported as mean \pm SD unless otherwise stated. A paired 1-tailed t-test was used to compare
242 the effect of the condition (HOT vs. CON) on T_{core} , T_{skin} and T_{musc} , MVC force, V_A ,
243 electrically-evoked RFD, GM shear modulus and tendon active stiffness. RFD_{0-200} , $\text{RFD}_{0-X_{\text{max}}}$,
244 the duration of $\text{RFD}_{0-X_{\text{max}}}$, peak fascicle shortening velocity, time to peak fascicle shortening
245 velocity, L_F at 90° (isometric position) and at 110° (passive dorsiflexion, before ballistic
246 contractions), joint and fascicle V_0 , joint and fascicle F_0 were compared between conditions
247 (HOT vs. CON) using a 2-tailed t-test. The effects of the condition (HOT, CON) and time
248 period (0-100 and 100-200 ms) on RFD were tested by a two-way analysis of variance
249 (ANOVA) with repeated measures (condition \times time period). Differences in V_F and fascicle
250 force during RFD, at 50, 100, 150 and 200 ms from MVC onset, were tested using two-way
251 ANOVAs (condition \times time) with repeated measures. The effects of condition (HOT, CON)
252 and load (0, 1.2, 2.6 kg) on joint velocity, plantar flexor force, V_F and fascicle force were
253 tested using two-way ANOVAs (condition \times load) with repeated measures. When the
254 sphericity assumption in repeated measures ANOVAs was violated (Mauchly's test), a
255 Geisser-Greenhouse correction was used. When appropriate, *post-hoc* analyses were
256 performed using a Bonferroni correction. Effect sizes were described in terms of partial eta-
257 squared (η^2_p , with $\eta^2_p \geq 0.06$ representing a moderate effect and $\eta^2_p \geq 0.14$ a large effect).
258 Statistical significance was set at $P < 0.05$.

259

260 **RESULTS**

261

262 ***Thermoregulatory responses***

263 Average T_{core} , T_{skin} and T_{muscle} were significantly higher in HOT than CON ($38.4 \pm 0.3^\circ\text{C}$,
264 $38.8 \pm 0.4^\circ\text{C}$ and $37.0 \pm 0.8^\circ\text{C}$ in HOT vs. $37.0 \pm 0.3^\circ\text{C}$, $34.7 \pm 0.7^\circ\text{C}$ and $34.0 \pm 1.1^\circ\text{C}$ in CON,
265 respectively; all $P < 0.001$, $\eta^2_p \geq 0.749$). There was no significant difference in body mass
266 between HOT and CON ($P = 0.890$, $\eta^2_p < 0.001$).

267

268 ***Impact of heat on muscle performance***

269 In reference to CON, MVC force did not reach statistical significance in HOT ($P = 0.052$, η^2_p
270 $= 0.176$; Table 1). VA was $4.6 \pm 8.7\%$ lower in HOT than CON ($P = 0.038$, $\eta^2_p = 0.239$; Table
271 1). Electrically-evoked RFD was faster in HOT than CON ($+16.9 \pm 32.8\%$, $P = 0.029$, $\eta^2_p =$
272 0.149 ; Table 1). RFD_{0-200} and $\text{RFD}_{0-X_{\text{max}}}$ were not significantly different between the two
273 conditions (all $P \geq 0.238$, $\eta^2_p \leq 0.016$). Two-way ANOVA revealed no main effect of
274 condition ($P = 0.647$, $\eta^2_p = 0.015$), while a significant main effect of time period ($P = 0.001$,
275 $\eta^2_p = 0.539$) and a condition \times time period interaction ($P < 0.001$, $\eta^2_p = 0.581$) were observed
276 on RFD during the time periods 0-100 and 100-200 ms. *Post-hoc* showed that RFD_{0-100} was
277 higher in HOT ($+48.2 \pm 62.7\%$; $P = 0.013$, $\eta^2_p = 0.088$), while $\text{RFD}_{100-200}$ remained unchanged
278 compared to CON ($P = 0.156$, $\eta^2_p = 0.027$).

279

280 ***Fascicle dynamics during electrically-evoked and voluntary contractions***

281 Initial L_F at which fascicle contracts did not change between 0° and 110° of plantar flexion
282 (all $P \geq 0.577$, $\eta^2_p \leq 0.024$; Table 1). No effect of condition on peak V_F in electrically-evoked
283 and voluntary isometric explosive contractions nor in time to peak shortening velocity were
284 found during RFD evaluation (all $P \geq 0.105$, $\eta^2_p \leq 0.105$; Table 1, Fig. 2). V_F increased (time
285 effect: $P < 0.001$, $\eta^2_p = 0.646$) between 0 and 100 ms and then decreased until 200 ms, with
286 neither a significant effect of condition nor time \times condition interaction (all $P \geq 0.092$, $\eta^2_p \leq$
287 0.172 ; Fig. 2C). Two-way ANOVA applied to fascicle force revealed an effect of time ($P <$
288 0.001 , $\eta^2_p = 0.880$), which increased from 0 to 200 ms, with neither main effect of condition
289 nor time \times condition interaction (all $P \geq 0.074$, $\eta^2_p \leq 0.285$; Fig. 2C).

290

291 ***Joint and ankle force-velocity relationship***

292 During ballistic contractions, a main effect of load ($P < 0.001$, $\eta^2_p = 0.960$) was found on joint
293 velocity, which decreased with increasing load. A main effect of condition, with a high effect
294 size ($P = 0.004$, $\eta^2_p = 0.513$) on data points, showed a rightward shift of the force-velocity
295 relationship, indicative of a higher force for a given velocity in HOT (+7.1±6.6%). There was
296 no condition \times load interaction effect ($P = 0.408$, $\eta^2_p = 0.072$; Fig. 3A). However, there was a
297 main effect of load ($P < 0.001$, $\eta^2_p = 0.934$) on fascicle shortening velocity, which decreased
298 with increasing load, without any effect of condition or condition \times load interaction (all $P \geq$
299 0.244, $\eta^2_p \leq 0.111$; Fig. 3B). Joint V_0 tended to increase ($P = 0.065$, $\eta^2_p = 0.036$; Table 1) and
300 fascicle V_0 remained unchanged across conditions ($P = 0.430$, $\eta^2_p = 0.006$; Table 1). A
301 significant main effect of load on plantar flexion and fascicle force was observed (all $P <$
302 0.001, $\eta^2_p \geq 0.892$), which increased with increasing load, without further effect (all $P \geq$
303 0.142, $\eta^2_p \leq 0.169$; Fig. 3). No difference in plantar flexor and fascicle F_0 was found between
304 HOT and CON (all $P \geq 0.266$, $\eta^2_p \leq 0.006$; Table 1).

305

306 *Muscle and tendon stiffness*

307 Shear modulus was significantly lower in HOT than CON (-11.7±22.2%; $P = 0.030$, $\eta^2_p =$
308 0.044; Fig. 4). Active Achilles tendon stiffness was lower in HOT than CON (-12.7±19.5%; P
309 = 0.038, $\eta^2_p = 0.099$; Fig. 5B).

310

311 **DISCUSSION**

312

313 The present study aimed to determine the effect of passive heat exposure on mechanical
314 properties of the muscle-tendon unit, in order to better understand the underlying mechanisms
315 involved in RFD improvements during electrically-evoked and voluntary contractions. Heat-
316 induced increases in T_{core} and T_{musc} accelerated the early phase of plantar flexor RFD (*i.e.*, <
317 100 ms from contraction onset), which was not accompanied by neither change in late and
318 global RFD (*i.e.*, 0-200 ms and 100-200 ms, respectively) nor in muscle fascicle force-
319 velocity properties (*i.e.*, peak fascicle shortening velocity, fascicle force at a given shortening
320 velocity). Conversely, soft tissues' stiffness decreased in warmer muscle.

321

322 *Influence of warmer muscle on muscle performance*

323 In line with previous research (9-11), MVC peak force tended to decrease and VA decreased
324 with increasing T_{core} . Yet, the decrease in MVC force did not reach statistical significance,
325 likely due to the lower amplitude of hyperthermia elicited in the present study ($\sim 38.4^{\circ}\text{C}$) as
326 compared to previous investigations [38.5°C - 39.5°C ; (9, 16, 40)]. These were similar
327 conditions to previous studies that investigated the effects of passive heat exposure on
328 voluntary RFD and their underlying mechanisms.

329 Heat exposure increased early voluntary RFD (*i.e.*, 0-100 ms; $+48.2\pm 62.7\%$), with no further
330 changes thereafter. The increase in voluntary RFD_{0-100} was greater than electrically-evoked
331 RFD ($+16.9\pm 32.8\%$), suggesting that neural effects occurred following heat exposure.
332 Previous studies reported an increase in voluntary RFD between 0 and 50 ms after contraction
333 onset after muscle heating (17, 18). In this early phase of RFD, the ability to produce force
334 rapidly, highly depends on motor unit recruitment and discharge rate (5). Elevated T_{musc} may
335 accelerate the opening and closing of voltage-gated sodium ions (Na^+) channels, thereby
336 decreasing potential amplitude, duration and area of action potential. These mechanisms could
337 lead to a faster depolarization onset and muscle fibre conduction velocity (41), resulting in
338 greater calcium ions (Ca^{2+}) release and re-uptake from the sarcoplasmic reticulum (26).
339 Alternatively, an increase in temperature is associated with a decrease in Ca^{2+} sensitivity (42).
340 However, Rodrigues et al. (18) recently suggested that passive heating may improve Ca^{2+}
341 sequestration kinetics, it is likely that this effect is different from the present findings obtained
342 after a whole body exposure in an environmental chamber. It is also well-established that
343 nerve conduction velocity increases with temperature (43). Neural drive is an important
344 determinant of rapid force production, especially in the early phase of contraction (4, 5).
345 Interestingly, this heat-induced effect on explosive force was concomitant to a trend for
346 increased fascicle shortening velocity ($+1.6 \pm 4.5 \text{ cm}\cdot\text{s}^{-1}$; Fig. 2C) over the initial 50 ms from
347 contraction onset. This finding may reflect a translation of improved neural drive to muscle
348 fascicle dynamics at the peripheral level. While $\text{RFD}_{0-X_{max}}$ was unchanged, the time period
349 required to achieve maximal RFD decreased with heat ($-19.3\pm 10.6\%$). This result strengthens
350 the crucial influence of temperature on the processes involved in the early phase of rapid force
351 production. Gordon et al. (19) demonstrated that early and middle phase of knee extensors
352 voluntary RFD were not affected by increased T_{core} elicited by whole body heat exposure (at
353 38.5 and 39.5°C). The difference with the present results may partly originate from the
354 different muscle groups investigated. Further studies are required to strongly conclude on the
355 effect of hyperthermia on plantar flexor muscles properties.

356 MVC peak force being an important determinant of voluntary RFD in the late phase of
357 contraction (4, 44), the trend to decreased MVC peak force in a hot environment may act as a
358 compensatory mechanism underlying the increase in RFD₀₋₁₀₀, leading to similar RFD
359 amplitude thereafter. From 100 to 200 ms, RFD was unchanged (Table 1). In the present
360 study, peak fascicle shortening velocity occurred in the first 100 ms from contraction onset in
361 both conditions. In addition, this parameter was unchanged during MVC performed in HOT
362 (Fig. 2C). These findings confirm the lack of influence of temperature on late RFD time-
363 course, which has been reported to be reflective of muscle mechanics and force-velocity
364 properties (6).

365

366 *Influence of warmer muscle on force-velocity relationships properties*

367 While joint F_0 , and V_0 were unchanged, increasing T_{core} during a ballistic contraction resulted
368 in a rightward shift of the joint force-velocity relationship, indicating a higher plantar flexor
369 force for a given joint velocity in a hot environment (Fig. 3A). A previous study reported a
370 higher wrist flexion angular velocity (45) in response to an increase in T_{musc} from ~22 to
371 ~37.5°C in *palmaris longus* and *flexor digitorum*, composed of a heterogeneous fibre type
372 composition (46, 47). Similarly, an increase in estimated T_{musc} from ~22 to ~37°C in *adductor*
373 *pollicis*, mainly composed by slow-twitch fibres (48), resulted in a higher angular velocity of
374 the thumb (27). Temperature is known to influence maximal shortening velocity to a greater
375 extent in slow-twitch compared to fast-twitch muscle fibres (12, 13). The balanced fibre type
376 composition of GM muscle (46) could thus partly explain the present increase in plantar
377 flexion angular velocity resulting from a T_{musc} increase. It is however difficult to determine to
378 what extent fibre type composition may account for temperature sensitivity, which has mainly
379 been addressed *in vitro*.

380 Heat did not alter fascicle peak force, maximal theoretical fascicle velocity or fascicle force-
381 velocity relationship of GM muscle (Fig. 3B). *In vitro*, a rise in ambient temperature has been
382 reported to increase the maximum muscle shortening velocity and force for a given velocity in
383 rodent and human muscle cell culture (12, 13). In the present study, the lack of a heat-induced
384 effect on the fascicle force-velocity relationship may originate from different amplitude of
385 T_{musc} changes in response to heat exposure (~34-37°C vs. ~10-35°C in the aforementioned
386 studies). In fact, the thermal dependency of maximum shortening velocity tends to decrease

387 with increasing temperature from ~6 to ~34°C (49). In the absence of additional information
388 beyond 34°C, *in vitro* data may not apply within the range of T_{musc} observed *in vivo*.

389

390 *Heat reduces soft tissues stiffness*

391 Heat exposure elicited a decrease in GM shear modulus ($-11.7 \pm 22.2\%$) compared with
392 thermoneutral condition. This temperature-induced effect may be attributed to changes in the
393 gap filament that have been shown to exhibit elastomer-like behaviour, particularly within the
394 more extensible region of the titin molecule (50). This alteration in muscle mechanical
395 properties may reduce the effectiveness of force transmission during active contractions,
396 thereby negatively impacting RFD amplitude.

397 Passive heat exposure also reduced active Achilles tendon stiffness measured during
398 contraction ($-12.3 \pm 19.3\%$). Previous studies reported increase passive maximal range of
399 motion without modifying muscle-tendon unit stiffness in response to local heat application
400 (51, 52). In the present study, heat exposure was systemic (*i.e.*, increase in ambient air
401 temperature), generating a larger physiological and biomechanical strain compared to
402 localized application [*e.g.*, hot water immersion, hot pack application (53)]. This may have
403 induced a deeper soft tissue heat exposure with putatively larger effects on tendon mechanical
404 properties.

405 An increase in elastic properties may reduce the efficiency of force transmission along the
406 muscle-tendon unit and the contribution of contractile properties in modulating force rapidly,
407 especially in the late phase of voluntary RFD (2, 7, 8). Therefore, the decreases in soft tissue
408 stiffness observed in warmer muscle could explain the unchanged, or even slightly reduced,
409 $\text{RFD}_{100-200}$ between conditions. The present results strongly suggest that alternative
410 mechanisms (*e.g.*, improved neural drive) may contribute to higher RFD amplitude.

411 Since passive tissue stiffness is involved in the production of angular velocity (28, 54), a
412 decrease in soft tissues' stiffness following heat exposure could explain the lack of effects of
413 heat on maximum joint velocity. Stiffness in soft tissues might also impact fascicle shortening
414 velocity, given that increasing the effective series elastic element stiffness showed a modest
415 reduction in the amplitude and velocity of active fascicle shortening of *lateral gastrocnemius*
416 and *soleus* muscle (55). However, initial L_F and fascicle dynamics were unchanged in the
417 present study (Fig. 2A-B, Table 1), despite more compliant soft tissues in the hot
418 environment. In turn, these heat-induced changes in muscle and tendon stiffness did not

419 impact initial LF, at 0° and 110°. Further, GM operated over fascicle lengths (5.6±0.5 cm)
420 that are centred on the plateau of the force-length relationship [*i.e.*, optimal lengths comprised
421 between 4.9±1.0 cm and 5.6±0.8 cm at 90°; (6)] in subjects with similar anthropometric data.
422 Given that RFD does not change over these muscle lengths (6), it is very unlikely that heat-
423 induced slight changes in operating fascicle length would have influenced RFD amplitude.
424 Although the starting position of the ankle was the same between conditions, reduced soft
425 tissue stiffness following heat exposure may reduce the energy restitution of the elastic
426 component during ballistic contractions. More compliant tissues could thus sustain larger
427 stresses, thereby shifting the amplitude of strain at which failure may occur (56, 57). Overall,
428 the use of heat to reduce muscle and tendon stiffness might thus potentially be valuable for
429 reducing the stress applied to the muscle during exercise and potentially reduce the risk of
430 strain injury.

431

432 ***Methodological considerations***

433 All measurements were done in the same testing session to allow data collection with an
434 ultrasound probe positioned at the same location. This experimental procedure strongly
435 improved the robustness of between-condition comparisons of muscle fascicle behaviour,
436 which represents a technical challenge in such environmental conditions. However, this
437 procedure was unable to randomize the temperature-dependent testing sequences. Previous
438 research reported that RFD does not change after a passive rest interval of 60 min (58). In line
439 with these data, our pilot experiments showed that all the measured parameters (*i.e.*, MVC
440 force, VA, electrically-evoked RFD, voluntary RFD over the different time periods, passive
441 shear modulus and active tendon stiffness) did not change over a time period (*i.e.*, ~127 min)
442 corresponding to the interval between pre- and post-tests included in the present experimental
443 design. Overall, these elements strongly suggest that the mechanical variables computed in
444 the present study were not affected by the order of the measurements, or the rest period,
445 between the two testing sessions.

446 One note to consider is that the force-velocity relationships were estimated from Hill's model,
447 fitted from maximal isometric force and three dynamic conditions performed upon very light
448 loading (at 0, 1.2 and 2.6 kg). Due to the logistical constraint associated with the use of an
449 isokinetic ergometer in an environmental chamber, we could not explore the *in vivo*
450 intermediate portion of the force-velocity relationship (28) in response to heat exposure.

451 Although not optimal, this approach included more conditions than a previous procedure (6)
452 and the maximal fascicle shortening velocity obtained in the thermoneutral condition using
453 our method ($32.7 \pm 6.2 \text{ cm.s}^{-1}$) was also similar to those obtained with nine tested loading
454 conditions [*i.e.*, $30.8 \pm 5.8 \text{ cm.s}^{-1}$ (28)]. Furthermore, the present inter-trial variability in
455 angular velocity was very low (*i.e.*, $1.96 \pm 1.48\%$; range: 0.01-5.95%). Overall, we are
456 confident about the reliability of this experimental procedure to investigate fascicle force-
457 velocity properties.

458 Voluntary activation was lower in a hot environment, suggesting acute neural adaptations in
459 response to heat. The current developments in high-density surface EMG electrodes and blind
460 source separation can be used to non-invasively extract the activity of a given pool of motor
461 units (59, 60). Using such an approach could represent a promising perspective built on the
462 current work and advance our understanding of the effects of heat on muscle force generation.
463 Another interesting perspective from this work would be to compare the impact of localised
464 calf heating on the neuromuscular properties presented in the present study to provide insights
465 into the role of central and peripheral neuromuscular adaptations to heat on muscle properties.

466

467 ***Conclusion***

468 This study explored for the first-time *in vivo* changes in muscle-tendon interactions elicited by
469 passive heat exposure. Increasing core and muscle temperatures tended to accelerate fascicle
470 shortening velocity during the 50 ms of voluntary explosive isometric contraction translating
471 into an improved rate of force development during the first 100 ms of a rapid contraction
472 onset. The fascicle force-velocity relationship and maximal fascicle shortening velocity were
473 not affected by heat while passive muscle and active tendon stiffness decreased, resulting in
474 an unchanged late and global phase of rate of force development. These findings evidence the
475 decoupled effects of heat on contractile and passive properties of the muscle-tendon unit, and
476 strongly encourage further investigations of the role of motor unit recruitment and discharge
477 rate found in the improved explosive force in response to heat exposure in humans.

478 **FIGURES LEGEND**

479 **Figure 1.** Experimental design and data collection (A). In hot (HOT) and control (CON)
480 conditions; MVC peak force, voluntary RFD (B), VA (C) and shear modulus of the GM were
481 assessed at 90° of ankle angle (D). Ramp contraction performed from 0 to 90% of MVC peak
482 force (E) assessed active Achille tendon stiffness. Fascicle dynamics were obtained from GM
483 ultrasound images acquired at 1000 Hz or 2000 Hz (A, F), to compute fascicle shortening
484 velocity (F). Joint and fascicle force-velocity relationships were built using ballistic
485 contractions at 0, 1.2, 2.6 kg and MVC peak force (G, H).

486 **Figure 2.** Fascicle shortening velocity during electrically-evoked (A) and MVC (B) and
487 fascicle force as a function of fascicle shortening velocity during RFD (C). Low and dark grey
488 areas represent SD, and the circles in panel C correspond to the values obtained at 50, 100,
489 150 and 200 ms from the contraction onset (n = 16 for A, n = 15 for B and n = 14 for C).

490 **Figure 3.** Joint (A) and fascicle force-velocity relationship (B). Filled area represents SD and
491 circles represent data obtained during MVC and during ballistic contractions performed
492 against 2.6, 1.2 and 0 kg (n = 13). *Significant effect of condition on joint velocity.

493 **Figure 4.** Shear modulus at rest in HOT and CON. The bold trace represents the mean change
494 of the whole sample (n = 15), box charts correspond to SD and dashed traces connect
495 individual values. *Significant difference between HOT and CON.

496 **Figure 5.** Force ± SD tendon force-elongation relationship (A) and active tendon stiffness
497 (B). The bold trace represents the mean change of tendon stiffness (n = 11), box charts
498 correspond to SD and dashed traces connect individual values. *Significant difference
499 between HOT and CON.

500 **ADDITIONAL INFORMATION**

501

502 **Data availability statement**

503 Subjects' consent did not include data availability in an open-access repository. Therefore, the
504 present data are available on request.

505

506 **Competing interest**

507 None of the authors has any conflicts of interest to declare.

508

509 **Author contributions**

510 The experiments were performed in the Laboratory Sport, Expertise and Performance (EA
511 7370), French Institute of Sport (INSEP), Paris, France. A.M., S.R., F.B. and G.G. conceived
512 and designed the research. All authors acquired the data. A.M., R.H., Y.D. and G.G. analysed
513 the data. A.M., S.R., F.B., and G.G. interpreted the results. A.M., S.R., F.B. and G.G.
514 prepared the figures. A.M. drafted the manuscript; A.M., S.R., F.B. and G.G. edited and
515 revised the manuscript. All authors have approved the final version of the submitted
516 manuscript for publication and are accountable for all aspects of the work. All persons
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519

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528

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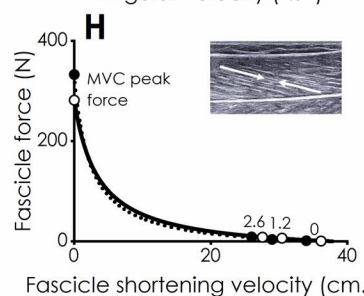
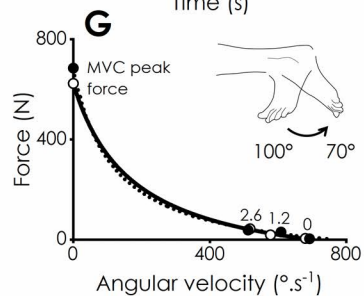
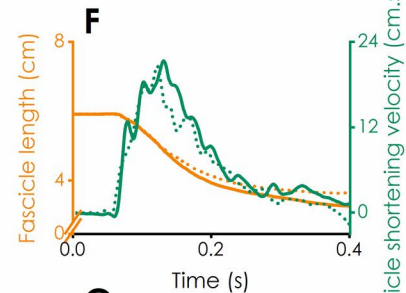
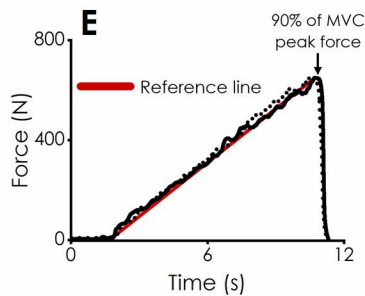
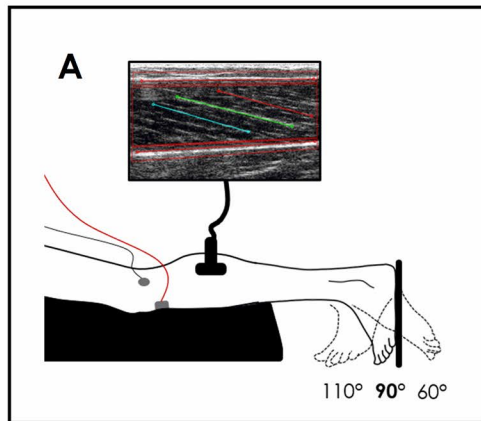
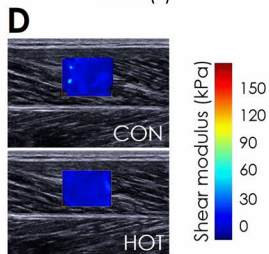
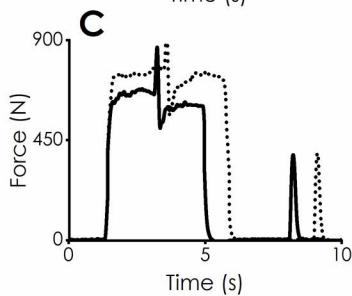
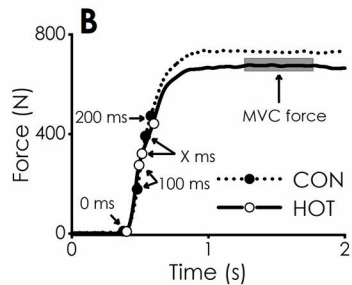
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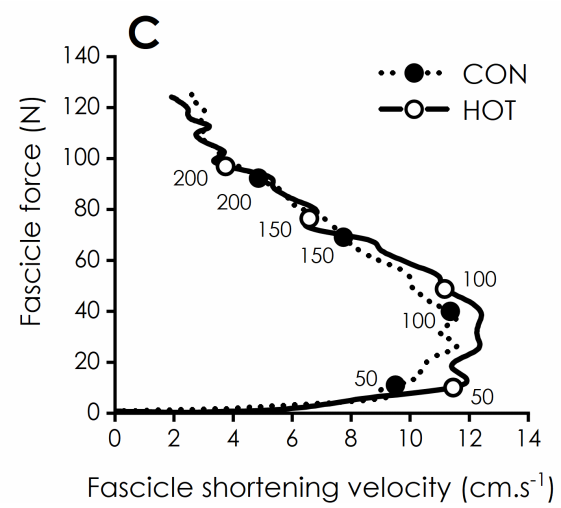
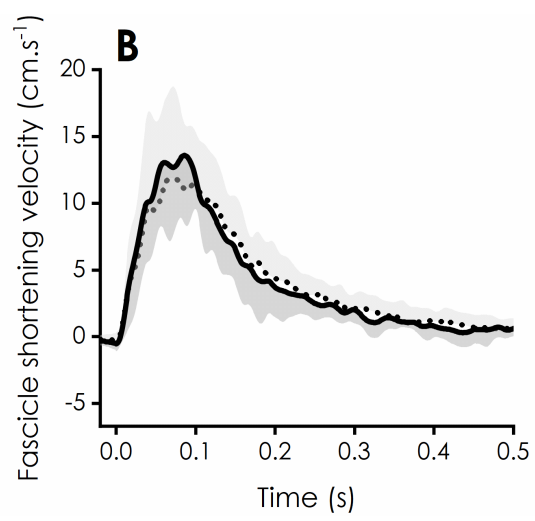
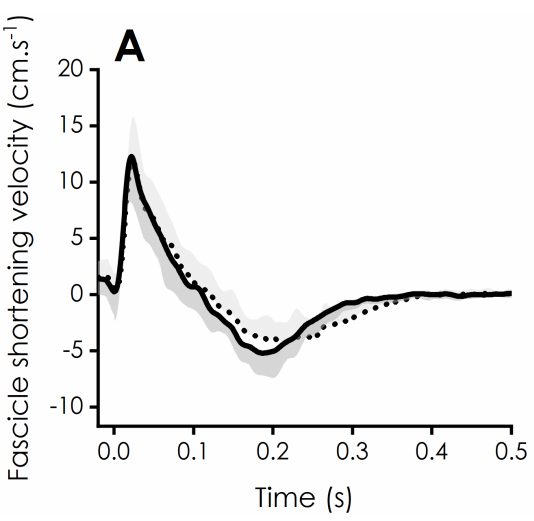
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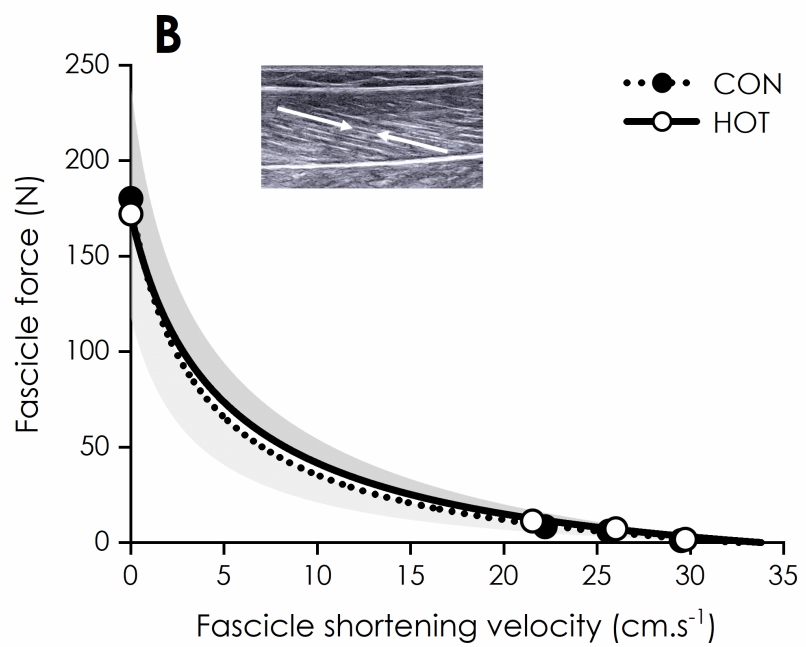
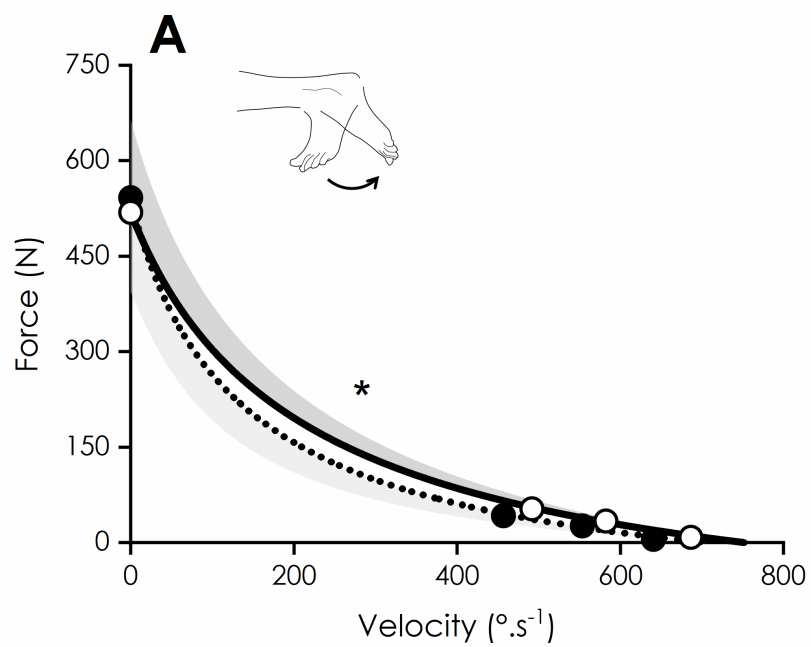
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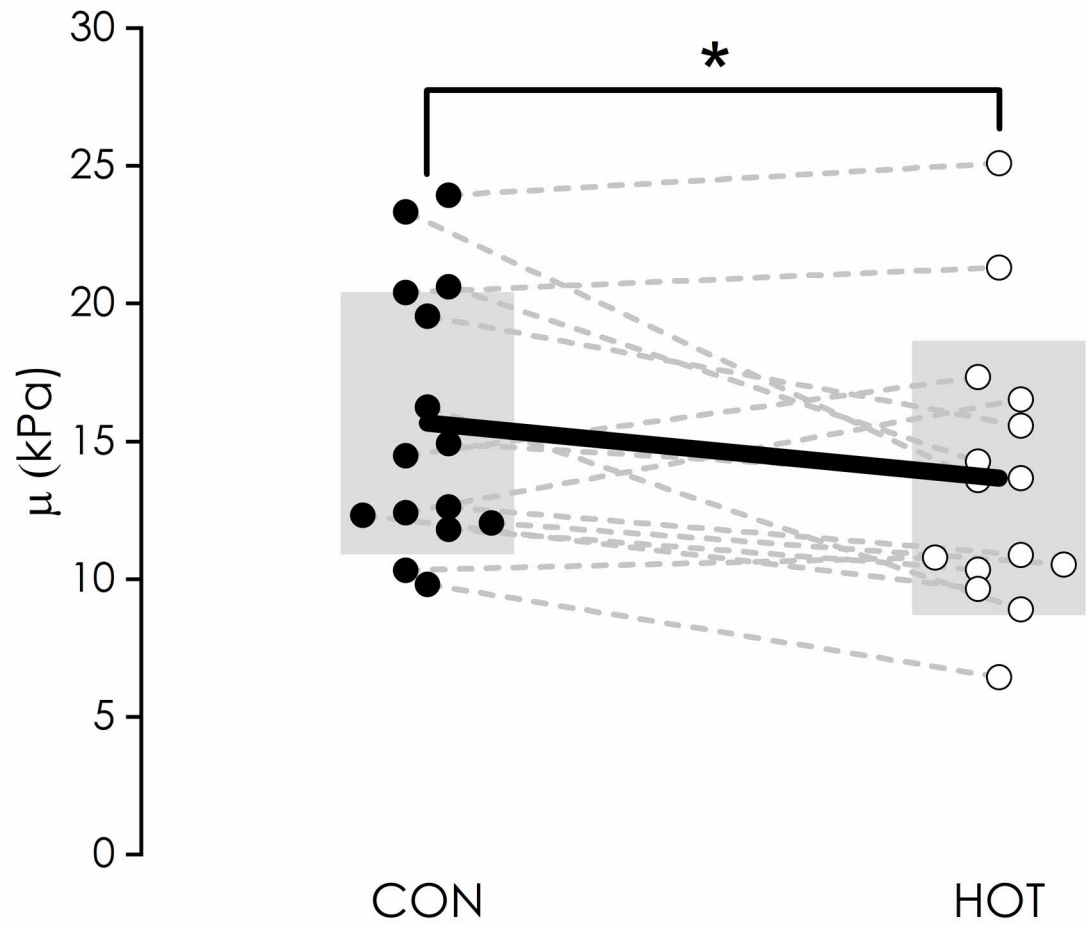
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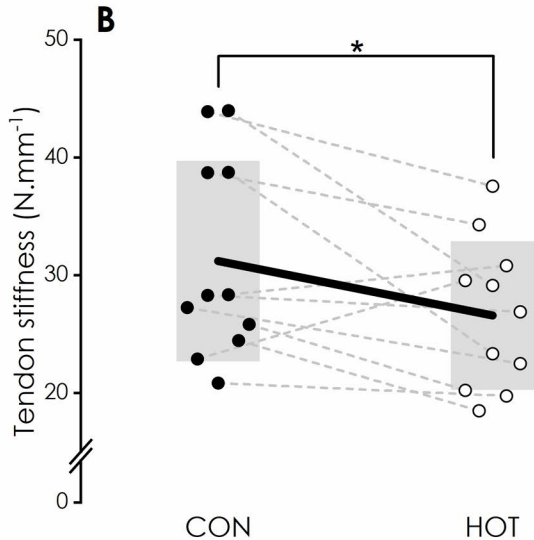
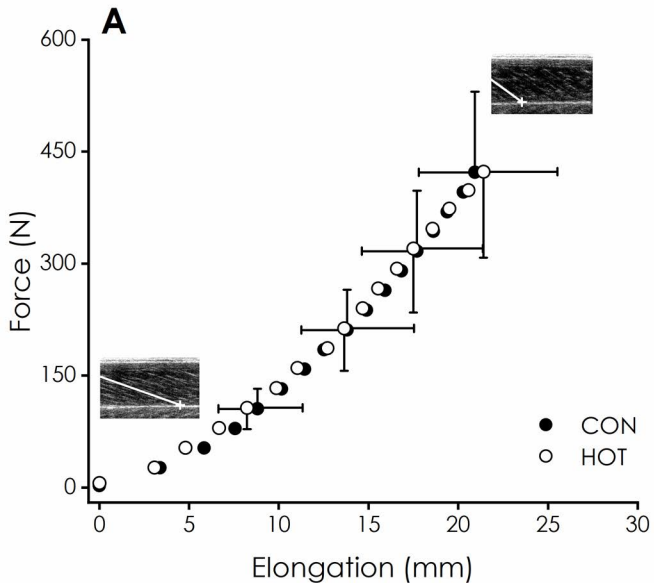


Table 1. Mechanical parameters and fascicle dynamics in hot (HOT) and control (CON) conditions.

	HOT	CON	n
<i>Mechanical parameters</i>			
MVC force (N)	531 ± 138	558 ± 128	15
VA (%)	93 ± 11*	97 ± 5	13
Electrically-evoked RFD (N.ms ⁻¹)	0.65 ± 0.11*	0.56 ± 0.12	16
RFD ₀₋₁₀₀ (N.s ⁻¹)	1397 ± 439*	1097 ± 554	15
RFD ₀₋₂₀₀ (N.s ⁻¹)	1560 ± 414	1526 ± 524	15
RFD ₁₀₀₋₂₀₀ (N.s ⁻¹)	1750 ± 607	1949 ± 620	15
RFD _{0-Xmax} (N.s ⁻¹)	1729 ± 488	1600 ± 563	15
Duration of RFD _{0-Xmax} (ms)	157 ± 26***	198 ± 42	15
V ₀ joint (°.s ⁻¹)	752 ± 130	707 ± 109	13
F ₀ joint (N)	519 ± 145	542 ± 148	13
<i>Fascicle behaviour</i>			
Initial L _F at 90° (cm)	5.61 ± 0.61	5.60 ± 0.68	16
Initial L _F at 110° (cm)	6.27 ± 0.63	6.30 ± 0.59	14
Peak V _F electrically-evoked (cm.s ⁻¹)	14.0 ± 2.1	13.6 ± 2.0	16
Peak V _F voluntary (cm.s ⁻¹)	15.8 ± 4.9	14.4 ± 5.3	14
Time to peak V _F voluntary (ms)	72.4 ± 17.8	88.6 ± 29.6	14
V ₀ fascicle (cm.s ⁻¹)	33.8 ± 8.5	32.7 ± 6.2	13
F ₀ fascicle (N)	172.1 ± 67.0	180.3 ± 62.5	13

Values are presented as mean ± SD. MVC, maximal voluntary contraction; VA, voluntary activation; RFD, rate of force development; RFD₀₋₁₀₀, rate of force development between MVC onset and 100 ms; RFD₀₋₂₀₀, rate of force development between MVC onset and 200 ms; RFD₁₀₀₋₂₀₀, rate of force development between 100 and 200 ms after MVC onset; RFD_{0-Xmax}, RFD from MVC onset to the maximal RFD; V₀, maximal theoretical velocity (joint and fascicle level); F₀, maximal theoretical force and fascicle force; V_F, fascicle shortening velocity; n, sample size, which has often been reduced due to missing data.

*Significant difference between HOT and CON, $P < 0.05$; ***, $P < 0.001$.