

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

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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			
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25 26				
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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  $34.0\pm1.1^{\circ}$ C) and passive heat exposure (HOT:  $47.4\pm1.8^{\circ}$ C, core temperature  $38.4\pm0.3^{\circ}$ C, 36 muscle temperature  $37.0\pm0.8$ °C) conditions. Maximal voluntary force changes did not reach 37 statistical significance (-5.0 $\pm$ 11.3%, P = 0.052) while voluntary activation significantly decreased (-4.6 $\pm$ 8.7%, P = 0.038) in HOT. Heat exposure significantly increased voluntary 38 RFD before 100 ms from contraction onset (+48.2 $\pm$ 62.7%; P = 0.013), without further 39 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 $\pm$ 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  $(P \le 0.030)$ . 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<sub>core</sub>), with its repercussion on 67 muscle temperature  $(T_{musc})$ , 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<sub>core</sub> or T<sub>musc</sub> 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<sub>musc</sub> 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 cycling (21). Although increasing  $T_{musc}$  has been reported to alter calcium ions (Ca<sup>2+</sup>) 74 sensitivity (22), an increase in T<sub>musc</sub> tends to improve muscle function, which has not been 75 attributed to its putative influence on  $Ca^{2+}$  sensitivity of the acto-myosin complex (23). This 76 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<sub>core</sub> and T<sub>musc</sub> 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*

Subjects were informed about the nature, aims and risks associated with the experimental procedure before giving their written consent. This study was approved by the Sud-Ouest et Outre-mer III ethics committee (reference: 3849) and conformed to the standards of the 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:  $69.8\pm9.9$ , kg, practicing  $5.5\pm3.2$  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

Two to four days after a familiarisation session, subjects underwent two identical testing sequences in a single session: the first sequence was in thermoneutral condition (CON;  $25.8\pm1.8^{\circ}$ C,  $33.6\pm8.6\%$  relative humidity [RH]); the second in a hot ambient condition (HOT;  $47.4\pm1.8^{\circ}$ C,  $18.5\pm4.7\%$  RH, after  $127\pm33$  min of heat exposure). The effect of heat was assessed on GM muscle-tendon properties and interactions (muscle fascicle dynamics during electrically-evoked and voluntary isometric RFD, joint and fascicle force-velocity relationships, muscle and tendon stiffness).

130

## 131 Equipment and procedure

132 Subjects lied prone with extended knees  $(0^{\circ})$ , their right ankle flexed at  $90^{\circ}$  (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° for dynamic contractions (i.e., ballistic contractions) or was firmly immobilized at 90° for 135 136 isometric contractions. The footplate was connected to a force sensor fixed below the plate at 137 the level of the 3<sup>rd</sup> 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 between the popliteal fossa and the centre of the lateral malleolus. The probe location was
considered appropriate when fascicles and aponeuroses were clearly visible across the image
(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  $\mu$ 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

flexion on the Bio2M ergometer, equipped with an angle sensor to provide ankle angle measurements (30), as previously described [Fig. 1A (6, 28)]. Three conditions (1 min rest) were tested in a randomised order: with 0 (five trials), 1.2 and 2.6 kg (three trials) attached to the pedal.

*Resting shear modulus.* The ultrasound scanner was used in shear wave elastography mode
(musculoskeletal preset) to measure (3 measurements per condition) the shear modulus (*i.e.*,
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<sub>core</sub> 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<sub>skin</sub>) as:  $0.3 \times \text{arm} + 0.3 \times \text{chest} + 0.2 \times \text{thigh} + 0.2 \times \text{shin}$ temperature (33). T<sub>musc</sub> of the contralateral GM was measured immediately before each 177 178 testing sequence, in a subsample of six subjects. T<sub>musc</sub> 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 (Xylocaïne, 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

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

190 Isometric contraction. The mechanical response to the five electrically-evoked stimulations was low-pass filtered (20 Hz, zero lag 3<sup>rd</sup> order Butterworth), analysed and averaged to 191 192 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  $\sim 1$  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 Hz, zero-lag 4<sup>th</sup> order Butterworth). The two trials resulting in the highest RFD from 197 198 contraction onset to 200 ms (RFD<sub>0-200</sub>) 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<sub>0-100</sub>), 0 to 200 ms (RFD<sub>0-200</sub>) and 100 to 200 ms (RFD<sub>100-200</sub>, [Fig. 1B]). For each 201 overlapping time interval from force onset, force was divided by the time to calculate RFD<sub>0</sub> to 202 'X' ms, to identify the maximal RFD (RFD<sub>0-Xmax</sub>; Fig. 1B). RFD<sub>0-Xmax</sub> 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 - superimposed twitch / potentiated
207 twitch) × 100. The highest VA value obtained was selected.

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

212 Joint and fascicle force-velocity relationship. Angular velocity was computed as the derivative of low-pass filtered (150 Hz, zero lag 3<sup>rd</sup> order Butterworth) ankle angle over time 213 214 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):

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

where F is force, V is velocity, a and b are coefficients, determined for each subject, using a fit with  $F_0$ , force and velocity values obtained at 0, 1.2 and 2.6 kg. The maximal theoretical velocity (V<sub>0</sub>) 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 ( $\mu$ ) 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. *Tendon stiffness.* The trial resulting in the lowest dispersion of force signal according to the targeted force during ramp contraction was considered for analysis (Fig. 1E). Displacement of the insertion of GM fascicle on the deep aponeurosis was manually measured (Image J, National Institutes of Health, Bethesda, USA), every 5% of MVC force, on the image (sampling frequency: 100 Hz) corresponding to targeted force level. The active stiffness of tendon corresponded to the ratio between the change in force and the displacement of the 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<sub>core</sub>, T<sub>skin</sub> and T<sub>muse</sub>, MVC force, VA, 243 electrically-evoked RFD, GM shear modulus and tendon active stiffness. RFD<sub>0-200</sub>, RFD<sub>0-Xmax</sub>, 244 the duration of RFD<sub>0-Xmax</sub>, 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<sub>0</sub>, joint and fascicle F<sub>0</sub> 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<sub>F</sub> 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<sub>F</sub> and fascicle force were tested using two-way ANOVAs (condition  $\times$  load) with repeated measures. When the 253 254 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  $(\eta^2_p, \text{ with } \eta^2_p \ge 0.06 \text{ representing a moderate effect and } \eta^2_p \ge 0.14 \text{ a large effect}).$ 258 Statistical significance was set at P < 0.05.

259

#### 260 RESULTS

261

#### 262 Thermoregulatory responses

Average  $T_{core}$ ,  $T_{skin}$  and  $T_{musc}$  were significantly higher in HOT than CON (38.4±0.3°C, 38.8±0.4°C and 37.0±0.8°C in HOT *vs.* 37.0±0.3°C, 34.7±0.7°C and 34.0±1.1°C in CON, respectively; all P < 0.001,  $\eta^2_p \ge 0.749$ ). There was no significant difference in body mass 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,  $\eta_p^2$ = 0.176; Table 1). VA was 4.6±8.7 % lower in HOT than CON (P = 0.038,  $\eta_p^2 = 0.239$ ; Table 270 271 1). Electrically-evoked RFD was faster in HOT than CON (+16.9±32.8%, P = 0.029,  $\eta_p^2 =$ 272 0.149; Table 1). RFD<sub>0-200</sub> and RFD<sub>0-Xmax</sub> were not significantly different between the two 273 conditions (all  $P \ge 0.238$ ,  $\eta_{P}^2 \le 0.016$ ). 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  $\eta_p^2 = 0.539$ ) and a condition × time period interaction (P < 0.001,  $\eta_p^2 = 0.581$ ) were observed 276 on RFD during the time periods 0-100 and 100-200 ms. Post-hoc showed that RFD<sub>0-100</sub> was 277 higher in HOT (+48.2±62.7%; P = 0.013,  $\eta_p^2 = 0.088$ ), while RFD<sub>100-200</sub> remained unchanged 278 compared to CON (P = 0.156,  $\eta_p^2 = 0.027$ ).

279

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

Initial L<sub>F</sub> at which fascicle contracts did not change between 0° and 110° of plantar flexion 281 282 (all  $P \ge 0.577$ ,  $\eta_p^2 \le 0.024$ ; Table 1). No effect of condition on peak V<sub>F</sub> in electrically-evoked 283 and voluntary isometric explosive contractions nor in time to peak shortening velocity were 284 found during RFD evaluation (all  $P \ge 0.105$ ,  $\eta_p^2 \le 0.105$ ; Table 1, Fig. 2). V<sub>F</sub> increased (time 285 effect: P < 0.001,  $\eta_p^2 = 0.646$ ) between 0 and 100 ms and then decreased until 200 ms, with 286 neither a significant effect of condition nor time × condition interaction (all  $P \ge 0.092$ ,  $\eta_p^2 \le$ 287 0.172; Fig. 2C). Two-way ANOVA applied to fascicle force revealed an effect of time ( $P \le 1$ 288 0.001,  $\eta_p^2 = 0.880$ ), which increased from 0 to 200 ms, with neither main effect of condition 289 nor time × condition interaction (all  $P \ge 0.074$ ,  $\eta^2_p \le 0.285$ ; 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 size (P = 0.004,  $\eta_p^2 = 0.513$ ) on data points, showed a rightward shift of the force-velocity 294 295 relationship, indicative of a higher force for a given velocity in HOT (+7.1±6.6%). There was 296 no condition × 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,  $\eta_p^2 = 0.934$ ) on fascicle shortening velocity, which decreased 298 with increasing load, without any effect of condition or condition  $\times$  load interaction (all  $P \ge$ 299 0.244,  $\eta_{p}^{2} \leq 0.111$ ; Fig. 3B). Joint V<sub>0</sub> tended to increase (P = 0.065,  $\eta_{p}^{2} = 0.036$ ; Table 1) and fascicle V<sub>0</sub> remained unchanged across conditions (P = 0.430,  $\eta^2_p = 0.006$ ; Table 1). A 300 301 significant main effect of load on plantar flexion and fascicle force was observed (all P <302 0.001,  $\eta^2_p \ge 0.892$ ), which increased with increasing load, without further effect (all  $P \ge 0.001$ ) 0.142,  $\eta_p^2 \le 0.169$ ; Fig. 3). No difference in plantar flexor and fascicle F<sub>0</sub> was found between 303 304 HOT and CON (all  $P \ge 0.266$ ,  $\eta_p^2 \le 0.006$ ; Table 1).

305

## 306 Muscle and tendon stiffness

Shear modulus was significantly lower in HOT than CON (-11.7±22.2%; P = 0.030,  $\eta^2_p = 0.044$ ; Fig. 4). Active Achilles tendon stiffness was lower in HOT than CON (-12.7±19.5%; P = 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<sub>core</sub> and T<sub>musc</sub> 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

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

329 Heat exposure increased early voluntary RFD (*i.e.*, 0-100 ms;  $+48.2\pm62.7\%$ ), with no further 330 changes thereafter. The increase in voluntary  $RFD_{0-100}$  was greater than electrically-evoked 331 RFD (+16.9±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<sup>+</sup>) 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 greater calcium ions  $(Ca^{2+})$  release and re-uptake from the sarcoplasmic reticulum (26). 338 Alternatively, an increase in temperature is associated with a decrease in  $Ca^{2+}$  sensitivity (42). 339 However, Rodrigues et al. (18) recently suggested that passive heating may improve Ca<sup>2+</sup> 340 341 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 increased fascicle shortening velocity (+1.6  $\pm$  4.5 cm.s<sup>-1</sup>; Fig. 2C) over the initial 50 ms from 346 347 contraction onset. This finding may reflect a translation of improved neural drive to muscle 348 fascicle dynamics at the peripheral level. While RFD<sub>0-Xmax</sub> 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 voluntary RFD were not affected by increased T<sub>core</sub> elicited by whole body heat exposure (at 352 353 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 RFD<sub>0-100</sub>, 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 higher wrist flexion angular velocity (45) in response to an increase in T<sub>musc</sub> from ~22 to 370 371  $\sim$ 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<sub>musc</sub> 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.

Heat did not alter fascicle peak force, maximal theoretical fascicle velocity or fascicle forcevelocity relationship of GM muscle (Fig. 3B). *In vitro*, a rise in ambient temperature has been reported to increase the maximum muscle shortening velocity and force for a given velocity in rodent and human muscle cell culture (12, 13). In the present study, the lack of a heat-induced effect on the fascicle force-velocity relationship may originate from different amplitude of  $T_{musc}$  changes in response to heat exposure (~34-37°C *vs.* ~10-35°C in the aforementioned studies). In fact, the thermal dependency of maximum shortening velocity tends to decrease 387 with increasing temperature from  $\sim 6$  to  $\sim 34^{\circ}$ 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*

Heat exposure elicited a decrease in GM shear modulus  $(-11.7\pm22.2\%)$  compared with thermoneutral condition. This temperature-induced effect may be attributed to changes in the gap filament that have been shown to exhibit elastomer-like behaviour, particularly within the more extensible region of the titin molecule (50). This alteration in muscle mechanical properties may reduce the effectiveness of force transmission during active contractions, thereby negatively impacting RFD amplitude.

397 Passive heat exposure also reduced active Achilles tendon stiffness measured during 398 contraction (-12.3±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 RFD<sub>100-200</sub> 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

impact initial LF, at 0° and 110°. Further, GM operated over fascicle lengths (5.6±0.5 cm) 419 420 that are centred on the plateau of the force-length relationship *[i.e.*, optimal lengths comprised 421 between  $4.9\pm1.0$  cm and  $5.6\pm0.8$  cm at  $90^{\circ}$ ; (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.*,  $\sim 127$  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. Although not optimal, this approach included more conditions than a previous procedure (6) and the maximal fascicle shortening velocity obtained in the thermoneutral condition using our method  $(32.7\pm6.2 \text{ cm.s}^{-1})$  was also similar to those obtained with nine tested loading conditions [*i.e.*,  $30.8\pm5.8 \text{ cm.s}^{-1}$  (28)]. Furthermore, the present inter-trial variability in angular velocity was very low (*i.e.*,  $1.96\pm1.48\%$ ; range: 0.01-5.95%). Overall, we are confident about the reliability of this experimental procedure to investigate fascicle forcevelocity 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

**Figure 1.** Experimental design and data collection (A). In hot (HOT) and control (CON) conditions; MVC peak force, voluntary RFD (B), VA (C) and shear modulus of the GM were assessed at 90° of ankle angle (D). Ramp contraction performed from 0 to 90% of MVC peak force (E) assessed active Achille tendon stiffness. Fascicle dynamics were obtained from GM ultrasound images acquired at 1000 Hz or 2000 Hz (A, F), to compute fascicle shortening velocity (F). Joint and fascicle force-velocity relationships were built using ballistic 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  $\pm$  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 517 designated as authors qualify for authorship, and all those who qualify for authorship are 518 listed.

519

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528

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	НОТ	CON	n
Mechanical parameters			
MVC force (N)	$531\pm138$	$558\pm128$	15
VA (%)	$93 \pm 11*$	$97\pm5$	13
Electrically-evoked RFD (N.ms <sup>-1</sup> )	$0.65\pm0.11*$	$0.56\pm0.12$	16
$RFD_{0-100} (N.s^{-1})$	$1397\pm439\texttt{*}$	$1097\pm554$	15
$ m RFD_{0-200}(N.s^{-1})$	$1560\pm414$	$1526\pm524$	15
$ m RFD_{100-200}(N.s^{-1})$	$1750\pm607$	$1949\pm620$	15
$RFD_{0-Xmax}(N.s^{-1})$	$1729\pm488$	$1600\pm563$	15
Duration of RFD <sub>0-Xmax</sub> (ms)	$157\pm26^{\boldsymbol{\ast\ast\ast\ast}}$	$198\pm42$	15
$V_0 \text{ joint } (\circ.s^{-1})$	$752\pm130$	$707\pm109$	13
F <sub>0</sub> joint (N)	$519\pm145$	$542\pm148$	13
Fascicle behaviour			
Initial L <sub>F</sub> at 90° (cm)	$5.61\pm0.61$	$5.60\pm0.68$	16
Initial L <sub>F</sub> at 110° (cm)	$6.27\pm0.63$	$6.30\pm0.59$	14
Peak V <sub>F</sub> electrically-evoked (cm.s <sup>-1</sup> )	$14.0\pm2.1$	$13.6\pm2.0$	16
Peak V <sub>F</sub> voluntary (cm.s <sup>-1</sup> )	$15.8\pm4.9$	$14.4\pm5.3$	14
Time to peak V <sub>F</sub> voluntary (ms)	$72.4 \pm 17.8$	$88.6\pm29.6$	14
$V_0$ fascicle (cm.s <sup>-1</sup> )	$33.8 \pm 8.5$	$32.7\pm6.2$	13
F <sub>0</sub> fascicle (N)	$172.1\pm67.0$	$180.3\pm62.5$	13

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

Values are presented as mean  $\pm$  SD. MVC, maximal voluntary contraction; VA, voluntary activation; RFD, rate of force development; RFD<sub>0-100</sub>, rate of force development between MVC onset and 100 ms; RFD<sub>0-200</sub>, rate of force development between MVC onset and 200 ms; RFD<sub>100-200</sub>, rate of force development between 100 and 200 ms after MVC onset; RFD<sub>0-Xmax</sub>, RFD from MVC onset to the maximal RFD; V<sub>0</sub>, maximal theoretical velocity (joint and fascicle level); F<sub>0</sub>, maximal theoretical force and fascicle force; V<sub>F</sub>, 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.