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1 **Influence of joint angle on muscle fascicle dynamics and rate of torque**  
2 **development during isometric explosive contractions**

3

4 **Running title: Muscle-tendon interactions and explosive strength**

5

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26

27 **Keywords:** explosive strength; muscle-tendon interactions; ultrafast ultrasound; muscle  
28 activation; force-velocity properties

29 **ABSTRACT**

30 This study investigated how joint angle influences fascicle shortening dynamics of  
31 gastrocnemius medialis (GM) during explosive contractions, and the resulting impact on rate  
32 of torque development (RTD). Sixteen participants performed six sets of five maximal  
33 explosive voluntary isometric plantar flexions at  $-20^\circ$ ,  $-10^\circ$ ,  $0^\circ$  (neutral position),  $10^\circ$ ,  $20^\circ$  and  
34  $30^\circ$  of ankle angle, and five no-load ballistic plantar flexions. RTD assessed over all time  
35 windows (from 0 to 200 ms) was significantly lower in extreme plantar flexed ( $\geq 20^\circ$ ) and  
36 dorsiflexed ( $-20^\circ$ ) positions compared to  $-10^\circ$ ,  $0^\circ$  ( $475 \pm 105 \text{ Nm}\cdot\text{s}^{-1}$ ) and  $10^\circ$ . At these neutral  
37 positions, RTD was maximal and muscle fascicles mainly operated over the plateau of the  
38 force-length relationship. At  $0^\circ$ , fascicle shortening velocity peaked at  $9.26 \pm 2.85 \text{ cm}\cdot\text{s}^{-1}$  (i.e.,  
39 28.2% of maximal shortening velocity measured during no-load ballistic condition). At 112  
40 ms after RTD onset, fascicle force reached  $208 \pm 78 \text{ N}$  (i.e., 85.6% of the theoretical  
41 maximum force at the corresponding shortening velocity) and was thereafter comprised  
42 within the 95% confidence interval of the force-velocity curve. This clearly indicates that  
43 muscle force reached the maximal force that accounts for the fascicle shortening velocity.  
44 These findings suggest that the dynamic behavior of muscle fascicles, and the associated  
45 fascicle shortening velocity, may influence the rapid force-generating capacity mainly from  
46 100 ms of RTD onset. The present study provides important information to better understand  
47 the determinants of human muscle performance during explosive tasks.

48

49 **New & Noteworthy**

- 50       • Ankle angle influences the operating muscle fascicle lengths of gastrocnemius  
51       medialis, and the rate of torque development during explosive isometric plantar  
52       flexions.
- 53       • The rate of torque development peaks in neutral angles where muscle fascicles shorten  
54       over the plateau of the force-length relationship.
- 55       • When fascicles operate over the plateau of the force-length relationship (neutral ankle  
56       positions), the force-velocity properties represent a limiting factor for the rapid force-  
57       generating capacity from 100 ms after the onset of explosive contractions.

## 58 INTRODUCTION

59 The ability of the human skeletal muscle to achieve maximal force production as  
60 quickly as possible is important for actions that involve explosive tasks or rapid adjustments  
61 in postural balance such as those encountered in sport-specific movement (1, 8, 37, 43). This  
62 capacity to produce explosive force is classically evaluated through the rate of torque  
63 development (RTD) achieved during a maximal voluntary isometric contraction (1, 30). RTD  
64 can be measured using a relatively simple setting (i.e., a force or torque sensor) as the  
65 variations of torque (or force) over various periods of time from the onset of torque (0 ms) to  
66 50-200 ms, (19, 44). Thus, RTD is widely used as a performance index in various populations  
67 (i.e., athletes, elderly, patients) and sports where the amount of time available for an increase  
68 in force is limited (e.g., athletics, team sports, combat sports) (37, 43, 49).

69 It is well established that RTD depends primarily on the neural system's ability to  
70 maximally and rapidly activate the available pool of motor units (15, 19). In particular, it has  
71 been recently shown that the motor neuron recruitment speed and the maximal rate at which  
72 motor neurons discharge action potentials in the initial phase of the contraction (0-50 ms)  
73 dictate the variability in RTD (16). Alternatively, additional factors, such as muscle fiber-type  
74 composition, architecture, muscle and tendon elastic properties have been suggested to  
75 influence RTD (5, 37, 52, 53). In a recent study, Massey et al. (40) reported small correlations  
76 between muscle-tendon unit relative stiffness and voluntary RTD, but no correlation with  
77 absolute and relative tendon stiffness. This demonstrated that other factors than tissue  
78 stiffness would influence RTD and confirmed the need for further experimental data to better  
79 understand the roles of these variables during voluntary explosive contraction (22, 37, 40).

80 One possible explanation of the difficulty to infer the influence of tendon mechanical  
81 properties on RTD is the fact that muscle and tendon inherently interact during contractions *in*  
82 *vivo*. Using ultrasound, several studies demonstrated that muscle fascicle behaviour can be

83 largely uncoupled from that of the behaviour of the muscle-tendon unit during various human  
84 movements thanks to the compliance of tendinous tissues (12, 20). As a basic illustration of  
85 this process, muscle fascicles were reported to shorten while tendinous tissues lengthen during  
86 isometric contractions of increasing intensity (29). This demonstrates that a non-isometric  
87 contraction is performed at the fibre level, while the muscle-tendon length remains constant  
88 (21, 29). These dynamic interactions between muscle and tendon may thus modify the range  
89 of lengths over which muscle fibres operate. A recent study nicely demonstrated that absolute  
90 knee extensor RTD was influenced by joint angle due to both alterations in neuromuscular  
91 activation and changes in contractile response [i.e., twitch and octet evoked responses; (34)].  
92 As recently shown for electrically-evoked contractions, the change in joint angle also  
93 influences the initial fascicle length (41). In addition, joint angle could influence the apparent  
94 stiffness of series elastic tissues and the interplay between these tissues and fascicles.  
95 However, to our knowledge, no study has investigated fascicle dynamics (i.e., length changes)  
96 during explosive isometric voluntary contractions. Such measurements may contribute to  
97 determine the changes in operating fascicle lengths involved over time during voluntary  
98 explosive contractions. Their comparison with force-length and force-velocity relationships  
99 could thereby give very important information about their influence on RFD performance  
100 (17). In addition, the influence of joint angle was not addressed for plantar flexors, while the  
101 long Achilles tendon plays an important role (23, 25). If confirmed, such hypothesis may  
102 contribute to bring new insights into the significant influence of joint angle on maximal and  
103 explosive strength (14, 47).

104         The present study aimed to examine the behaviour of *gastrocnemius medialis* (GM)  
105 muscle fascicle during a voluntary RTD test. Maximal explosive isometric contractions of  
106 plantar flexor muscles were performed at various ankle positions (from -20° in dorsiflexion to  
107 30° of plantar flexion). Given the significant changes in fascicle length reported during

108 isometric contractions in humans (21, 29, 45), our objectives were twofold: (i) to determine  
109 the influence of ankle angle on the fascicle length shortening and RTD achieved during an  
110 explosive contraction; (ii) to investigate how this dynamic behaviour of muscle fascicle and  
111 its shortening velocity may influence RTD (by referring to the force-velocity relationship) in a  
112 joint configuration that elicits fascicle shortening over the plateau of the force-length  
113 relationship.

114

## 115 **METHODS**

### 116 *Participants*

117 Ten males and six females (age:  $23.2 \pm 2.7$  years, height:  $175.3 \pm 6.4$  cm, body mass:  $70.2 \pm$   
118  $12.6$  kg), with no history of ankle disorder or injury, participated in this study. All volunteers  
119 were informed about the nature, aims and risks associated with the experimental procedure  
120 before giving their written consent to participate. The study was approved by the local ethics  
121 committee (2017-A03117-46) and conformed to the standards of the Declaration of Helsinki.

122

### 123 *Experimental design*

124 All participants attended one familiarization session and one testing session a few days later.  
125 During these sessions, after a 10-minute standardized warm-up, participants performed 5  
126 ballistic plantar flexions with no external load (load = 0 kg) on a specific ergometer composed  
127 of a specific rotational footplate (Bio2M, Compiègne, France). Participants then performed  
128 six sets of five repetitions of explosive voluntary isometric contractions to reach maximal  
129 force of the plantar flexor muscles in a randomized order at various ankle angles (from  $-20^\circ$  in  
130 dorsiflexion to  $30^\circ$  in plantar flexion) on an Eracles-system mechatronic ergometer (Eracles-  
131 Technology, Compiègne, France; Fig. 1). RTD and MVC peak torque were assessed on the  
132 same repetitions to avoid fatigue occurrence. We performed pilot analyses that showed no

133 significant difference between these metrics assessed during the same contractions when  
134 sufficient time was allowed to the participants were instructed to push “as fast and as hard as  
135 possible” with sufficient time (5 s) to then achieve MVC torque plateau (37). We performed  
136 pilot analyses that showed no significant difference in peak MCV torque between trials  
137 performed in this condition and in a conventional MVC measurement. Therefore, we think  
138 that this issue marginally influenced our results. At the end of the protocol, two passive  
139 dorsiflexion cycles were performed on the same ergometer at  $1^{\circ}\cdot\text{s}^{-1}$  to estimate triceps surae  
140 moment arm (see moment arm section) and to subtract the passive torque to the raw torque in  
141 order to obtain the active torque to build the active force-length relationship (see data  
142 processing). During each explosive contraction performed at each ankle angle (Fig.1),  
143 mechanical parameters (i.e., torque, displacement, velocity), muscle fascicle length and  
144 velocity of GM, surface electromyography (EMG) activity of *gastrocnemius lateralis* (GL),  
145 *soleus* (SOL) and *tibialis anterior* (TA) were simultaneously recorded.

146

#### 147 ***Equipment and procedure***

148 *Voluntary isometric explosive contractions.* Voluntary isometric explosive contractions were  
149 performed on an Eracles-system mechatronic ergometer (Eracles-Technology, Compiègne,  
150 France) previously described (23). Participants were placed in prone position, with the knee  
151 fully extended ( $0^{\circ}$ : full knee extension) and firmly attached to the ergometer by harness. The  
152 axis of right ankle rotation was aligned to the motor axis. The starting position of the ankle  
153 was randomly set at various angles:  $-20^{\circ}$ ,  $-10^{\circ}$ ,  $0^{\circ}$ ,  $10^{\circ}$ ,  $20^{\circ}$  and  $30^{\circ}$  ( $0^{\circ}$ : foot perpendicular to  
154 tibia; positive positions in plantar flexion direction; Fig. 2). Participants were instructed to  
155 contract “as fast and hard as possible” in order to reach maximal torque from a relaxed  
156 condition (37) after a standardized 3-second countdown with a visual feedback of the force  
157 trace and oral feedback of their RTD score measured from 0 to 200 ms after torque onset.



158 Five repetitions of 5-s duration interspaced by a 2-min rest period were performed per ankle  
159 angle condition, and the 3 best trials were considered for analysis (see below). The residual  
160 joint rotation during contractions was measured using a goniometer (Biometrics, Gometz-le-  
161 Châtel, France) fixed to the ankle. Since the ergometer was rigid, potential change in ankle  
162 angle was due mainly to slight heel movement on the platform. The pre-contraction torque  
163 was consistently verified in order to avoid any pre-activation or counter-movement prior to  
164 explosive contractions. In the case of pre-tension or countermovement, the trial was discarded  
165 from the analysis.

166

167 *Passive torque.* The passive plantar flexor torque-angle relationship was assessed during the  
168 tendon excursion method (3, 35) in dorsiflexion direction on the same ergometer and in the  
169 same position as for voluntary isometric contractions. Footplate rotation was set at  $1^{\circ} \cdot s^{-1}$  over  
170 the maximal range of motion in plantar flexion and dorsiflexion for each individual (i.e., from  
171  $42 \pm 8^{\circ}$  to  $-27 \pm 9^{\circ}$  on average).

172

173 *Moment arm.* Length of the triceps surae moment arm was measured using the tendon  
174 excursion method (3, 39) during the measure of passive torque, to determine fascicle force.  
175 Displacement of fascicle insertion on deep aponeurosis was observed by ultrasound (32). The  
176 length of the *triceps surae* moment arm was considered as the slope of the linear regression  
177 between deep aponeurosis displacement (in cm) and change in ankle angle ( $-10^{\circ}$  to  $20^{\circ}$ ;  $r^2 =$   
178  $0.99 \pm 0.04$ ).

179

180 *No-load ballistic contraction.* In order to determine maximal fascicle shortening velocity  
181 ( $V_{\max}$ ), participants performed maximal dynamic plantar flexions with no external load on a  
182 specific ergometer composed of a rotational footplate and a bench (Bio2M, Compiègne,

183 France) (33) as previously described and used (24, 25) . The starting position of the ankle was  
184 set at  $-20^\circ$  of dorsiflexion. Participants were instructed to contract “as fast as possible” from  
185 rest over the whole range of motion (i.e.,  $50^\circ$ ). Participants performed five trials with a rest of  
186 1’ between repetitions. When they thought they could achieve a faster movement, an  
187 additional trial was performed, with a maximum of 10 trials to avoid fatigue. The fascicle  
188 shortening velocity reached during RTD was expressed relatively to  $V_{\max}$ .

189

### 190 ***Data collection and processing***

191 *Mechanical data.* Joint angle, angular velocity and torque were recorded at 2000 Hz using an  
192 analog-to-digital converter designed by our laboratory (Custom DT, INSEP, Paris, France).  
193 Mechanical signals were analysed using custom-written scripts (Origin 9.1, OriginLab  
194 corporation, USA). First, signals were low-pass filtered (150 Hz, zero-lag 4<sup>th</sup> order  
195 Butterworth). Then, we determined the onset of contraction during RTD using the torque  
196 signal according to the systematic approach proposed by Tillin et al. (51). The onset of torque  
197 production was manually determined as previously described by Tillin et al. (49) before low-  
198 pass filtering. First, recordings where the baseline (resting) torque was not stable (i.e.,  $> 0.5$   
199 N.m the preceding 100 ms) were discarded. Second signals were checked with a consistent  
200 scale (e.g. 500 ms vs. 1 N). Third, the investigator placed manually a dashed line on the apex  
201 of the last peak/trough before the signal deflected from the baseline noise. RTD was  
202 calculated as the rising torque divided by the time windows [i.e., a straight line: from 0 to 200  
203 ms (RTD<sub>0-200</sub>), from 0 to 50 ms (RTD<sub>0-50</sub>) from 50 to 100 ms (RTD<sub>50-100</sub>), and from 100 to  
204 200 ms (RTD<sub>100-200</sub>)]. Mean displacement of the heel was monitored using an electronic  
205 goniometer (Biometrics, Gometz-le-Châtel, France). The mean displacement was measured at  
206 respectively  $1 \pm 1^\circ$ ,  $1 \pm 1^\circ$ ,  $1 \pm 2^\circ$ ,  $2 \pm 2^\circ$ ,  $2 \pm 2^\circ$  and  $2 \pm 2^\circ$  at respectively  $30^\circ$ ,  $20^\circ$ ,  $10^\circ$ ,  $0^\circ$ , -  
207  $10^\circ$  and  $-20^\circ$ . When detachment of the heel was above  $5^\circ$ , the trial was not considered. For

208 each set of five contractions performed at a given starting angle, the three trials resulting in  
209 the highest  $RTD_{0-200}$  were averaged for further analysis. The peak torque corresponded to the  
210 highest peak torque value obtained among the five explosive isometric contraction performed  
211 in each ankle angle position. Maximal angular velocity during the no-load condition  
212 corresponded to the averaged value measured from  $-10^\circ$  to  $20^\circ$  of plantar flexion (25).

213

214 *Ultrasound.* An ultrafast ultrasound scanner (Aixplorer, Supersonic Imagine, Aix en  
215 Provence, France) coupled with a linear transducer array (4-15 MHz, SuperLinear 15-4,  
216 Vermon, Tours, France) was used to acquire ultrasonic raw data from the GM muscle at a  
217 sampling frequency of 1000 Hz for RTD and 2000 Hz for the no-load condition. The  
218 ultrasonic raw data were used to create B-mode images (depth = 30 to 50 mm, width = 55  
219 mm; in order to visualize the whole muscle thickness for each participant) by applying  
220 conventional beamforming through Matlab software (Version, The Mathworks, Natick, MA).  
221 The ultrasound probe was placed on the skin surface at 30% of the distance between the  
222 popliteal fossa area and the centre of the lateral malleolus. A specific cast was used during  
223 contractions to keep the probe in the same location throughout the measurements. Changes in  
224 GM fascicle length (Fig. 2A) and pennation angle were assessed in every frame over 500 ms  
225 using the automatic tracking method proposed by Farris and Lichtwark (18) and low-pass  
226 filtered (50 Hz) using a 3<sup>rd</sup> order Butterworth filter. Fascicle shortening was calculated in  
227 every frame over the same time window used to determine RTD (i.e., 200 ms), over the whole  
228 range of motion in the passive condition to build the fascicle force-length relationship.  
229 Fascicle shortening velocity (Fig. 2C) was computed as the first-time derivative of fascicle  
230 length.  $V_{max}$  was calculated as the peak obtained during the no-load condition (25). Total  
231 plantar flexion force was calculated from the torque divided by the Achilles tendon moment

232 arm. Fascicle force was then calculated from the GM muscle force [i.e., 20.9% of total plantar  
233 flexion force (13)], divided by the cosine of the pennation angle.

234

235 *Active force-length relationship.* According to the method proposed by Hoffman et al. (28),  
236 the parallel elastic component was considered parallel to the contractile element only. Thus,  
237 the individual fascicle force-length curve was determined by fitting passive fascicle torque  
238 data to the following equation (28):

$$Passive\ force = Ae^{kL_f}$$

239 where A is constant, k is the stiffness of the curve and  $L_f$  the fascicle length.

240 To build the fascicle total force-length relationship, the peak fascicle force and the  
241 corresponding fascicle length when GM fascicle force was maximal were extracted for each  
242 ankle angle condition (30°, 20°, 10°, 0°, -10°, -20° of plantar flexion; Fig. 2D). For each  
243 point, the x-coordinate corresponded to the fascicle length measured when GM fascicle force  
244 was maximal. The y-coordinate corresponded to the peak fascicle force minus the passive  
245 force measured at the same fascicle length on the passive force-length curve (28). The active  
246 force-length relationship was fitted using the previously suggested methods (11, 28). A  
247 Levenberg-Marquardt algorithm was used to calculate five parameters (Origin 9.1, OriginLab  
248 corporation, USA): the maximal force, the fascicle length at the maximal force (i.e., optimal  
249 fascicle length,  $L_0$ ), the roundness, the skewness, and the width of the relationship. No  
250 constraints were used, excepted when the fitted relationship resulted in non-physiological data  
251 (see discussion section). The optimal fascicle length and maximal force were then used to  
252 build the normalized force-length relationship for each individual and the whole sample of  
253 participants.

254

255 *Force-velocity relationship.* Neutral ankle position (0°) is the most-commonly used condition  
256 to assess plantar flexion MVC torque and RTD, and resulted in the highest RTD values.  
257 Therefore, peak fascicle force elicited during MVC performed at 0° condition ( $F_{max}$ ) was used  
258 as the maximal theoretical force for each individual (i.e.,  $F_0$  of the force-velocity relationship;  
259 Fig. 2E). This relationship was modelled using the hyperbolic equation (27):

$$V = b * (F_{max} - F) / (F + a)$$

260 where F is force, V is velocity, and a and b are constants.

261 This model was fitted to experimental data that included  $F_{max}$  measured during RTD  
262 evaluation performed at 0° and  $V_{max}$  assessed during no-load ballistic contractions (Fig. 2E).  
263 The values of coefficients a (202.0) and b (17.0) were determined using the following  
264 equation:

$$a = k * F_{max}$$

$$b = k * V_{max}$$

265 where k is a constant.

266 The value of coefficient k (0.51) was determined from the mean force-velocity relationship  
267 obtained in a previous study on participants with similar anthropometrical characteristics and  
268 physical activity (24, 25). We determined the time point at which the mean fascicle force-  
269 velocity data obtained during RTD testing crossed the lower limit of 95% confidence interval  
270 of the mean force-velocity relationship.

271

272 *EMG.* Surface EMG activity was recorded using a wireless remote unit (Zerowire, Aurion,  
273 Italy), on GL, SOL and TA muscles. The skin was shaved, gently abraded and cleaned with a  
274 solution of ether, acetone and alcohol to minimize inter-electrode impedance. The bipolar,  
275 silver/silver chloride, surface disc electrodes (Blue Sensor N-00-S/25, Medicotest, France)  
276 were placed with a center distance of 2 cm. Electrodes were placed longitudinally with respect

277 to the underlying muscle fibre arrangement and located according to the Surface EMG for the  
278 Non-Invasive Assessment of Muscles recommendation's (SENIAM) (26). EMG signals were  
279 pre-amplified (input impedance: 20 MX; common mode-rejection ratio: 90 dB; gain: 1000;  
280 bandwidth: 10–500 Hz), digitized and sampled at 2000 Hz. All EMG signals were first band-  
281 pass filtered (high pass: 10 Hz, 3<sup>rd</sup> order Butterworth filter, low pass: 400 Hz, 3<sup>rd</sup> order  
282 Butterworth, filtered forward–backward filtering for zero phase shifting). EMG signals  
283 obtained during RTD was analysed as the root mean square (RMS) with a 10 ms moving  
284 rectangular window to produce a RMS envelope. During MVC, RMS EMG was calculated  
285 using a 500-ms moving rectangular windows. The maximal RMS EMG amplitude measured  
286 during maximal isometric contraction performed at the corresponding tested plantar flexion  
287 angle was selected as the reference to normalize EMG data at the same testing angle. GL and  
288 SOL EMG RMS were averaged over different time windows: between 0 ms and 50 ms,  
289 between 50 ms and 100 ms, between 100 ms and 200 ms and between 0ms and 200 ms.

290

### 291 *Statistical analysis*

292 All statistical analyses were performed with Statistica (StatSoft, Tulsa, Oklahoma, USA). All  
293 data being normally distributed (Shapiro-Wilk's test), all results are expressed as means  $\pm$  s.d.  
294 Statistical significance was set at  $P < 0.05$ . The potential effects of ankle angle (-20°, -10°, 0°,  
295 10°, 20° and 30°) on peak GM fascicle force, fascicle length corresponding to peak force,  
296 fascicle length corresponding to the onset of RTD (in passive condition, before the onset of  
297 the contraction), fascicle length changes over the first 200 ms, peak fascicle shortening  
298 velocity and time to peak shortening velocity were determined by one-way ANOVAs (angle  
299 effect) with repeated measures. The effects of ankle angle (-20°, -10°, 0°, 10°, 20° and 30°)  
300 and time period (0-50, 50-100 and 100-200 ms) on RTD were tested by a two-way ANOVA  
301 (angle  $\times$  time period) with repeated measures. Differences in muscle activation were tested for

302 each muscle (GL and SOL) using two two-way ANOVAs (time  $\times$  angle) with repeated  
303 measures. The 95% confidence interval was calculated for the force-velocity relationship  
304 (mean bias: 95%, mean difference:  $\pm 1.96$  s.d.). When the sphericity assumption in repeated  
305 measures ANOVAs was violated (Mauchly's test), a Geisser-Greenhouse correction was  
306 used. *Post-hoc* tests were performed by means of Newman-Keuls procedures for comparison  
307 between time points.

308

## 309 **RESULTS**

### 310 *Effect of joint angle on RTD*

311 Figure 3A shows changes in torque during RTD evaluation for all tested angles over time.  
312 The two-way ANOVA showed significant main effects of angle ( $P < 0.001$ ), time period ( $P <$   
313  $0.001$ ) and time period  $\times$  angle interaction ( $P < 0.001$ ) on RTD (Table 1). *Post-hoc* showed  
314 that no significant effect was found on RTD<sub>0-50</sub> between  $-10^\circ$ ,  $0^\circ$  and  $10^\circ$  ( $P = 0.29$ ). These  
315 values were significantly higher than RTD<sub>0-50</sub> measured at  $-20^\circ$  ( $P < 0.03$ ) ( $17 \pm 6\%$ ), which  
316 was significantly higher than the values obtained at  $20^\circ$  and  $30^\circ$  ( $33 \pm 16\%$  and  $57 \pm 28\%$ ,  
317 respectively;  $P < 0.005$ ). We found no significant differences in RTD<sub>50-100</sub> between  $-10^\circ$ ,  $0^\circ$   
318 and  $10^\circ$  ( $P = 0.83$ ), and these values were significantly higher than those obtained at  $-20^\circ$  and  
319  $20^\circ$  ( $17 \pm 4\%$  and  $20 \pm 6\%$ , respectively;  $P < 0.04$ ), which were significantly higher than  
320 RTD<sub>50-100</sub> achieved at  $30^\circ$  ( $28 \pm 13\%$ ;  $P < 0.001$ ). RTD<sub>100-200</sub> measured at  $0^\circ$ ,  $-10^\circ$  and  $-20^\circ$   
321 were significantly higher than the values obtained at  $10^\circ$  ( $11 \pm 4\%$ ;  $P = 0.02$ ), which was  
322 significantly higher than the values obtained at  $20^\circ$  and  $30^\circ$  ( $12 \pm 3\%$  and  $33 \pm 3\%$ ;  $P < 0.02$ ).

323

### 324 *Effect of joint angle on fascicle length and velocity changes during RTD evaluation*

325 At the two extreme ankle angle positions, GM fascicle operated from  $3.6 \pm 0.7$  cm to  $2.8 \pm 0.6$   
326 at  $30^\circ$  and from  $7.0 \pm 1.2$  cm to  $5.8 \pm 1.3$  cm at  $-20^\circ$  (Fig. 3). These fascicle length changes

327 were significantly different between all conditions (angle effect;  $P < 0.05$ ), showing the  
328 substantial effect of the ankle angle on this parameter. In all conditions, fascicle shortening  
329 occurred mainly in the first 200 ms, corresponding to  $0.67 \pm 0.37$  cm,  $1.02 \pm 0.38$  cm,  $1.22 \pm$   
330  $0.49$  cm,  $1.21 \pm 0.48$  cm,  $1.06 \pm 0.40$  cm and  $0.85 \pm 0.33$  cm for angles of  $-20^\circ$ ,  $-10^\circ$ ,  $0^\circ$ ,  $10^\circ$ ,  
331  $20^\circ$  and  $30^\circ$ , respectively. Fascicle shortening was significantly lower at  $-20^\circ$  than in other  
332 conditions ( $P < 0.003$ ). Peak fascicle shortening velocity showed a significant angle effect ( $P$   
333  $< 0.001$ ), with a maximal value achieved at  $0^\circ$  ( $10.8 \pm 3.8$  cm.s<sup>-1</sup>) and minimal at  $20^\circ$  ( $6.7 \pm$   
334  $3.7$  cm.s<sup>-1</sup>; Table 1). Peak shortening velocity was significantly lower at  $-20^\circ$  than at  $-10^\circ$ ,  $0^\circ$ ,  
335  $10^\circ$ ,  $20^\circ$  and  $30^\circ$  ( $P < 0.001$ ).

336

### 337 ***RTD performance in relation with force-length relationship***

338 In addition to the effect on muscle fascicle length changes, we observed a significant effect of  
339 angle on peak fascicle force ( $P < 0.001$ ) reached during RTD evaluation. Values ranged  
340 between  $180 \pm 49$  N at  $30^\circ$  and  $568 \pm 177$  N at  $-20^\circ$  (Fig. 4). *Post-hoc* revealed that maximal  
341 forces did not differ significantly between  $-20^\circ$ ,  $-10^\circ$  ( $565 \pm 129$  N) and  $0^\circ$  ( $520 \pm 114$  N;  $P =$   
342  $0.08$ ; Fig. 4). Maximal fascicle forces produced at these angles were higher than values  
343 obtained in plantar flexion positions at  $10^\circ$ ,  $20^\circ$  and  $30^\circ$  ( $P < 0.001$ ). The figure 4 allowed to  
344 determine whether the average changes in fascicle length during RTD occurred over the  
345 ascending limb, descending limb or the plateau of the force-length relationship. On average,  
346 muscle fascicle operated over the ascending limb during RTD at  $30^\circ$  and  $20^\circ$ , while it was  
347 over the descending limb at  $-20^\circ$ . Changes in fascicle length during RTD performed at  $10$  and  
348  $-10^\circ$  were mainly comprised between the ascending limb and the plateau at  $10^\circ$  and between  
349 the descending limb and the plateau at  $-10^\circ$ . Finally, the fascicles operated over the plateau  
350 when RTD was performed at  $0^\circ$ .



351 The individual changes in length during RTD were analysed to further confirm these results  
352 (Fig. 5). First, this individual analysis showed that the changes in fascicle length that occurred  
353 during RTD at 30° and 20° corresponded to the ascending limb for all the participants.  
354 Inversely, the changes in fascicle length during RTD performed at -20° corresponded to the  
355 descending limb for all the participants excepted for 3/16 (i.e., participants # 4, 11 and 16) for  
356 which muscle fascicles operated over the plateau in this condition. Second, at 10°, fascicle  
357 length changes occurred over the ascending limb for 9/16 participants (#1, 2, 3, 4, 5, 10, 11,  
358 14, 16), the plateau for 6/16 participants (#7, 8, 9, 12, 13, 15), and the descending limb for  
359 1/16 participant (#6). In the same way, the changes in length during RTD at -10°  
360 corresponded to the ascending limb for 1/16 participants (#11), the plateau for 7/16  
361 participants (# 2, 3, 4, 5, 9, 10, 16) and the descending limb for 8/16 participants (#1, 6, 7, 8,  
362 12, 13, 14, 15). Third, the changes in fascicle length during RTD at 0° corresponded to the  
363 ascending limb for 1/16 participant (#11), the plateau for 11/16 participants (#1, 2, 3, 4, 5, 8,  
364 9, 10, 12, 14, 16) and the descending limb for 4/16 participants (#6, 7, 13, 15).

365

### 366 ***RTD performance in relation with fascicle force-velocity relationship***

367 The 0° condition elicited a fascicle shortening range centred over optimal GM fascicle length  
368 values commonly reported in voluntary contractions (i.e., ~5 cm, Fig. 2D). The average force-  
369 velocity relationship of GM is displayed in Figure 6. The theoretical maximal fascicle force  
370 and maximal fascicle shortening velocity obtained from this relationship reached  $521 \pm 115$  N  
371 and  $33.3 \pm 8.8$  cm.s<sup>-1</sup>, respectively. At 50 ms after the onset of RTD evaluation, the measured  
372 fascicle force ( $51 \pm 30$  N) was low compared to the theoretical maximal force the individuals  
373 were able to produce at the corresponding fascicle-shortening velocity ( $278 \pm 61$  N, Fig. 6).  
374 Between 50 and 100 ms, the force increased up to  $177 \pm 73$  N (i.e., 72.5% of the theoretical  
375 maximum force at this corresponding specific shortening velocity) while the shortening

376 velocity continued to increase and reached a plateau corresponding to  $9.26 \pm 2.85 \text{ cm}\cdot\text{s}^{-1}$  (i.e.,  
377 28.2% of  $V_{\text{max}}$ ). At 112 ms, fascicle force reached  $208 \pm 78 \text{ N}$  (i.e., 85.6% of the theoretical  
378 maximum force at this velocity) and was thereafter comprised within the 95% confidence  
379 interval of the force-velocity relationship up to  $F_{\text{max}}$ .

380

381 **Muscle activity.** GL mean muscle activity showed no significant effect of angle ( $P = 0.6$ ) and  
382 time  $\times$  angle interaction ( $P = 0.2$ ), with a significant effect of time ( $P < 0.001$ ; Fig. 3D, Table  
383 1). *Post-hoc* showed that GL mean activity between 50 and 100 ms was significantly higher  
384 than activity measured 0 and 50 ms and between 100 and 200 ms ( $P < 0.001$ ).

385 SOL mean muscle activity showed the significant effect of angle ( $P < 0.001$ ), time ( $P <$   
386  $0.001$ ) and time  $\times$  angle interaction ( $P = 0.001$ , Table 1). *Post-hoc* showed than SOL activity  
387 was significantly higher at  $-20^\circ$ ,  $-10^\circ$  and  $0^\circ$  than at  $20^\circ$  and  $30^\circ$  ( $P < 0.02$ ). SOL mean  
388 activity between 0 and 50 ms was significantly lower than between 50 and 100 ms or between  
389 100 and 200 ms ( $P < 0.001$ ).

390

## 391 **DISCUSSION**

392 The present study aimed to determine the influence of joint angle on the plantar flexor  
393 RTD and associated fascicle dynamics measured during an explosive isometric contraction. In  
394 line with our hypothesis, the results revealed a significant shortening of GM fascicles during  
395 explosive isometric contractions, which was significantly influenced by joint angle. RTD  
396 measured over a 200-ms period reached higher values at  $10^\circ$ ,  $0^\circ$  and  $10^\circ$  than in dorsiflexed ( $-$   
397  $20^\circ$ ) and plantar flexed ( $20^\circ$  and  $30^\circ$ ) positions. This could mainly originate from the fact that  
398 GM fascicles operate over the plateau of the force-length relationship in these neutral  
399 conditions (i.e., centred on optimal fascicle length). At  $0^\circ$ , fascicle-shortening velocity  
400 reached  $\sim 28.2\%$  of  $V_{\text{max}}$  at 89 ms from RTD onset. This finding reflects that the substantial

401 fascicle shortening that occurs in the isometric condition causes a decrease in maximal  
402 fascicle force-generating capacity, according to the force-velocity relationship.

403 Plantar flexor RTD values ( $346 \pm 38 \text{ N.m.s}^{-1}$  and  $417 \pm 137 \text{ N.m.s}^{-1}$  for RTD<sub>0-50</sub> and  
404 RTD<sub>0-200</sub>, respectively) were comprised within the ranges of RTD measures obtained during  
405 ankle plantar flexions [i.e., from 200 to 610  $\text{Nm.s}^{-1}$  (9, 46)]. In line with previous data  
406 obtained on knee extensor muscles (34), our results show that the impact of ankle joint angle  
407 on RTD follows an inverted 'U' relationship at any specific time point. To our knowledge, this  
408 effect has never been reported for plantar flexors, while our results corroborate previous  
409 studies focused on knee extensor muscles (2, 14). In the latter study, a change in ability to  
410 produce force rapidly was associated with changes in muscle activation. These previous  
411 findings are in accordance with the concomitant increase in EMG activity of SOL [i.e. main  
412 contributor to planter flexor force (13)], and RFD observed in the present study at  $-20^\circ$ ,  $-10^\circ$   
413 and  $0^\circ$  than  $20^\circ$  and  $30^\circ$ . However, our results showed no significant effect of ankle angle on  
414 average GL EMG activity across different time windows (Table 1). It is important to note that  
415 GM and antagonist activity were not measured, which precludes to strongly conclude on the  
416 influence of joint angle on muscle activation during RTD evaluation.

417 We observed a significant fascicle shortening during explosive isometric contractions,  
418 regardless of ankle position (Fig. 3 and 4). Such a non-isometric behaviour of the fascicle  
419 provides an additional evidence of the decoupling between muscle fibres (which shorten) and  
420 tendon (which stretches) observed during various motor tasks [i.e., walking, running,  
421 jumping, single-joint dynamic contractions (21, 29)]. The significant effect of joint angle on  
422 RTD can be interpreted with respect to the muscle fascicle shortening potential and the  
423 associated muscle force-generating capacity, which depend on the initial muscle-tendon  
424 length configuration (7, 28, 38).

425           The mean operating fascicle length during RTD<sub>0-200</sub> performed at 0° was comprised  
426 between  $5.87 \pm 0.84$  cm and  $4.64 \pm 0.99$  cm, which strongly corresponds to the optimal length  
427 condition to produce force for GM muscle [Fig. 4; (28)]. Although a substantial variability  
428 was found between individuals, this finding was confirmed by individual analyses (Fig. 5). At  
429 30° and 20°, muscle fascicles shortened over the ascending limb of the active force-length  
430 relationship, thereby limiting force and RTD. The resulting RTD in these conditions was  
431 significantly lower compared to the values elicited in neutral conditions where fascicles  
432 operated over the plateau (Fig. 4; Table 1). In the same way, at -20° (dorsiflexed ankle  
433 position), RTD values were lower than those obtained at 0° (Table 1). In this condition, GM  
434 fascicle mainly operated over the descending limb of the force-length relationship. Therefore,  
435 due to a decrease in the maximal force ability over the fascicle operating length, our results  
436 strongly support that the force-length properties can contribute to limit the amount of RTD  
437 achieved at 30°, 20° and -20°. Nevertheless, this mechanism should be considered together  
438 with the potential impact of ankle angle on neural activation (17, 41). For intermediate angles  
439 (10° and -10°), the fascicle shortening during RTD was between the ascending, descending  
440 limb and the plateau. Therefore, the influence of the force-length relationship is more  
441 mitigated for these conditions. Interestingly, while a trend was observed, RTD did not  
442 significantly differ between 10°, 0° and -10°. As a whole, these results demonstrated that  
443 using a neutral ankle position around 0° for RTD evaluation ensures a maximal force-  
444 generating capacity in respect to the force-length relationship, and a minimal influence of the  
445 force-length properties on the amount of produced muscle force. This finding is important  
446 because it was the condition to further analyse the 0° condition by investigating the force  
447 development in light of the force-velocity properties.

448           Our results enable the identification of different phases of RTD performed in this 0°  
449 neutral condition. Firstly, from 0 to 50 ms, mean EMG activity (Table 1) and fascicle force

450 generated at the associated fascicle velocity was divergent from the maximal EMG activity  
451 and the maximal force-velocity capacities of individuals. Therefore, in this phase, RTD may  
452 be mainly related to the activation dynamics. Indeed, Del Vecchio et al. (16) showed that the  
453 individual ability to produce force rapidly in this early phase of RTD is highly dependent on  
454 motor unit recruitment and discharge rate. Secondly, from 50 to 100 ms, the mean fascicle  
455 force generated at the associated velocity progressively approached the force-velocity  
456 relationship (Fig. 6). During this phase, EMG activity was significantly higher than in the  
457 other time windows. Thus, in this phase, explosive strength still depends on activation and  
458 progressively on the force-velocity properties. Thirdly, after ~100 ms, the mean fascicle force  
459 generated at the associated fascicle velocity measured during RTD matched with the maximal  
460 force-velocity properties (Fig. 6).

461         These results confirm previous results obtained on knee extensor muscles (14). In the  
462 latter study, the response to an evoked octet was reported as the primary determinant of force  
463 development from 50 to 100 ms, suggesting that contractile properties of the muscle-tendon  
464 unit may influence the force increase from 50 ms after the onset of contraction. Moreover, in  
465 our study, fascicle force in the later part of RTD (after 200 ms) is strongly related to the  
466 maximal isometric force-generating capacity as demonstrated by the force-velocity values  
467 measured close to  $F_{max}$ . This result supports previous reports of an increasing influence of  
468 maximal voluntary isometric torque on RTD measured over this later period of contraction (4,  
469 19). The later putative intervention of contractile properties in plantar flexors may reflect the  
470 influence of their pennate architecture as contractile forces are less directly transmitted to the  
471 tendon than in less pennated muscles [e.g. knee extensors (48)]. Inversely, the gearing effect  
472 allowed by fascicle pennation has been suggested to limit fascicle shortening velocity for  
473 reaching a given muscle-tendon unit shortening velocity, which could increase RTD (6, 10).  
474 How these two processes are involved in force rise remain to be elucidated.

475           The impact of fascicle dynamics on RTD could be influenced by the stiffness of the  
476 elastic tissues (19, 36, 37, 41). Waugh et al. (53) showed that Achilles tendon stiffness could  
477 account for up to 35% of the variability in RTD normalized to its peak value, while Kubo (31)  
478 suggested that the link between changes in tendon properties and RTD may be divergent.  
479 Mayfield, et al. (41, 42) showed a modest decrease in fascicle shortening velocity with  
480 increasing the effective stiffness (manipulated by applying a rapid rotation of the foot at the  
481 onset of contraction) during electrically-evoked RTD, thereby increasing force-generating  
482 capacity. During voluntary contractions, the present protocol placed the elastic tissues in a  
483 configuration where their passive stiffness increased when the ankle was in dorsiflexed  
484 angles. The present study confirms that this rise in tendon stiffness in dorsiflexed positions  
485 reduces fascicle shortening velocity (Table 1). However, although the decrease in fascicle  
486 velocity is theoretically beneficial for producing high levels of force rapidly, mean RTD was  
487 significantly lower at  $-20^\circ$  over each time window compared to  $0^\circ$ . This finding suggests that  
488 the impairment of the force-generating capacity during RTD in dorsiflexed ankle  
489 configuration is mainly related to the fact that fascicles are forced to operate over the  
490 descending limb of the force-length relationship. This result clearly shows the interplay  
491 between tendon stiffness and fascicle mechanics that remain very difficult to dissociate *in vivo*  
492 and may in turn substantially contribute to the observed variability between individuals.  
493 Future research is required to find the best compromise between the mechanical properties of  
494 both tendinous and contractile tissues, and thereby optimize fascicle dynamics for RTD  
495 performance.

496           The fits applied to the active voluntary force-length relationships were done in the  
497 same way than in previous published papers (11, 28). However, it should be kept in mind that  
498 it requires the calculation of five parameters. For such fits, we cannot fully ascertain that the  
499 real solution was found by optimization due to possible local minima. Thus, the fit should be

500 rather considered as an estimation about the theoretical force-length relationship. This should  
501 not be considered as a main issue given that the parameters extracted from the fits were not  
502 used in the present paper, excepted  $F_0$  and  $L_0$  for the average normalized force-length  
503 relationship (Fig. 4B). In addition, for three participants (#11, 13 and 16, Fig. 5), the  $L_0$  was  
504 extrapolated in regards to the measured data points. Thus, the normalized force-length  
505 relationship should be considered with caution. The force-velocity relationship was estimated  
506 from Hill's model that was fitted on the basis of measured values of maximal force and  
507 maximal shortening velocity. First, we assume that the fascicle velocity reached during no-  
508 load ballistic plantar flexions is representative of the theoretical maximal velocity value (5).  
509 Indeed, previous studies from our group have shown this method to be effective in assessing  
510 the active  $V_{\max}$  that muscle fascicles can achieve *in vivo* (7, 23, 25). Second, the curvature  
511 coefficients were taken from the mean values of a previous study (25). Ideally, the fascicle  
512 force-velocity curvature coefficient could be individualized from data collected under  
513 different loading conditions (25). The inclusion of concentric contractions at various  
514 velocities would have also permitted to consider the intricate influence of both length and  
515 velocity changes on RTD at intermediate shortening velocities using a 3-D force-length-  
516 velocity relationship (50, 52). However, in the present study, it was not possible to add the  
517 conditions required for this procedure due to the increased of fatigue due to this protocol.  
518 Nevertheless, compared to the study by Hauraix et al. (25), participants had similar (i)  
519 anthropometrical characteristics, (ii) maximal velocity (i.e.,  $30.8 \text{ cm}\cdot\text{s}^{-1}$  vs.  $33.3 \pm 8.8 \text{ cm}\cdot\text{s}^{-1}$ )  
520 and (iii) maximal force ( $420 \text{ N}$  vs.  $520 \pm 115 \text{ N}$ ). Therefore, we are confident that our  
521 approach is sufficiently robust to interpret the force and fascicle shortening velocity obtained  
522 during isometric RTD testing in light of the mean force-velocity relationship.

523

524 **Conclusion**

525           The present study demonstrates that joint angle substantially influence the rate of torque  
526 development, associated fascicle length changes and shortening velocity expressed during  
527 explosive maximal isometric plantar flexions. Force-length properties mainly account for the  
528 effect of ankle angle on RTD, which peaked around the neutral ankle positions where  
529 fascicles operated over the plateau of the fascicle force-length relationship. After ~100 ms  
530 from the onset of RTD, the fascicle force was very close to its maximal theoretical value  
531 considering the associated shortening velocity (i.e., according to the force-velocity  
532 relationship). While an initial phase is required to initiate the tendon stretch and maximally  
533 activate the muscle, RTD is mainly influenced by muscle mechanics and the force-velocity  
534 properties from 100 ms after RTD onset. This contribution of contractile properties to the  
535 ability to generate force rapidly may also be modulated by the mechanical properties of elastic  
536 tissues due to the inherent interplay between muscle and tendon *in vivo*. The present study  
537 provides important information to better understand the determinants of human muscle  
538 performance during explosive tasks. In the long term, it can be used to implement  
539 individualized training programs and improve explosive strength.



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545

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553

554 **DISCLOSURES**

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

556

557 **AUTHOR CONTRIBUTIONS**

558 R.H., A.N., S.D. and G.G. conception and design of research; R.H. and T.P. performed  
559 experiments. R.H., T.P., A.N., S.D. and G.G. analysed data; R.H., T.P., A.N., S.D. and G.G.  
560 interpreted results of experiments; R.H., A.N., S.D. and G.G. prepared figures; R.H. drafted  
561 manuscript; R.H., A.N., S.D. and G.G. edited and revised manuscript; R.H., T.P., A.N., S.D.  
562 and G.G. approved final version of manuscript.

563 **Table 1. Rate of torque development, peak fascicle velocity, and mean EMG activity in gastrocnemius lateralis and soleus muscles**  
 564 **measured at different ankle angles.**

Ankle angle	-20° <sup>(a)</sup>	-10° <sup>(b)</sup>	0° <sup>(c)</sup>	10° <sup>(d)</sup>	20° <sup>(e)</sup>	30° <sup>(f)</sup>
<b>RTD (Nm.s<sup>-1</sup>)</b>						
0-200 ms	320 ± 91 <sup>cef</sup>	354 ± 117 <sup>ef</sup>	389 ± 94 <sup>aef</sup>	329 ± 94 <sup>ef</sup>	265 ± 66 <sup>abcdcf</sup>	194.5 ± 53 <sup>abcde</sup>
0-50 <sup>hi</sup> ms	141 ± 61 <sup>bcddef</sup>	208 ± 127 <sup>aef</sup>	178 ± 105 <sup>aef</sup>	203 ± 113 <sup>aef</sup>	106 ± 53 <sup>bdc</sup>	81 ± 45 <sup>bdc</sup>
50-100 <sup>g</sup> ms	413 ± 136 <sup>bcdcf</sup>	496 ± 210 <sup>f</sup>	549 ± 178 <sup>aef</sup>	483 ± 168 <sup>f</sup>	388 ± 150 <sup>cf</sup>	280 ± 129 <sup>abcde</sup>
100-200 <sup>g</sup> ms	361 ± 128 <sup>ef</sup>	357 ± 128 <sup>ef</sup>	414 ± 98 <sup>def</sup>	317 ± 81 <sup>cf</sup>	284 ± 60 <sup>abcf</sup>	210 ± 59 <sup>abcde</sup>
<b>Peak Fascicle velocity (cm.s<sup>-1</sup>)</b>	6.1 ± 3.4 <sup>bcddef</sup>	8.6 ± 4.0 <sup>a</sup>	10.8 ± 3.8 <sup>a</sup>	10.6 ± 3.0 <sup>a</sup>	9.8 ± 3.2 <sup>a</sup>	8.6 ± 3.4 <sup>a</sup>
<b>Mean EMG GL (% RMS max)</b>						
0-200 ms	69.7 ± 11.0	64.6 ± 24.6	62.3 ± 18.4	65.7 ± 21.0	62.2 ± 18.7	72.0 ± 17.1
0-50 <sup>h</sup> ms	67.2 ± 27.9	68.3 ± 37	58.6 ± 27.8	66.1 ± 27.1	53.1 ± 21.3	61.8 ± 25.0
50-100 <sup>gi</sup> ms	87.0 ± 19.7	78.6 ± 35.1	72.9 ± 23.2	75.5 ± 24.4	69.7 ± 24.0	76.9 ± 20.1
100-200 <sup>h</sup> ms	62.5 ± 22.3 <sup>g</sup>	57.8 ± 18.6 <sup>g</sup>	60.5 ± 19.2 <sup>g</sup>	62.7 ± 18.1 <sup>g</sup>	64.5 ± 17.3 <sup>abc</sup>	76.3 ± 16.6 <sup>abc</sup>
<b>Mean EMG SOL (% RMS max)</b>						
0-200 ms	57.4 ± 23.6	51.7 ± 27.1	50.7 ± 23.6	43.4 ± 19.0	36.8 ± 14.9	37.8 ± 18.8
0-50 <sup>hi</sup> ms	21.3 ± 12.5	16.9 ± 7.8	14.9 ± 8.2	13.3 ± 7.4	12.2 ± 6.8	14.4 ± 7.8
50-100 <sup>g</sup> ms	71.2 ± 33.5	78.6 ± 50.1	62.0 ± 32.1	52.9 ± 30.1	41.0 ± 19.5	40.5 ± 24.5
100-200 <sup>g</sup> ms	65.5 ± 22.3	59.2 ± 28.4	63.2 ± 31.4	53.9 ± 21.9	47.0 ± 18.9	48.2 ± 23.9

565

566

567 Values are mean ± SD (n = 16).

568 <sup>a</sup>, <sup>b</sup>, <sup>c</sup>, <sup>d</sup>, <sup>e</sup> and <sup>f</sup>: significantly different than -20°, -10°, 0°, 10°, 20°, and 30°, respectively [*P* < 0.05; two-way ANOVA, main effect: ankle angle (-  
 569 20°, -10°, 0°, 10°, 20°, 30°)].

570 <sup>g</sup>, <sup>h</sup> and <sup>i</sup>: significantly different than RTD<sub>0-50</sub>, RTD<sub>50-100</sub> and RTD<sub>100-200</sub>, respectively [*P* < 0.05; one-way ANOVA, main effects: ankle angle (-  
 571 20°, -10°, 0°, 10°, 20°, 30°) × time period (0-50, 50-100, 100-200 ms)].

572 MVC: maximal voluntary contraction; RMS: root mean square.

573

574

575 **FIGURES LEGENDS**

576

577 **Figure 1. Individual patterns of collected signals during RTD testing.** Plantar flexor  
578 torque was recorded by a mechatronic ergometer triggered by a high-frame rate ultrasound  
579 scanner. Fascicle length and pennation angle were measured on ultrasound images processed  
580 using automatic tracking software. Fascicle length was differentiated ~~derived~~ to obtain  
581 fascicle velocity. Electromyographic (EMG) activity of *gastrocnemius lateralis* and *soleus*  
582 were recorded in time with ultrasound images and mechanical signals. The time  
583 corresponding to the onset of torque development (first arrow) was manually determined  
584 using the method proposed by (54).

585 **Figure 2. Methodological approach used to obtain individual force-length and force**  
586 **velocity relationship. Force-length at MVC peak torque (D):** *Gastrocnemius medialis*  
587 fascicle length (A) was recorded during RTD at different conditions (-20, -10, 0, 10, 20 and  
588 30°) using ultrasound. Fascicle force (B) was calculated from torque recordings, moment arm  
589 and pennation angle. Force-length at MVC peak torque (D) was built from the fascicle length  
590 corresponding at peak fascicle force (black circle for peak at 0°, A) and associated fascicle  
591 force (green circle for peak at 0°, B) minus the passive force produced at fascicle length  
592 corresponding to peak fascicle force (31). The range of fascicle shortening at 0° plotted as a  
593 green trace (green-black circle).

594 **Force-velocity relationship (E):** Fascicle velocity (C) was calculated from fascicle length  
595 derivative. For the sake of clarity, only fascicle velocity at 0° during RTD (green line) and  
596 during ballistic condition (dashed line) are presented here. From peak fascicle velocity (red  
597 circle, C) and force values (green circle, B), the individual force-velocity relationship was  
598 build (black trace in E). The curvature coefficient of the slope was defined using previous  
599 mean data collected by our group on a similar sample of participants (27). Fascicle shortening  
600 velocity during RTD was plotted as a rainbow trace, with the colour scale illustrating time  
601 from 0 ms (red) to 600 ms (purple).

602 **Figure 3. Mean (n =16) Torque (A), *gastrocnemius medialis* fascicle length (B), fascicle**  
603 **velocity (C) and GL RMS EMG time-courses (D) at various angles during RTD.** Mean  
604 torque was presented without the effect of passive tension.

605 **Figure 4. Raw (A) and normalized (B) mean active force-length relationship** obtained  
606 during maximal contractions performed at -20°, -10°, 0°, 10°, 20° and 30° of ankle angle  
607 assuming the model B from Hoffman et al. [(29); n = 16]. The force-length relationship was  
608 normalized (B) using the maximal force ( $F_0$ ) and the optimal fascicle length ( $L_0$ ) obtained  
609 using individual fits. Colour traces represents the time-course of force and fascicle length  
610 changes that occurred during the evaluation of rate of torque development (RTD; i.e., from 0  
611 N force to maximal values on the force-length relationship). The three black circles represent  
612 the values achieved at 50, 100 and 200 ms during RTD. Fascicle forces values obtained at -  
613 20°, -10° and 0° were significantly higher than values obtained at 10°, 20° and 30° [ $P <$   
614 0.001; one-way ANOVA, main effect: ankle angle (-20°, -10°, 0°, 10°, 20° and 30°)].

615 **Figure 5. Individual active force-length relationship** obtained during maximal contractions  
616 performed at -20°, -10°, 0°, 10°, 20° and 30° of ankle angle assuming the model B from  
617 Hoffman et al. 2012 for the 16 participants (P).

618 **Figure 6. Force-velocity relationship** (black line) with associated lower 95% confidence  
619 interval. The curvature coefficient of the slope was defined using previous mean data  
620 collected by our group on a similar sample of participants (n = 16) (27). Fascicle force and  
621 shortening velocity measured at 0° of ankle angle during RTD was plotted as a rainbow trace,  
622 with the color scale illustrating time from 0 ms (red) to 600 ms (purple). The three black  
623 marks represents the mean fascicle length at 50, 100 and 200 ms from the onset of RTD  
624 testing.

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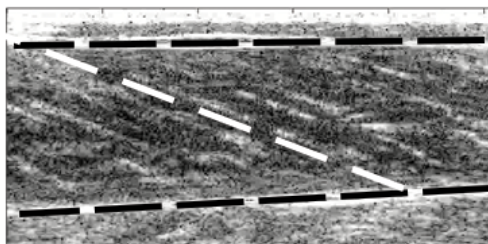
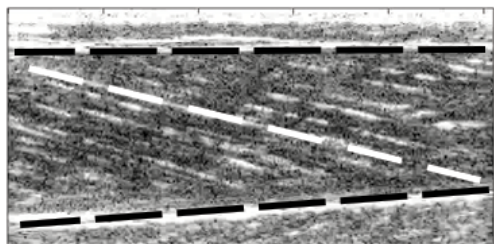
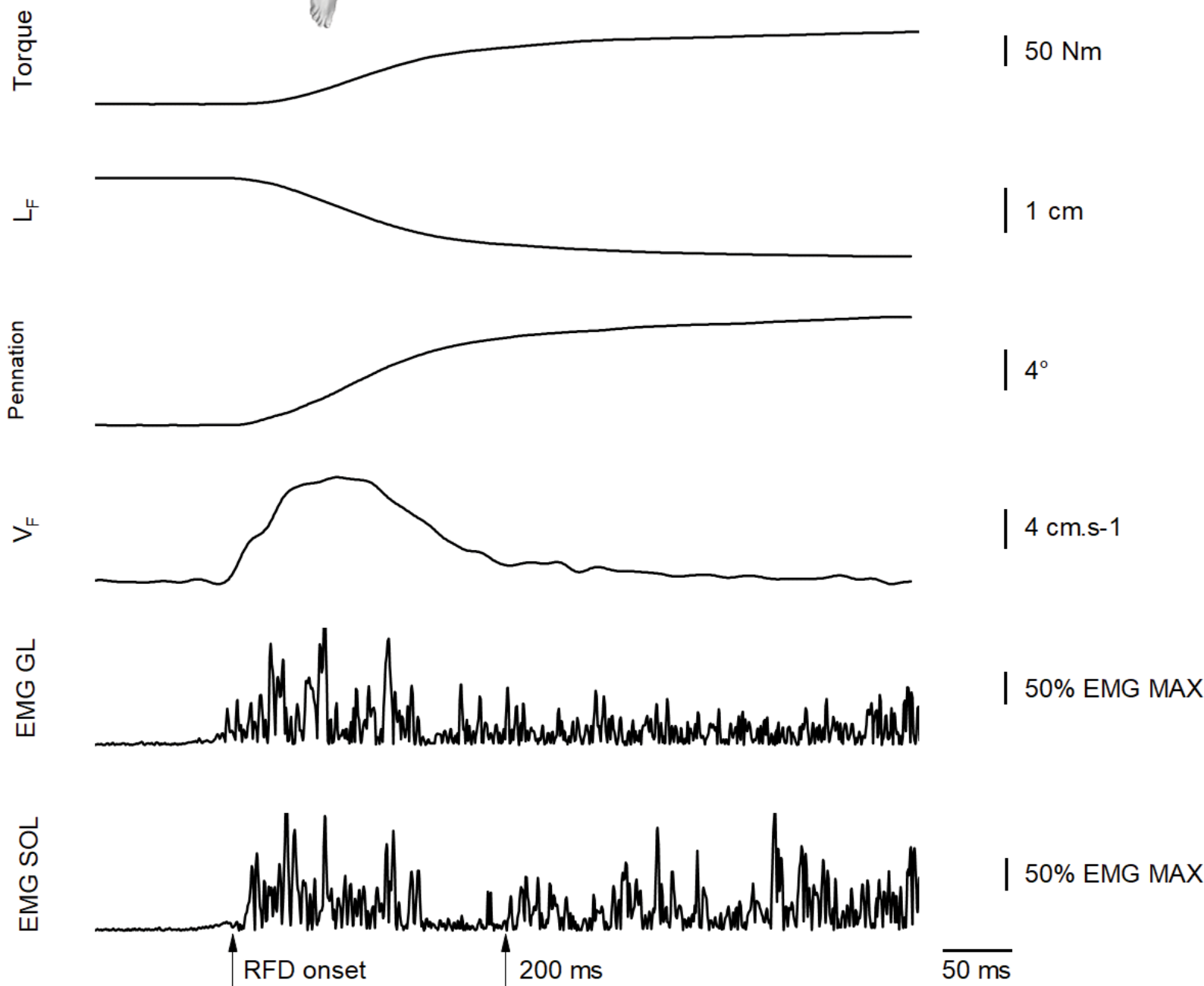
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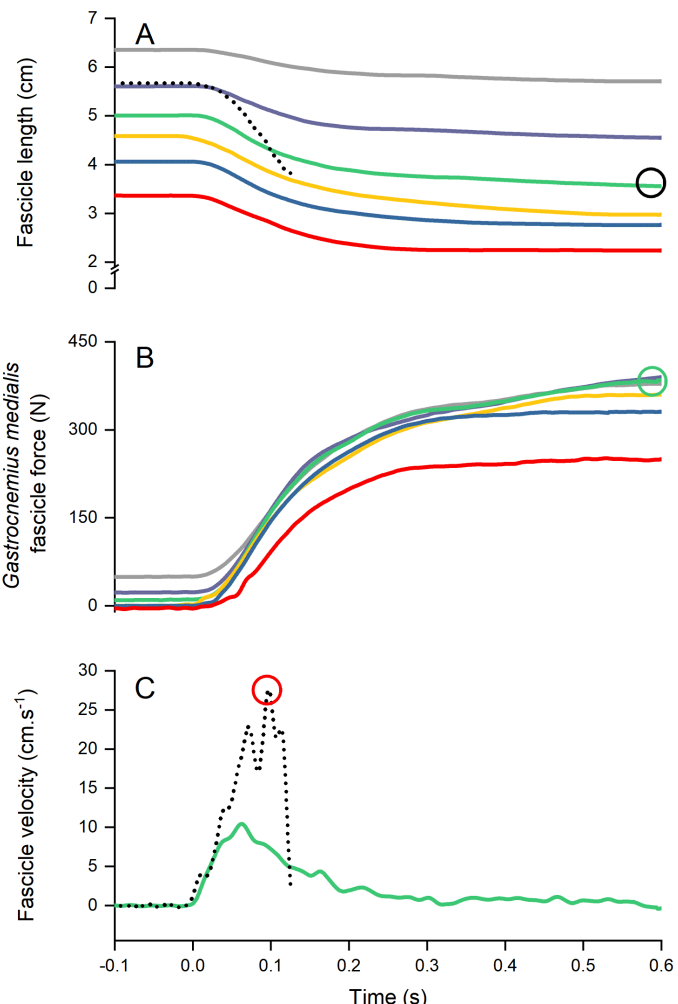
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RFD conditions:  
 ● -20° ● -10° ● 0° ● 10° ● 20° ● 30°  
 Ballistic condition :  
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