

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

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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
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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°, -10°, 0° (neutral position), 10°, 20° and 34 30° 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 dorsiflexed (- 20°) positions compared to -10, 0° (475 $\pm$ 105 Nm.s<sup>-1</sup>) and 10°. At these neutral 36 37 positions, RTD was maximal and muscle fascicles mainly operated over the plateau of the force-length relationship. At 0°, fascicle shortening velocity peaked at 9.26±2.85 cm.s<sup>-1</sup> (i.e., 38 39 28.2% of maximal shortening velocity measured during no-load ballistic condition). At 112 ms after RTD onset, fascicle force reached  $208 \pm 78$  N (i.e., 85.6% of the theoretical 40 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 muscle force reached the maximal force that accounts for the fascicle shortening velocity. 43 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.

### 49 New & Noteworthy

- Ankle angle influences the operating muscle fascicle lengths of gastrocnemius
   medialis, and the rate of torque development during explosive isometric plantar
   flexions.
- The rate of torque development peaks in neutral angles where muscle fascicles shorten
  over the plateau of the force-length relationship.
- When fascicles operate over the plateau of the force-length relationship (neutral ankle
   positions), the force-velocity properties represent a limiting factor for the rapid force 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 isometric contractions in humans (21, 29, 45), our objectives were twofold: (i) to determine the influence of ankle angle on the fascicle length shortening and RTD achieved during an explosive contraction; (ii) to investigate how this dynamic behaviour of muscle fascicle and its shortening velocity may influence RTD (by referring to the force-velocity relationship) in a joint configuration that elicits fascicle shortening over the plateau of the force-length relationship.

114

115 METHODS

116 Participants

Ten males and six females (age:  $23.2 \pm 2.7$  years, height:  $175.3 \pm 6.4$  cm, body mass:  $70.2 \pm 12.6$  kg), with no history of ankle disorder or injury, participated in this study. All volunteers were informed about the nature, aims and risks associated with the experimental procedure before giving their written consent to participate. The study was approved by the local ethics 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, Compiegne, 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° in 130 dorsiflexion to 30° 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 dorsiflexion cycles were performed on the same ergometer at  $1^{\circ}$ .s<sup>-1</sup> to estimate triceps surae 139 140 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 (Eraclès-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 was randomly set at various angles: -20°, -10°, 0°, 10°, 20° and 30° (0°: foot perpendicular to 153 154 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  $1^{\circ}$ .s<sup>-1</sup> 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° to 20°;  $r^2 =$ 178 0.99 ± 0.04).

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,

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

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 corporation, USA). First, signals were low-pass filtered (150 Hz, zero-lag 4<sup>th</sup> order 194 195 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., > 0.5199 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° and -20°. When detachment of the heel was above 5°, the trial was not considered. For each set of five contractions performed at a given starting angle, the three trials resulting in the highest  $RTD_{0-200}$  were averaged for further analysis. The peak torque corresponded to the highest peak torque value obtained among the five explosive isometric contraction performed in each ankle angle position. Maximal angular velocity during the no-load condition 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 = 55219 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 filtered (50 Hz) using a 3<sup>rd</sup> order Butterworth filter. Fascicle shortening was calculated in 226 227 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 length.  $V_{max}$  was calculated as the peak obtained during the no-load condition (25). Total 230 231 plantar flexion force was calculated from the torque divided by the Achilles tendon moment arm. Fascicle force was then calculated from the GM muscle force [i.e., 20.9% of total plantar

flexion force (13)], divided by the cosine of the pennation angle.

234

Active force-length relationship. According to the method proposed by Hoffman et al. (28),
the parallel elastic component was considered parallel to the contractile element only. Thus,
the individual fascicle force-length curve was determined by fitting passive fascicle torque
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 ankle angle condition (30°, 20°, 10°, 0°, -10°, -20° of plantar flexion; Fig. 2D). For each 242 243 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.

*Force-velocity relationship.* Neutral ankle position (0°) is the most-commonly used condition to assess plantar flexion MVC torque and RTD, and resulted in the highest RTD values. Therefore, peak fascicle force elicited during MVC performed at 0° condition ( $F_{max}$ ) was used as the maximal theoretical force for each individual (i.e.,  $F_0$  of the force-velocity relationship; 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.

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

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

where k is a constant.

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

271

*EMG.* Surface EMG activity was recorded using a wireless remote unit (Zerowire, Aurion,
Italy), on GL, SOL and TA muscles. The skin was shaved, gently abraded and cleaned with a
solution of ether, acetone and alcohol to minimize inter-electrode impedance. The bipolar,
silver/silver chloride, surface disc electrodes (Blue Sensor N-00-S/25, Medicotest, France)
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 bandpass filtered (high pass: 10 Hz, 3<sup>rd</sup> order Butterworth filter, low pass: 400 Hz, 3<sup>rd</sup> order 281 282 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  $(-20^\circ, -10^\circ, 0^\circ, 10^\circ, 20^\circ \text{ and } 30^\circ)$ 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 ach muscle (GL and SOL) using two two-way ANOVAs (time  $\times$  angle) with repeated measures. The 95% confidence interval was calculated for the force-velocity relationship (mean bias: 95%, mean difference:  $\pm 1.96$  s.d.). When the sphericity assumption in repeated measures ANOVAs was violated (Mauchly's test), a Geisser-Greenhouse correction was used. *Post-hoc* tests were performed by means of Newman-Keuls procedures for comparison 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 < 0.001) 313 0.001) and time period  $\times$  angle interaction (P < 0.001) on RTD (Table 1). Post-hoc showed that no significant effect was found on  $\text{RTD}_{0.50}$  between  $-10^{\circ}$ ,  $0^{\circ}$  and  $10^{\circ}$  (P = 0.29). These 314 315 values were significantly higher than  $\text{RTD}_{0.50}$  measured at -20° (P < 0.03) (17 ± 6%), which was significantly higher than the values obtained at 20° and 30° (33  $\pm$  16% and 57  $\pm$  28%, 316 317 respectively; P < 0.005). We found no significant differences in RTD<sub>50-100</sub> between -10°, 0° 318 and  $10^{\circ}$  (P = 0.83), and these values were significantly higher than those obtained at -20° and 319  $20^{\circ}$  (17 ± 4% and  $20 \pm 6\%$ , respectively; P < 0.04), which were significantly higher than 320 RTD<sub>50-100</sub> achieved at 30° (28  $\pm$  13%; P < 0.001). RTD<sub>100-200</sub> measured at 0°, -10° and -20° 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  $2.8 \pm 0.6$ 

at 30° and from 7.0  $\pm$  1.2 cm to 5.8  $\pm$  1.3 cm at -20° (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,  $1.22 \pm$ 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  $-20^{\circ}$ ,  $-10^{\circ}$ ,  $0^{\circ}$ ,  $10^{\circ}$ , 330 331  $20^{\circ}$  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< 0.001), with a maximal value achieved at 0° (10.8 ± 3.8 cm.s<sup>-1</sup>) and minimal at 20° (6.7 ± 333 3.7 cm.s<sup>-1</sup>; Table 1). Peak shortening velocity was significantly lower at  $-20^{\circ}$  than at  $-10^{\circ}$ ,  $0^{\circ}$ , 334 335  $10^{\circ}$ ,  $20^{\circ}$  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 ± 129 N) and  $0^\circ$  (520 ± 114 N; P =342 0.08; Fig. 4). Maximal fascicle forces produced at these angles were higher than values obtained in plantar flexion positions at  $10^\circ$ ,  $20^\circ$  and  $30^\circ$  (P < 0.001). The figure 4 allowed to 343 344 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° and 20°, while it was 347 over the descending limb at -20°. Changes in fascicle length during RTD performed at 10 and  $-10^{\circ}$  were mainly comprised between the ascending limb and the plateau at  $10^{\circ}$  and between 348 the descending limb and the plateau at -10°. Finally, the fascicles operated over the plateau 349 350 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. Inversely, the changes in fascicle length during RTD performed at -20° corresponded to the 354 355 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, 14, 16), the plateau for 6/16 participants (#7, 8, 9, 12, 13, 15), and the descending limb for 358 1/16 participant (#6). In the same way, the changes in length during RTD at  $-10^{\circ}$ 359 360 corresponded to the ascending limb for 1/16 participants (#11), the plateau for 7/16361 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  $0^{\circ}$  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 and  $33.3 \pm 8.8$  cm.s<sup>-1</sup>, respectively. At 50 ms after the onset of RTD evaluation, the measured 371 372 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  $9.26 \pm 2.85$  cm.s<sup>-1</sup> (i.e.,

377 28.2% of  $V_{max}$ ). At 112 ms, fascicle force reached 208 ± 78 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  $F_{max}$ .

380

381 *Muscle activity.* GL mean muscle activity showed no significant effect of angle (P = 0.6) and 382 time × 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).

SOL mean muscle activity showed the significant effect of angle (P < 0.001), time (P < 0.001) and time × angle interaction (P = 0.001, Table 1). *Post-hoc* showed than SOL activity was significantly higher at -20°, -10° and 0° than at 20° and 30° (P < 0.02). SOL mean activity between 0 and 50 ms was significantly lower than between 50 and 100 ms or between 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°, fascicle-shortening velocity reached ~28.2 % of  $V_{max}$  at 89 ms from RTD onset. This finding reflects that the substantial 400

401 fascicle shortening that occurs in the isometric condition causes a decrease in maximal402 fascicle force-generating capacity, according to the force-velocity relationship.

Plantar flexor RTD values  $(346 \pm 38 \text{ N.m.s}^{-1} \text{ and } 417 \pm 137 \text{ N.m.s}^{-1} \text{ for } \text{RTD}_{0.50} \text{ and}$ 403 RTD<sub>0-200</sub>, respectively) were comprised within the ranges of RTD measures obtained during 404 ankle plantar flexions [i.e., from 200 to 610 Nm.s<sup>-1</sup> (9, 46)]. In line with previous data 405 406 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° than 20° and 30°. 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).

between $5.87 \pm 0.84$ cm and $4.64 \pm 0.99$ cm, which strongly corresponds to the optimal length condition to produce force for GM muscle [Fig. 4; (28)]. Although a substantial variability was found between individuals, this finding was confirmed by individual analyses (Fig. 5). At 30° and 20°, muscle fascicles shortened over the ascending limb of the active force-length relationship, thereby limiting force and RTD. The resulting RTD in these conditions was significantly lower compared to the values clicited in neutral conditions where fascicles operated over the plateau (Fig. 4; Table 1). In the same way, at $-20^\circ$ (dorsiflexed ankle position), RTD values were lower than those obtained at 0° (Table 1). In this condition, GM fascicle mainly operated over the descending limb of the force-length relationship. Therefore, due to a decrease in the maximal force ability over the fascicle operating length, our results strongly support that the force-length properties can contribute to limit the amount of RTD achieved at $30^\circ$ , $20^\circ$ and $-20^\circ$ . Nevertheless, this mechanism should be considered together with the potential impact of ankle angle on neural activation (17, 41). For intermediate angles ( $10^\circ$ and $-10^\circ$ ), the fascicle shortening during RTD was between the ascending, descending limb and the plateau. Therefore, the influence of the force-length relationship is more mitigated for these conditions. Interestingly, while a trend was observed, RTD did not significantly differ between $10^\circ$ , $0^\circ$ and $-10^\circ$ . As a whole, these results demonstrated that using a neutral ankle position around $0^\circ$ for RTD evaluation ensures a maximal force- generating capacity in respect to the force-length relationship, and a minimal influence of the force-length properties on the amount of produced muscle force. This finding is important because it was the condition to further analyse the $0^\circ$ condition by investigating the force 447 development in light of the force-velocity properties.	425	The mean operating fascicle length during RTD <sub>0-200</sub> performed at 0° was comprised
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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  $\sim 100$  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 measured close to F<sub>max</sub>. This result supports previous reports of an increasing influence of 467 468 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° over each time window compared to 0°. 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.

The fits applied to the active voluntary force-length relationships were done in the same way than in previous published papers (11, 28). However, it should be kept in mind that it requires the calculation of five parameters. For such fits, we cannot fully ascertain that the 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<sub>0</sub> and L<sub>0</sub> 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) anthropometrical characteristics, (ii) maximal velocity (i.e.,  $30.8 \text{ cm.s}^{-1} \text{ vs.} 33.3 \pm 8.8 \text{ cm.s}^{-1}$ ) 519 520 and (iii) maximal force (420 N vs.  $520 \pm 115$  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 substantial 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 performance during explosive tasks. In the long term, it can be used to implement 538 539 individualized training programs and improve explosive strength.

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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° (c)	10° <sup>(d)</sup>	20° <sup>(e)</sup>	30° <sup>(f)</sup>
RTD (Nm.s <sup>-1</sup> )						
0-200 ms	320 ± 91 <sup>cef</sup>	354 ± 117 <sup>et</sup>	389 ± 94 <sup>aet</sup>	329 ± 94 <sup>ef</sup>	265 ± 66 <sup>abcdf</sup>	194.5 ± 53 <sup>abcde</sup>
0-50 <sup>hi</sup> ms	141 ± 61 <sup>bcdef</sup>	208 ± 127 <sup>aef</sup>	178 ± 105 <sup>aet</sup>	203 ± 113 <sup>aef</sup>	106 ±53 <sup>bdc</sup>	$81 \pm 45^{bdc}$
50-100 <sup>g</sup> ms	413 ± 136 <sup>bcdf</sup>	$496 \pm 210^{\circ}$	549 ± 178 <sup>aet</sup>	$483 \pm 168^{t}$	388 ± 150 <sup>ct</sup>	280 ± 129 <sup>abcde</sup>
100-200 <sup>g</sup> ms	361 ± 128 <sup>ef</sup>	357 ± 128 <sup>et</sup>	414 ± 98 <sup>def</sup>	317 ± 81 <sup>cf</sup>	284 ± 60 <sup>abcf</sup>	$210 \pm 59^{abcde}$
Peak Fascicle velocity (cm.s <sup>-1</sup> )						
	6.1 ± 3.4 <sup>bcdef</sup>	$8.6 \pm 4.0^{a}$	$10.8 \pm 3.8^{a}$	$10.6 \pm 3.0^{a}$	$9.8 \pm 3.2^{a}$	8.6 + 3.4 <sup>a</sup>
Mean EMG GL (% RMS max)						
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	76.3 ± 16.6
Mean EMG SOL (% RMS max)	de	de	de		abc	abc
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>n</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>9</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

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566

567 Values are mean  $\pm$  SD (n = 16).

568 a, b, c, d, e and f: 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  $RTD_{0-50}$ ,  $RTD_{50-100}$  and  $RTD_{100-200}$ , respectively [P < 0.05; one-way ANOVA, main effects: ankle angle (-

571  $20^{\circ}, -10^{\circ}, 0^{\circ}, 10^{\circ}, 20^{\circ}, 30^{\circ}) \times \text{time period } (0-50, 50-100, 100-200 \text{ ms})].$ 

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

573

### 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  $0^{\circ}$  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).

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

605 Figure 4. Raw (A) and normalized (B) mean active force-length relationship obtained during maximal contractions performed at -20°, -10°, 0°, 10°, 20° and 30° of ankle angle 606 607 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 the values achieved at 50, 100 and 200 ms during RTD. Fascicle forces values obtained at -612 613  $20^{\circ}$ ,  $-10^{\circ}$  and  $0^{\circ}$  were significantly higher than values obtained at  $10^{\circ}$ ,  $20^{\circ}$  and  $30^{\circ}$  [P < 614 0.001; one-way ANOVA, main effect: ankle angle  $(-20^\circ, -10^\circ, 0^\circ, 10^\circ, 20^\circ \text{ and } 30^\circ)$ ].

Figure 5. Individual active force-length relationship obtained during maximal contractions
performed at -20°, -10°, 0°, 10°, 20° and 30° of ankle angle assuming the model B from
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.

#### 625 **REFERENCES**

626 Aagaard P, Simonsen EB, Andersen JL, Magnusson P, and Dyhre-Poulsen P. 1. 627 Increased rate of force development and neural drive of human skeletal muscle following resistance training. J Appl Physiol 93: 1318-1326, 2002. 628 629 Alexander RM, and Bennet-Clark HC. Storage of elastic strain energy in muscle 2. 630 and other tissues. Nature 265: 114-117, 1977. 631 An KN, Takahashi K, Harrigan TP, and Chao EY. Determination of muscle 3. 632 orientations and moment arms. J Biomech Eng 106: 280-282, 1984. 633 4. Andersen LL, and Aagaard P. Influence of maximal muscle strength and intrinsic 634 muscle contractile properties on contractile rate of force development. Eur J Appl Physiol 96: 635 46-52, 2006. Andersen LL, Andersen JL, Zebis MK, and Aagaard P. Early and late rate of force 636 5. 637 development: differential adaptive responses to resistance training? Scand J Med Sci Sports 638 20: e162-169, 2010. 639 6. Azizi E, and Deslauriers AR. Regional heterogeneity in muscle fiber strain: the role 640 of fiber architecture. Front Physiol 5: 303, 2014. 641 Beaumatin N, Hauraix H, Nordez A, Hager R, Rabita G, Guilhem G, and Dorel 7. 642 S. Maximal shortening velocity during plantar flexion: Effects of pre-activity and initial 643 stretching state. Scand J Med Sci Sports 28: 1361-1370, 2018. 644 Behan FP, Pain MTG, and Folland JP. Explosive voluntary torque is related to 8. 645 whole-body response to unexpected perturbations. J Biomech 81: 86-92, 2018. 646 9. Behm DG, Whittle J, Button D, and Power K. Intermuscle differences in activation. 647 Muscle Nerve 25: 236-243, 2002. 648 10. Brainerd EL, and Azizi E. Muscle fiber angle, segment bulging and architectural 649 gear ratio in segmented musculature. J Exp Biol 208: 3249-3261, 2005. 650 11. Brennan SF, Cresswell AG, Farris DJ, and Lichtwark GA. The effect of muscle-651 tendon unit vs. fascicle analyses on vastus lateralis force-generating capacity during constant 652 power output cycling with variable cadence. Journal of applied physiology (Bethesda, Md : 653 1985) 124: 993-1002, 2018. 654 12. Cronin NJ, and Lichtwark G. The use of ultrasound to study muscle-tendon function 655 in human posture and locomotion. Gait Posture 37: 305-312, 2013. 656 13. Crouzier M, Lacourpaille L, Nordez A, Tucker K, and Hug F. Neuromechanical 657 coupling within the human triceps surae and its consequence on individual force-sharing 658 strategies. J Exp Biol 221: 2018. de Ruiter CJ, Kooistra RD, Paalman MI, and de Haan A. Initial phase of maximal 659 14. 660 voluntary and electrically stimulated knee extension torque development at different knee 661 angles. J Appl Physiol 97: 1693-1701, 2004. de Ruiter CJ, Vermeulen G, Toussaint HM, and de Haan A. Isometric knee-662 15. 663 extensor torque development and jump height in volleyball players. Med Sci Sports Exerc 39: 664 1336-1346, 2007. 665 Del Vecchio A, Negro F, Holobar A, Casolo A, Folland JP, Felici F, and Farina D. 16. 666 You are as fast as your motor neurons: speed of recruitment and maximal discharge of motor 667 neurons determine the maximal rate of force development in humans. J Physiol 597: 2445-668 2456, 2019. 669 Duchateau J, and Enoka RM. Human motor unit recordings: Origins and insight into 17. 670 the integrated motor system. Brain Res 2011. Farris DJ, and Lichtwark GA. UltraTrack: Software for semi-automated tracking of 671 18. 672 muscle fascicles in sequences of B-mode ultrasound images. Comput Methods Programs

673 *Biomed* 128: 111-118, 2016.

674 19. Folland JP, Buckthorpe MW, and Hannah R. Human capacity for explosive force 675 production: neural and contractile determinants. Scand J Med Sci Sports 24: 894-906, 2014. 676 Fukunaga T, Kawakami Y, Kubo K, and Kanehisa H. Muscle and tendon 20. 677 interaction during human movements. Exerc Sport Sci Rev 30: 106-110, 2002. 678 21. Fukunaga T, Kawakami Y, Kuno S, Funato K, and Fukashiro S. Muscle 679 architecture and function in humans. J Biomech 30: 457-463, 1997. 680 Gerstner GR, Giuliani HK, Mota JA, and Ryan ED. Age-related reductions in 22. 681 muscle quality influence the relative differences in strength and power. Exp Gerontol 99: 27-682 34, 2017. 683 23. Hager R, Dorel S, Nordez A, Rabita G, Couturier A, Hauraix H, Duchateau J, 684 and Guilhem G. The slack test does not assess maximal shortening velocity of muscle 685 fascicles in humans. J Exp Biol 221: 2018. 686 24. Hauraix H, Nordez A, and Dorel S. Shortening behavior of the different components 687 of muscle-tendon unit during isokinetic plantar flexions. J Appl Physiol 115: 1015-1024, 688 2013. 689 25. Hauraix H, Nordez A, Guilhem G, Rabita G, and Dorel S. In vivo maximal 690 fascicle-shortening velocity during plantar flexion in humans. Journal of applied physiology 691 (Bethesda, Md: 1985) 119: 1262-1271, 2015. 692 26. Hermens HJ, Freriks B, Disselhorst-Klug C, and Rau G. Development of 693 recommendations for SEMG sensors and sensor placement procedures. J Electromyogr 694 Kinesiol 10: 361-374, 2000. 695 27. Hill AV. The heat of shortening and the dynamic constants of muscle. *Proceedings of* 696 the Royal Society of London Series B - Biological Sciences 126: 136-195, 1997. 697 Hoffman BW, Lichtwark GA, Carroll TJ, and Cresswell AG. A comparison of two 28. Hill-type skeletal muscle models on the construction of medial gastrocnemius length-tension 698 699 curves in humans in vivo. J Appl Physiol 113: 90-96, 2012. 700 Ito M, Kawakami Y, Ichinose Y, Fukashiro S, and Fukunaga T. Nonisometric 29. 701 behavior of fascicles during isometric contractions of a human muscle. J Appl Physiol 85: 702 1230-1235, 1998. 703 30. Kawakami Y, Ichinose Y, and Fukunaga T. Architectural and functional features of 704 human triceps surae muscles during contraction. J Appl Physiol 85: 398-404, 1998. 705 31. Kubo K, Kanehisa H, and Fukunaga T. Effects of resistance and stretching training 706 programmes on the viscoelastic properties of human tendon structures in vivo. J Physiol 538: 707 219-226, 2002. 708 32. Kubo K, Kanehisa H, Kawakami Y, and Fukanaga T. Growth changes in the 709 elastic properties of human tendon structures. Int J Sports Med 22: 138-143, 2001. 710 33. Lambertz D, Paiva MG, Marinho SM, Aragao RS, Barros KM, Manhaes-de-711 Castro R, Khider N, and Canon F. A reproducibility study on musculotendinous stiffness 712 quantification, using a new transportable ankle ergometer device. J Biomech 41: 3270-3273, 713 2008. 714 34. Lanza MB, Balshaw TG, and Folland JP. Explosive strength: effect of knee-joint 715 angle on functional, neural, and intrinsic contractile properties. Eur J Appl Physiol 119: 1735-716 1746, 2019. 717 35. Lee SS, and Piazza SJ. Built for speed: musculoskeletal structure and sprinting 718 ability. J Exp Biol 212: 3700-3707, 2009. 719 Lichtwark GA, and Wilson AM. Is Achilles tendon compliance optimised for 36. 720 maximum muscle efficiency during locomotion? J Biomech 40: 1768-1775, 2007. 721 Maffiuletti NA, Aagaard P, Blazevich AJ, Folland J, Tillin N, and Duchateau J. 37. 722 Rate of force development: physiological and methodological considerations. Eur J Appl

723 *Physiol* 2016.

724 38. Maganaris CN. Imaging-based estimates of moment arm length in intact human 725 muscle-tendons. Eur J Appl Physiol 91: 130-139, 2004. 726 Maganaris CN. A predictive model of moment-angle characteristics in human 39. 727 skeletal muscle: application and validation in muscles across the ankle joint. J Theor Biol 230: 728 89-98, 2004. 729 Massev GJ, Balshaw TG, Maden-Wilkinson TM, Tillin NA, and Folland JP. The 40. 730 influence of patellar tendon and muscle-tendon unit stiffness on quadriceps explosive strength 731 in man. Exp Physiol 2017. 732 41. Mayfield DL, Cresswell AG, and Lichtwark GA. Effects of series elastic 733 compliance on muscle force summation and the rate of force rise. J Exp Biol 2016. 734 Mayfield DL, Lichtwark GA, Cronin NJ, Avela J, and Cresswell AG. Doublet 42. 735 potentiation in the triceps surae is limited by series compliance and dynamic fascicle 736 behavior. Journal of applied physiology (Bethesda, Md: 1985) 119: 807-816, 2015. 737 Palmer TB, Hawkey MJ, Thiele RM, Conchola EC, Adams BM, Akehi K, Smith 43. 738 DB, and Thompson BJ. The influence of athletic status on maximal and rapid isometric 739 torque characteristics and postural balance performance in Division I female soccer athletes 740 and non-athlete controls. Clin Physiol Funct Imaging 35: 314-322, 2015. 741 Penailillo L, Blazevich A, Numazawa H, and Nosaka K. Rate of force development 44. 742 as a measure of muscle damage. Scand J Med Sci Sports 25: 417-427, 2015. 743 45. Reeves ND, and Narici MV. Behavior of human muscle fascicles during shortening 744 and lengthening contractions in vivo. J Appl Physiol 95: 1090-1096, 2003. 745 Ricard MD, Ugrinowitsch C, Parcell AC, Hilton S, Rubley MD, Sawyer R, and 46. 746 **Poole CR**. Effects of rate of force development on EMG amplitude and frequency. Int J Sports Med 26: 66-70, 2005. 747 748 Rousanoglou EN, Herzog W, and Boudolos KD. Moment-Angle Relations in the 47. 749 Initial Time of Contraction. Int J Sports Med 31: 651-655, 2010. 750 Spector SA, Gardiner PF, Zernicke RF, Roy RR, and Edgerton VR. Muscle 48. 751 architecture and force-velocity characteristics of cat soleus and medial gastrocnemius: 752 implications for motor control. J Neurophysiol 44: 951-960, 1980. 753 49. Tillin NA, Jimenez-Reves P, Pain MT, and Folland JP. Neuromuscular 754 performance of explosive power athletes versus untrained individuals. Med Sci Sports Exerc 755 42: 781-790, 2010. 756 50. Tillin NA, Pain MT, and Folland JP. Contraction type influences the human ability 757 to use the available torque capacity of skeletal muscle during explosive efforts. Proc Biol Sci 758 279: 2106-2115, 2012. 759 51. Tillin NA, Pain MT, and Folland JP. Identification of contraction onset during 760 explosive contractions. Response to Thompson et al. "Consistency of rapid muscle force 761 characteristics: Influence of muscle contraction onset detection methodology" [J 762 Electromyogr Kinesiol 2012;22(6):893-900]. J Electromyogr Kinesiol 2013. 763 Tillin NA, Pain MTG, and Folland JP. Contraction speed and type influences rapid 52. 764 utilisation of available muscle force: neural and contractile mechanisms. J Exp Biol 221: 765 2018. 766 53. Waugh CM, Korff T, Fath F, and Blazevich AJ. Rapid force production in children 767 and adults: mechanical and neural contributions. Med Sci Sports Exerc 45: 762-771, 2013.











