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Running title: Muscle-tendon interactions and explosive strength

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ABSTRACT

This study investigated how joint angle influences fascicle shortening dynamics of gastrocnemius medialis (GM) during explosive contractions, and the resulting impact on rate of torque development (RTD). Sixteen participants performed six sets of five maximal explosive voluntary isometric plantar flexions at -20°, -10°, 0° (neutral position), 10°, 20° and 30° of ankle angle, and five no-load ballistic plantar flexions. RTD assessed over all time windows (from 0 to 200 ms) was significantly lower in extreme plantar flexed (≥20°) and dorsiflexed (- 20°) positions compared to -10, 0° (475±105 $Nm.s^{-1}$) and 10°. At these neutral 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 $cm.s^{-1}$ (i.e., 28.2% of maximal shortening velocity measured during no-load ballistic condition). At 112 ms after RTD onset, fascicle force reached 208 ± 78 N (i.e., 85.6% of the theoretical maximum force at the corresponding shortening velocity) and was thereafter comprised 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. These findings suggest that the dynamic behavior of muscle fascicles, and the associated fascicle shortening velocity, may influence the rapid force-generating capacity mainly from 100 ms of RTD onset. The present study provides important information to better understand the determinants of human muscle performance during explosive tasks.

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.

INTRODUCTION

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

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

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

The present study aimed to examine the behaviour of *gastrocnemius medialis* (GM) muscle fascicle during a voluntary RTD test. Maximal explosive isometric contractions of plantar flexor muscles were performed at various ankle positions (from -20° in dorsiflexion to 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.

METHODS

Participants

Ten males and six females (age: 23.2 ± 2.7 years, height: 175.3 ± 6.4 cm, body mass: 70.2 ± 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.

Experimental design

All participants attended one familiarization session and one testing session a few days later. During these sessions, after a 10-minute standardized warm-up, participants performed 5 ballistic plantar flexions with no external load (load = 0 kg) on a specific ergometer composed of a specific rotational footplate (Bio2M, Compiegne, France). Participants then performed six sets of five repetitions of explosive voluntary isometric contractions to reach maximal force of the plantar flexor muscles in a randomized order at various ankle angles (from -20° in dorsiflexion to 30° in plantar flexion) on an Eracles-system mechatronic ergometer (Eracles-Technology, Compiègne, France; Fig. 1). RTD and MVC peak torque were assessed on the same repetitions to avoid fatigue occurrence. We performed pilot analyses that showed no significant difference between these metrics assessed during the same contractions when sufficient time was allowed to the participants were instructed to push “as fast and as hard as possible” with sufficient time (5 s) to then achieve MVC torque plateau (37). We performed pilot analyses that showed no significant difference in peak MCV torque between trials performed in this condition and in a conventional MVC measurement. Therefore, we think that this issue marginally influenced our results. At the end of the protocol, two passive dorsiflexion cycles were performed on the same ergometer at $1°.s^{-1}$ to estimate triceps surae moment arm (see moment arm section) and to subtract the passive torque to the raw torque in order to obtain the active torque to build the active force-length relationship (see data processing). During each explosive contraction performed at each ankle angle (Fig.1), mechanical parameters (i.e., torque, displacement, velocity), muscle fascicle length and velocity of GM, surface electromyography (EMG) activity of *gastrocnemius lateralis* (GL), *soleus* (SOL) and *tibialis anterior* (TA) were simultaneously recorded.

Equipment and procedure

Voluntary isometric explosive contractions. Voluntary isometric explosive contractions were performed on an Eracles-system mechatronic ergometer (Eraclès-Technology, Compiègne, France) previously described (23). Participants were placed in prone position, with the knee fully extended (0°: full knee extension) and firmly attached to the ergometer by harness. The 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 tibia; positive positions in plantar flexion direction; Fig. 2). Participants were instructed to contract “as fast and hard as possible” in order to reach maximal torque from a relaxed condition (37) after a standardized 3-second countdown with a visual feedback of the force trace and oral feedback of their RTD score measured from 0 to 200 ms after torque onset.

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

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

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

No-load ballistic contraction. In order to determine maximal fascicle shortening velocity (V_{max}), participants performed maximal dynamic plantar flexions with no external load on a 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° 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_{max}.

Data collection and processing

Mechanical data. Joint angle, angular velocity and torque were recorded at 2000 Hz using an analog-to-digital converter designed by our laboratory (Custom DT, INSEP, Paris, France). Mechanical signals were analysed using custom-written scripts (Origin 9.1, OriginLab corporation, USA). First, signals were low-pass filtered (150 Hz, zero-lag 4th order Butterworth). Then, we determined the onset of contraction during RTD using the torque signal according to the systematic approach proposed by Tillin et al. (51). The onset of torque production was manually determined as previously described by Tillin et al. (49) before low-pass filtering. First, recordings where the baseline (resting) torque was not stable (i.e., > 0.5 N.m the preceding 100 ms) were discarded. Second signals were checked with a consistent scale (e.g. 500 ms vs. 1 N). Third, the investigator placed manually a dashed line on the apex of the last peak/trough before the signal deflected from the baseline noise. RTD was calculated as the rising torque divided by the time windows [i.e., a straight line: from 0 to 200 ms ($RTD_{0–200}$), from 0 to 50 ms (RTD_{0-50}) from 50 to 100 ms (RTD_{50-100}), and from 100 to 200 ms ($RTD_{100-200}$)]. Mean displacement of the heel was monitored using an electronic goniometer (Biometrics, Gometz-le-Châtel, France). The mean displacement was measured at respectively 1 ± 1°, 1 ± 1°, 1 ± 2°, 2 ±2°, 2 ± 2° and 2 ± 2° at respectively 30°, 20°, 10°, 0°, -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° to 20° of plantar flexion (25).

Ultrasound. An ultrafast ultrasound scanner (Aixplorer, Supersonic Imagine, Aix en Provence, France) coupled with a linear transducer array (4-15 MHz, SuperLinear 15-4, Vermon, Tours, France) was used to acquire ultrasonic raw data from the GM muscle at a sampling frequency of 1000 Hz for RTD and 2000 Hz for the no-load condition. The ultrasonic raw data were used to create B-mode images (depth = 30 to 50 mm, width = 55 mm; in order to visualize the whole muscle thickness for each participant) by applying conventional beamforming through Matlab software (Version, The Mathworks, Natick, MA). The ultrasound probe was placed on the skin surface at 30% of the distance between the popliteal fossa area and the centre of the lateral malleolus. A specific cast was used during contractions to keep the probe in the same location throughout the measurements. Changes in GM fascicle length (Fig. 2A) and pennation angle were assessed in every frame over 500 ms using the automatic tracking method proposed by Farris and Lichtwark (18) and low-pass filtered (50 Hz) using a 3rd order Butterworth filter. Fascicle shortening was calculated in every frame over the same time window used to determine RTD (i.e., 200 ms), over the whole range of motion in the passive condition to build the fascicle force-length relationship. 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 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.

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):

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

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

To build the fascicle total force-length relationship, the peak fascicle force and the 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 point, the x-coordinate corresponded to the fascicle length measured when GM fascicle force was maximal. The y-coordinate corresponded to the peak fascicle force minus the passive force measured at the same fascicle length on the passive force-length curve (28). The active force-length relationship was fitted using the previously suggested methods (11, 28). A Levenberg-Marquardt algorithm was used to calculate five parameters (Origin 9.1, OriginLab corporation, USA): the maximal force, the fascicle length at the maximal force (i.e., optimal fascicle length, L_0), the roundness, the skewness, and the width of the relationship. No constraints were used, excepted when the fitted relationship resulted in non-physiological data (see discussion section). The optimal fascicle length and maximal force were then used to build the normalized force-length relationship for each individual and the whole sample of 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):

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

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 force-velocity data obtained during RTD testing crossed the lower limit of 95% confidence interval of the mean force-velocity relationship.

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

Statistical analysis

All statistical analyses were performed with Statistica (StatSoft, Tulsa, Oklahoma, USA). All data being normally distributed (Shapiro-Wilk's test), all results are expressed as means ± s.d. Statistical significance was set at $P < 0.05$. The potential effects of ankle angle (-20°, -10°, 0°, 10°, 20° and 30°) on peak GM fascicle force, fascicle length corresponding to peak force, fascicle length corresponding to the onset of RTD (in passive condition, before the onset of the contraction), fascicle length changes over the first 200 ms, peak fascicle shortening velocity and time to peak shortening velocity were determined by one-way ANOVAs (angle effect) with repeated measures. The effects of ankle angle (-20°, -10°, 0°, 10°, 20° and 30°) and time period (0-50, 50-100 and 100-200 ms) on RTD were tested by a two-way ANOVA (angle × time period) with repeated measures. Differences in muscle activation were tested for each muscle (GL and SOL) using two two-way ANOVAs (time × angle) with repeated measures. The 95% confidence interval was calculated for the force-velocity relationship (mean bias: 95%, mean difference: ±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.

RESULTS

Effect of joint angle on RTD

Figure 3A shows changes in torque during RTD evaluation for all tested angles over time. The two-way ANOVA showed significant main effects of angle ($P < 0.001$), time period ($P < 0.001$) and time period × angle interaction ($P < 0.001$) on RTD (Table 1). *Post-hoc* showed that no significant effect was found on $RTD_{0\text{-}50}$ between -10°, 0° and 10° ($P = 0.29$). These values were significantly higher than $RTD_{0\text{-}50}$ measured at -20° ($P < 0.03$) (17 ± 6%), which was significantly higher than the values obtained at 20° and 30° (33 ± 16% and 57 ± 28%, respectively; $P < 0.005$). We found no significant differences in $RTD_{50\text{-}100}$ between -10°, 0° and 10° ($P = 0.83$), and these values were significantly higher than those obtained at -20° and 20° (17 ± 4% and 20 ± 6%, respectively; $P < 0.04$), which were significantly higher than $RTD_{50\text{-}100}$ achieved at 30° (28 ± 13%; $P < 0.001$). $RTD_{100\text{-}200}$ measured at 0°, -10° and -20° were significantly higher than the values obtained at 10° (11 ± 4%; $P = 0.02$), which was significantly higher than the values obtained at 20° and 30° (12 ± 3% and 33 ± 3%; $P < 0.02$).

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

At the two extreme ankle angle positions, GM fascicle operated from 3.6 ± 0.7 cm to 2.8 ± 0.6 at 30° and from 7.0 ± 1.2 cm to 5.8 ± 1.3 cm at -20° (Fig. 3). These fascicle length changes were significantly different between all conditions (angle effect; $P < 0.05$), showing the substantial effect of the ankle angle on this parameter. In all conditions, fascicle shortening occurred mainly in the first 200 ms, corresponding to 0.67 ± 0.37 cm, 1.02 ± 0.38 cm, 1.22 ± 0.49 cm, 1.21 ± 0.48 cm, 1.06 ± 0.40 cm and 0.85 ± 0.33 cm for angles of -20°, -10°, 0°, 10°, 20° and 30°, respectively. Fascicle shortening was significantly lower at -20° than in other 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 $cm.s^{-1}$) and minimal at 20° (6.7 ± 3.7 $cm.s^{-1}$; Table 1). Peak shortening velocity was significantly lower at -20° than at -10°, 0°, 10°, 20° and 30° ($P < 0.001$).

RTD performance in relation with force-length relationship

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

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

RTD performance in relation with fascicle force-velocity relationship

The 0° condition elicited a fascicle shortening range centred over optimal GM fascicle length values commonly reported in voluntary contractions (i.e., ~5 cm, Fig. 2D). The average force-velocity relationship of GM is displayed in Figure 6. The theoretical maximal fascicle force and maximal fascicle shortening velocity obtained from this relationship reached 521 ± 115 N and 33.3 ± 8.8 $cm.s^{-1}$, respectively. At 50 ms after the onset of RTD evaluation, the measured fascicle force (51 ± 30 N) was low compared to the theoretical maximal force the individuals were able to produce at the corresponding fascicle-shortening velocity (278 ± 61 N, Fig. 6). Between 50 and 100 ms, the force increased up to 177 ± 73 N (i.e., 72.5% of the theoretical maximum force at this corresponding specific shortening velocity) while the shortening velocity continued to increase and reached a plateau corresponding to 9.26 ± 2.85 $cm.s^{-1}$ (i.e., 28.2% of V_{max}). At 112 ms, fascicle force reached 208 ± 78 N (i.e., 85.6% of the theoretical maximum force at this velocity) and was thereafter comprised within the 95% confidence interval of the force-velocity relationship up to F_{max}.

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

DISCUSSION

The present study aimed to determine the influence of joint angle on the plantar flexor RTD and associated fascicle dynamics measured during an explosive isometric contraction. In line with our hypothesis, the results revealed a significant shortening of GM fascicles during explosive isometric contractions, which was significantly influenced by joint angle. RTD measured over a 200-ms period reached higher values at 10°, 0° and 10° than in dorsiflexed (-20°) and plantar flexed (20° and 30°) positions. This could mainly originate from the fact that GM fascicles operate over the plateau of the force-length relationship in these neutral 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 fascicle shortening that occurs in the isometric condition causes a decrease in maximal fascicle force-generating capacity, according to the force-velocity relationship.

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

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

The mean operating fascicle length during RTD_{0-200} performed at 0° was comprised between 5.87 ± 0.84 cm and 4.64 ± 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 elicited in neutral conditions where fascicles operated over the plateau (Fig. 4; Table 1). In the same way, at -20° (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°, 20° and -20°. Nevertheless, this mechanism should be considered together with the potential impact of ankle angle on neural activation (17, 41). For intermediate angles (10° and -10°), 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°, 0° and -10°. As a whole, these results demonstrated that using a neutral ankle position around 0° 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° condition by investigating the force development in light of the force-velocity properties.

Our results enable the identification of different phases of RTD performed in this 0° neutral condition. Firstly, from 0 to 50 ms, mean EMG activity (Table 1) and fascicle force generated at the associated fascicle velocity was divergent from the maximal EMG activity and the maximal force-velocity capacities of individuals. Therefore, in this phase, RTD may be mainly related to the activation dynamics. Indeed, Del Vecchio et al. (16) showed that the individual ability to produce force rapidly in this early phase of RTD is highly dependent on motor unit recruitment and discharge rate. Secondly, from 50 to 100 ms, the mean fascicle force generated at the associated velocity progressively approached the force-velocity relationship (Fig. 6). During this phase, EMG activity was significantly higher than in the other time windows. Thus, in this phase, explosive strength still depends on activation and progressively on the force-velocity properties. Thirdly, after ~100 ms, the mean fascicle force generated at the associated fascicle velocity measured during RTD matched with the maximal force-velocity properties (Fig. 6).

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

The impact of fascicle dynamics on RTD could be influenced by the stiffness of the elastic tissues (19, 36, 37, 41). Waugh et al. (53) showed that Achilles tendon stiffness could account for up to 35% of the variability in RTD normalized to its peak value, while Kubo (31) suggested that the link between changes in tendon properties and RTD may be divergent. Mayfield, et al. (41, 42) showed a modest decrease in fascicle shortening velocity with increasing the effective stiffness (manipulated by applying a rapid rotation of the foot at the onset of contraction) during electrically-evoked RTD, thereby increasing force-generating capacity. During voluntary contractions, the present protocol placed the elastic tissues in a configuration where their passive stiffness increased when the ankle was in dorsiflexed angles. The present study confirms that this rise in tendon stiffness in dorsiflexed positions reduces fascicle shortening velocity (Table 1). However, although the decrease in fascicle velocity is theoretically beneficial for producing high levels of force rapidly, mean RTD was significantly lower at -20° over each time window compared to 0°. This finding suggests that the impairment of the force-generating capacity during RTD in dorsiflexed ankle configuration is mainly related to the fact that fascicles are forced to operate over the descending limb of the force-length relationship. This result clearly shows the interplay between tendon stiffness and fascicle mechanics that remain very difficult to dissociate *in vivo* and may in turn substantially contribute to the observed variability between individuals. Future research is required to find the best compromise between the mechanical properties of both tendinous and contractile tissues, and thereby optimize fascicle dynamics for RTD 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 rather considered as an estimation about the theoretical force-length relationship. This should not be considered as a main issue given that the parameters extracted from the fits were not used in the present paper, excepted F_0 and L_0 for the average normalized force-length relationship (Fig. 4B). In addition, for three participants (#11, 13 and 16, Fig. 5), the L_0 was extrapolated in regards to the measured data points. Thus, the normalized force-length relationship should be considered with caution. The force-velocity relationship was estimated from Hill's model that was fitted on the basis of measured values of maximal force and maximal shortening velocity. First, we assume that the fascicle velocity reached during no-load ballistic plantar flexions is representative of the theoretical maximal velocity value (5). Indeed, previous studies from our group have shown this method to be effective in assessing the active V_{max} that muscle fascicles can achieve *in vivo* (7, 23, 25). Second, the curvature coefficients were taken from the mean values of a previous study (25). Ideally, the fascicle force-velocity curvature coefficient could be individualized from data collected under different loading conditions (25). The inclusion of concentric contractions at various velocities would have also permitted to consider the intricate influence of both length and velocity changes on RTD at intermediate shortening velocities using a 3-D force-length-velocity relationship (50, 52). However, in the present study, it was not possible to add the conditions required for this procedure due to the increased of fatigue due to this protocol. Nevertheless, compared to the study by Hauraix et al. (25), participants had similar (i) anthropometrical characteristics, (ii) maximal velocity (i.e., 30.8 $cm.s^{-1}$ *vs*. 33.3 ± 8.8 $cm.s^{-1}$) and (iii) maximal force (420 N *vs*. 520 ± 115 N). Therefore, we are confident that our approach is sufficiently robust to interpret the force and fascicle shortening velocity obtained during isometric RTD testing in light of the mean force-velocity relationship.

Conclusion

The present study demonstrates that joint angle substantial influence the rate of torque development, associated fascicle length changes and shortening velocity expressed during explosive maximal isometric plantar flexions. Force-length properties mainly account for the effect of ankle angle on RTD, which peaked around the neutral ankle positions where fascicles operated over the plateau of the fascicle force-length relationship. After ~100 ms from the onset of RTD, the fascicle force was very close to its maximal theoretical value considering the associated shortening velocity (i.e., according to the force-velocity relationship). While an initial phase is required to initiate the tendon stretch and maximally activate the muscle, RTD is mainly influenced by muscle mechanics and the force-velocity properties from 100 ms after RTD onset. This contribution of contractile properties to the ability to generate force rapidly may also be modulated by the mechanical properties of elastic tissues due to the inherent interplay between muscle and tendon *in vivo*. The present study 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 individualized training programs and improve explosive strength.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

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

Ankle angle	-20° $^{(a)}$	-10° $^{(b)}$	0° $^{(c)}$	10°$^{(d)}$	20°$^{(e)}$	30°$^{(f)}$
RTD (Nm.s^{-1})						
0-200 ms	320 ± 91^{cef}	354 ± 117^{ef}	389 ± 94^{aef}	329 ± 94^{ef}	265 ± 66^{abcdf}	194.5 ± 53^{abcde}
0-50^{hi} ms	141 ± 61^{bcdef}	208 ± 127^{aef}	178 ± 105^{aef}	203 ± 113^{aef}	106 ±53^{bdc}	81 ± 45^{bdc}
50-100^{g} ms	413 ± 136^{bcdf}	496 ± 210^{f}	549 ± 178^{aef}	483 ± 168^{f}	388 ± 150^{cf}	280 ± 129^{abcde}
100-200^{g} ms	361 ± 128^{ef}	357 ± 128^{ef}	414 ± 98^{def}	317 ± 81^{cf}	284 ± 60^{abcf}	210 ± 59^{abcde}
Peak Fascicle velocity (cm.s^{-1})						
	6.1 ± 3.4^{bcdef}	8.6 ± 4.0^{a}	10.8 ± 3.8^{a}	10.6 ± 3.0^{a}	9.8 ± 3.2^{a}	8.6 + 3.4^{a}
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^{h} 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^{gi} 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^{h} ms	62.5 ± 22.3^{g} ^{de}	57.8 ± 18.6^{g} ^{de}	60.5 ± 19.2^{g} ^{de}	62.7 ± 18.1^{g}	64.5 ± 17.3 ^{abc}	76.3 ± 16.6 ^{abc}
Mean EMG SOL (% RMS max)						
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^{hi} 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^{g} 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^{g} 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

Values are mean ± SD (n = 16).

^{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 (-20°, -10°, 0°, 10°, 20°, 30°)].

^{g}, ^{h} and ^{i}: significantly different than RTD_{0-50}, RTD_{50-100} and $RTD_{100-200}$, respectively [*P* < 0.05; one-way ANOVA, main effects: ankle angle (-20°, -10°, 0°, 10°, 20°, 30°) × time period (0-50, 50-100, 100-200 ms)].

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

FIGURES LEGENDS

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

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

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

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 assuming the model B from Hoffman et al. [(29); n = 16)]. The force-length relationship was normalized (B) using the maximal force (F_0) and the optimal fascicle length (L_0) obtained using individual fits. Colour traces represents the time-course of force and fascicle length changes that occurred during the evaluation of rate of torque development (RTD; i.e., from 0 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 -20°, -10° and 0° were significantly higher than values obtained at 10°, 20° and 30° [P < 0.001; one-way ANOVA, main effect: ankle angle (-20°, -10°, 0°, 10°, 20° and 30°)].

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).

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

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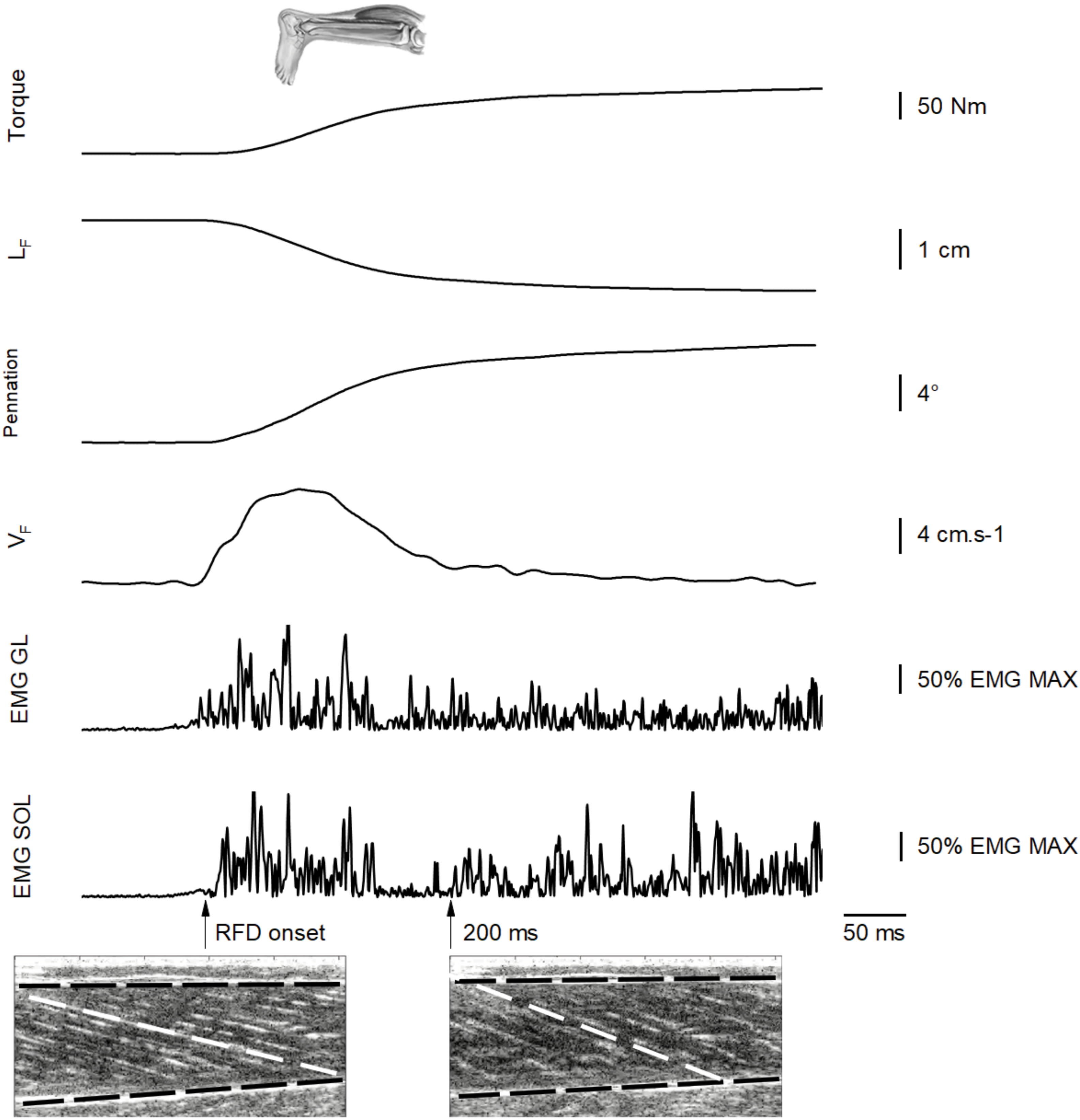
Torque
50 Nm
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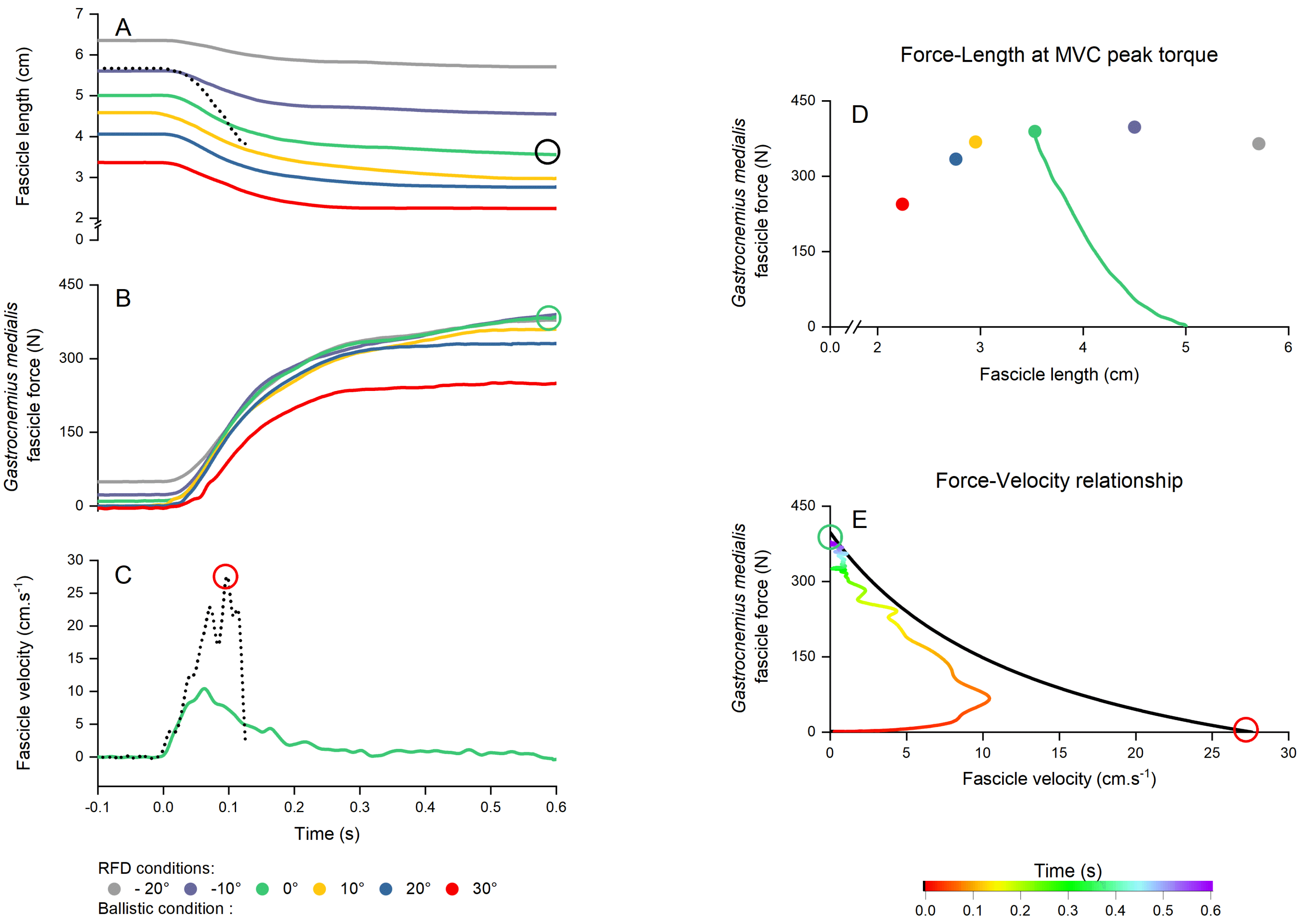
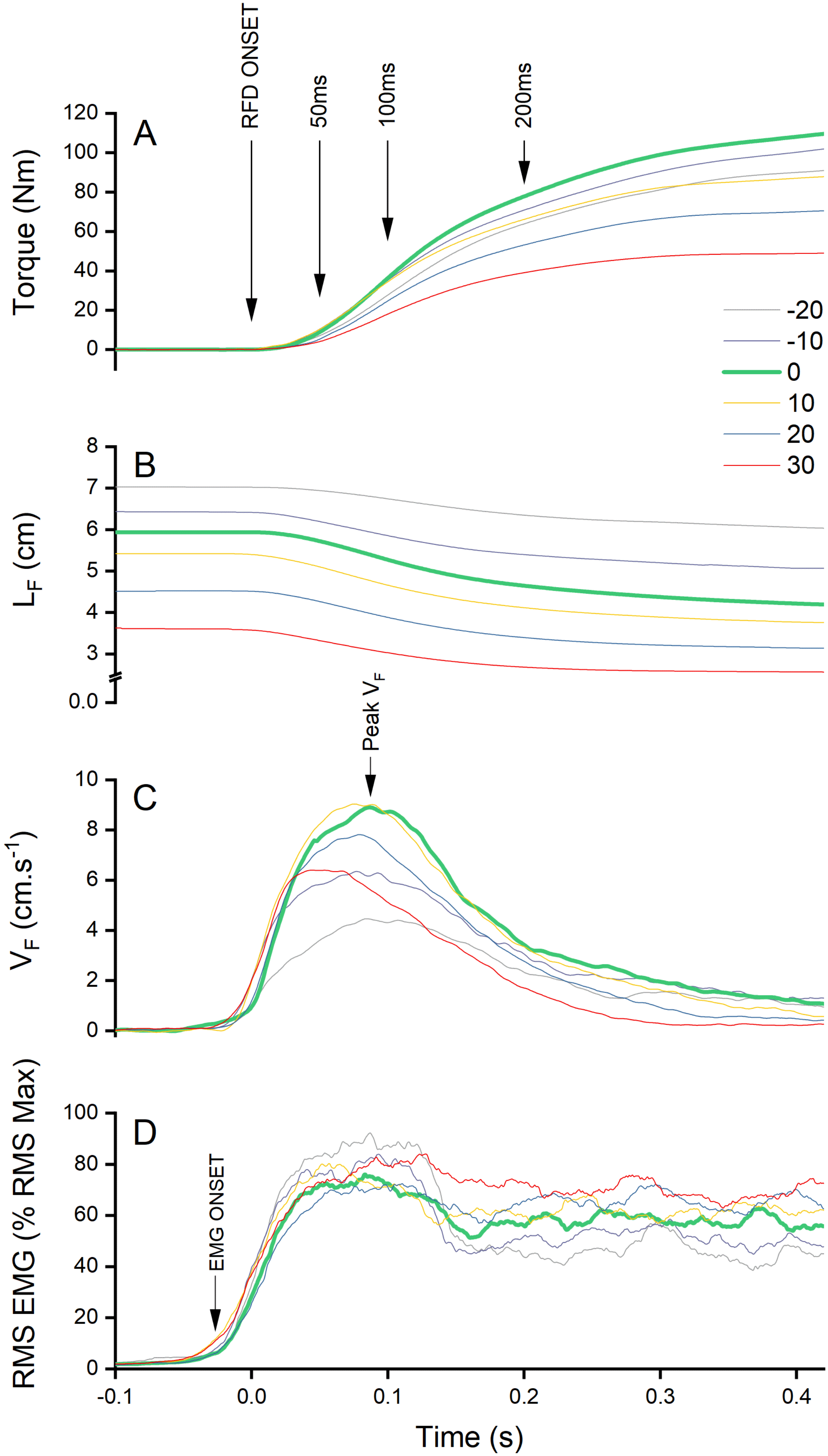
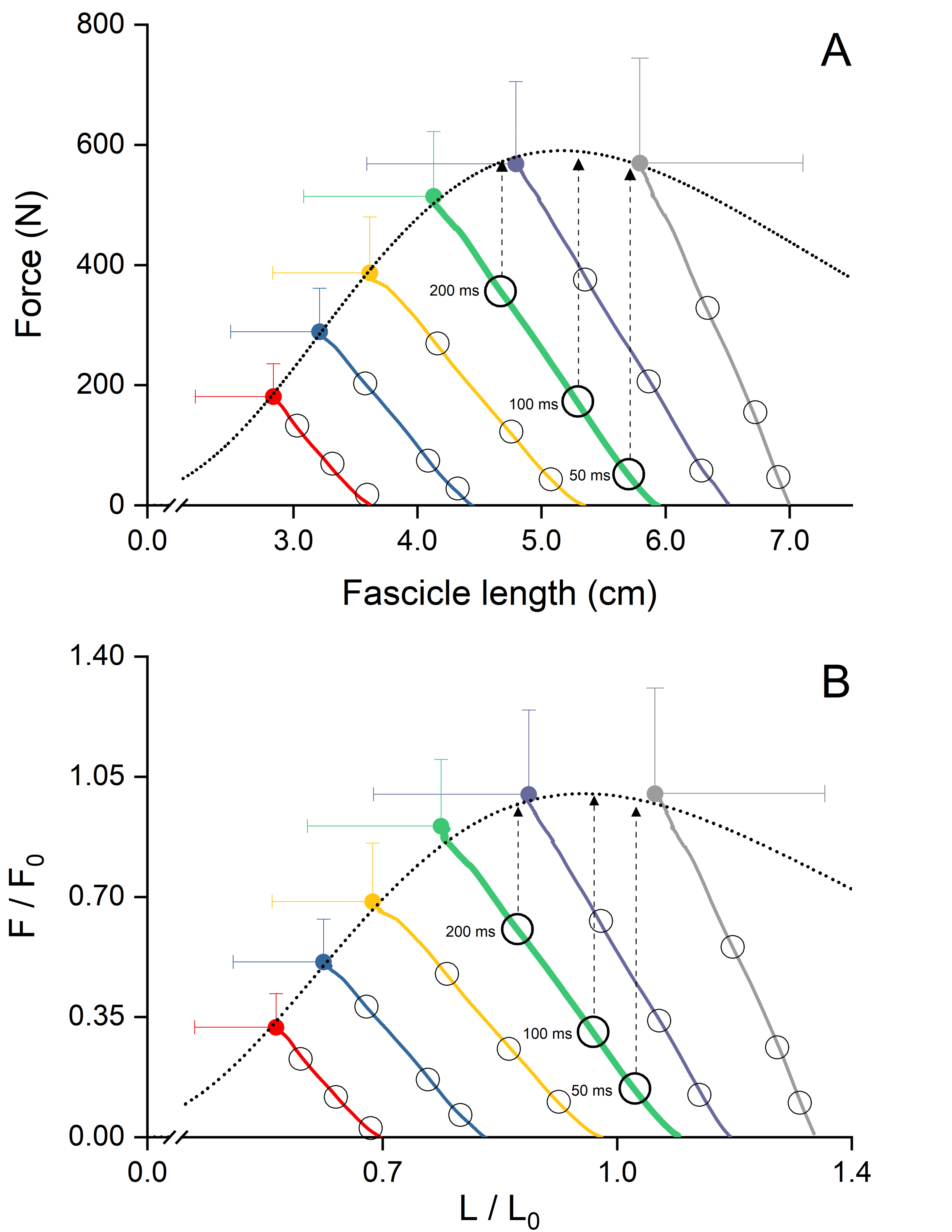
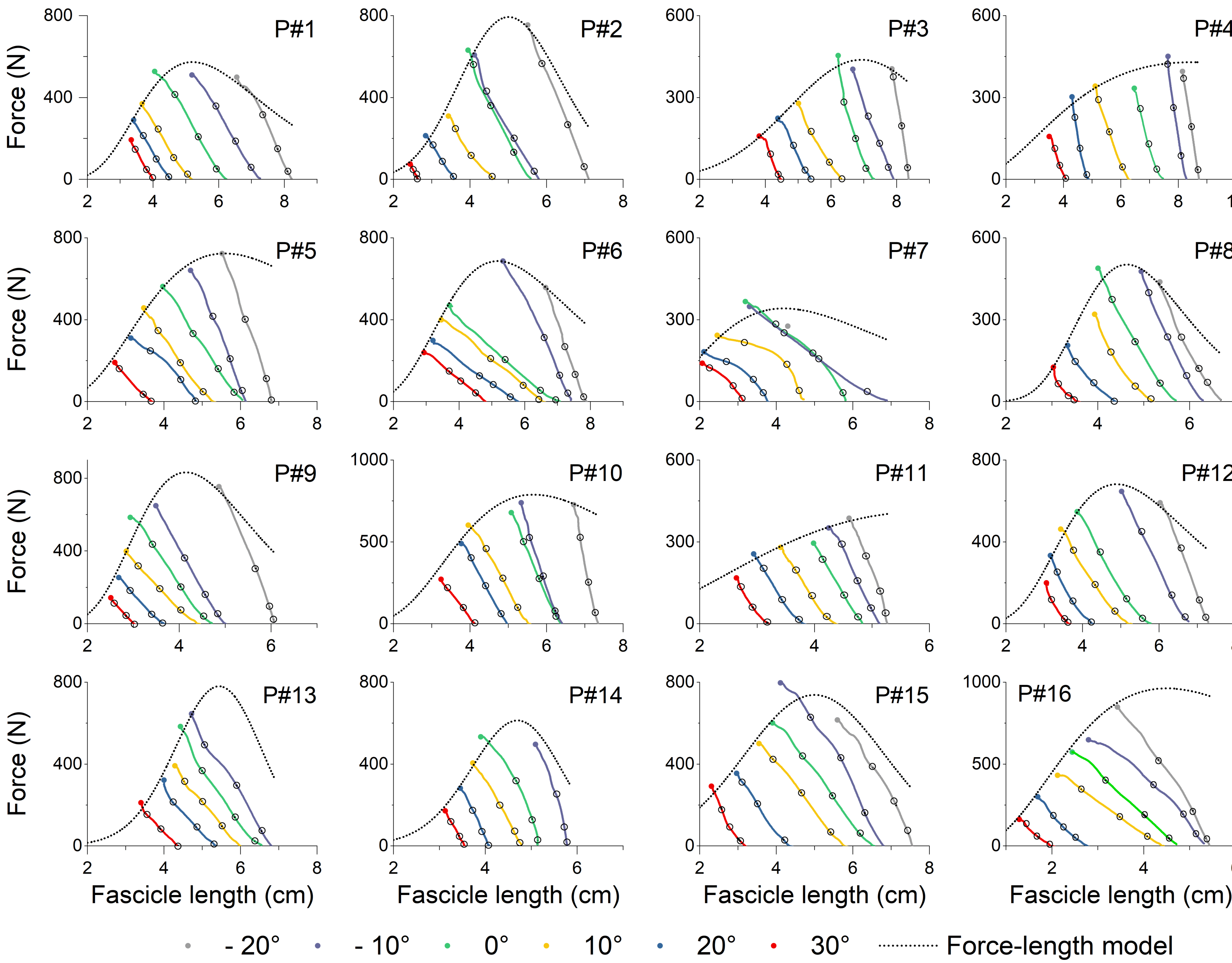


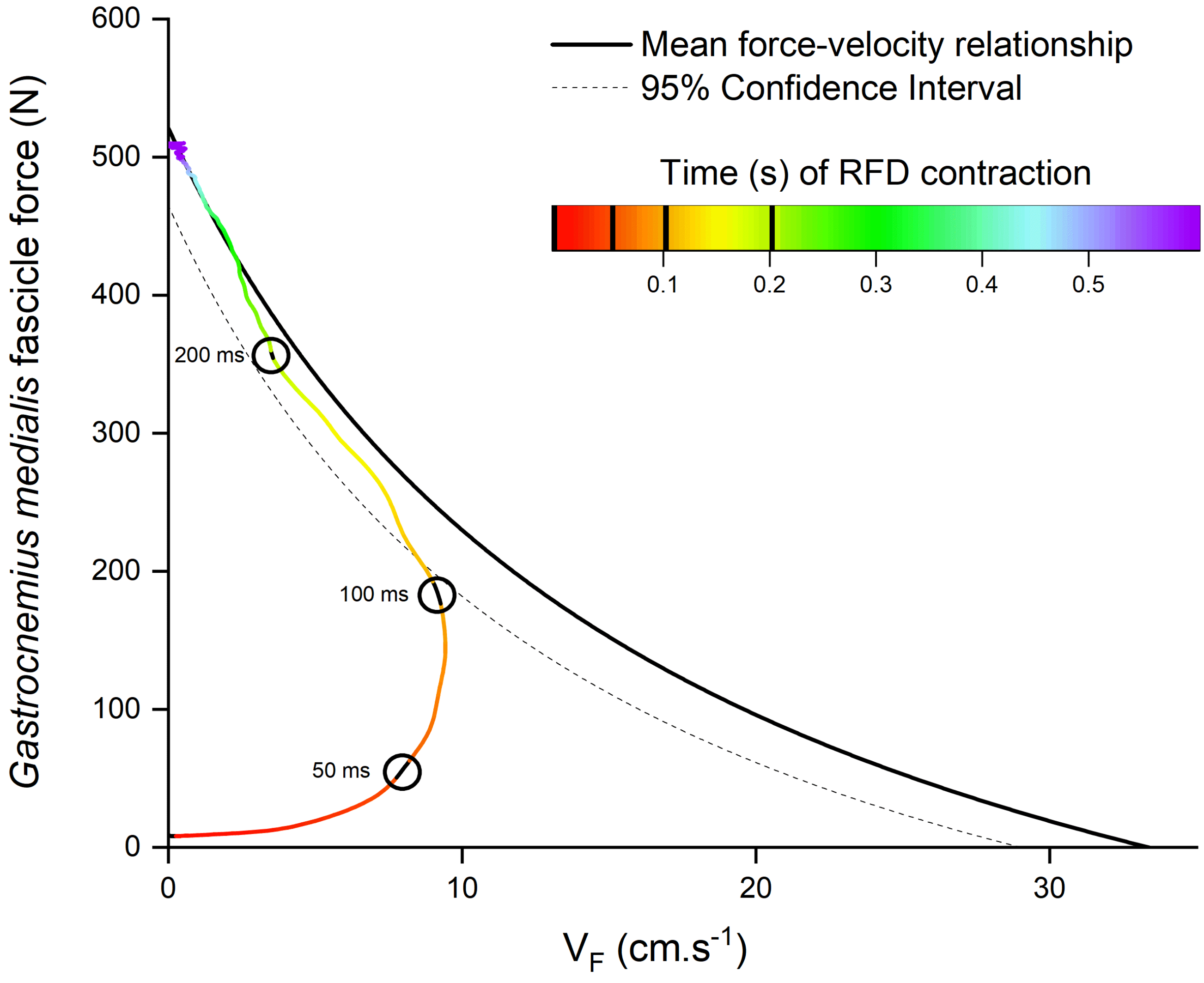
A
Fascicle length (cm)
B
Gastrocnemius medialis fascicle force (N)
C
Fascicle velocity (cm.s-1)
Time (s)
RFD conditions:
- 20° -10° 0° 10° 20° 30°
Ballistic condition :
Force-Length at MVC peak torque
D
Gastrocnemius medialis fascicle force (N)
Fascicle length (cm)
Force-Velocity relationship
E
Gastrocnemius medialis fascicle force (N)
Fascicle velocity (cm.s-1)
Time (s)



RFD ONSET
50ms
100ms
200ms
A
Torque (Nm)
-20
-10
0
10
20
30
B
L_F (cm)
Peak V_F
C
V_F (cm.s^{-1})
D
RMS EMG (% RMS Max)
EMG ONSET
Time (s)


A
800
600
400
200
0
Force (N)
0.0
3.0
4.0
5.0
6.0
7.0
Fascicle length (cm)
200 ms
100 ms
50 ms
B
1.40
1.05
0.70
0.35
0.00
F / F0
0.0
0.7
1.0
1.4
L / L0
200 ms
100 ms
50 ms


P#1
P#2
P#3
P#4
P#5
P#6
P#7
P#8
P#9
P#10
P#11
P#12
P#13
P#14
P#15
P#16
Force (N)
Fascicle length (cm)
- 20°
- 10°
0°
10°
20°
30°
Force-length model



Mean force-velocity relationship
95% Confidence Interval
Time (s) of RFD contraction
0.1
0.2
0.3
0.4
0.5
200 ms
100 ms
50 ms
Gastrocnemius medialis fascicle force (N)
600
500
400
300
200
100
0
0
10
20
30
V_F (cm.s^-1)