



# Faster intrinsic rate of torque development in elbow flexors than knee extensors: Effect of muscle architecture?

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## ABSTRACT

We studied the effect of pennate vs. fusiform muscle architecture on the rate of torque development (RTD) by examining the predominately fusiform elbow flexors (EF) and highly-pennate knee extensors (KE). Seventeen male volunteers ( $28.4 \pm 6.2$  years) performed explosive isometric EF and KE contractions (MVCs). Biceps brachii and vastus lateralis fascicle angles were measured to confirm their architecture, and both the rate of voluntary muscle activation (root-mean-square EMG in the 50 ms before contraction onset; EMG<sub>50</sub>) and electromechanical delay (EMD; depicting muscle-tendon series elasticity) were assessed as control variables to account for their influence on RTD. MVC torque, early (RTD<sub>50</sub>) and late (RTD<sub>200</sub>) RTDs were calculated and expressed as absolute and normalized values. Absolute MVC torque (+412%), RTD<sub>50</sub> (+215%), and RTD<sub>200</sub> (+427%) were significantly ( $p < 0.001$ ) higher in KE than EF. However, EF RTD<sub>50</sub> was faster (+178%) than KE after normalization ( $p = 0.02$ ). EMG<sub>50</sub> and EMD did not differ between muscle groups. The results suggest that the faster absolute RTD in KE is largely associated with its higher maximal torque capacity, however in the absence of differences in rates of muscle activation, fiber type, and EMD the fusiform architecture of EF may be considered a factor allowing its faster early RTD relative to strength capacity.

## 1. Introduction

Muscle architecture is the main mechanical factor underpinning muscle maximal strength and contraction velocity (Blazevich, 2006; Lieber and Fridén, 2000). According to the muscle fibers' arrangements, muscles can be classified into two general types: fusiform and pennate (Lieber and Fridén, 2000). Fascicles of fusiform muscles run parallel to the muscle's line of action (Gans and Gaunt, 1991; Lieber and Fridén, 2000), whereas fascicles in pennate muscles run at an angle to the aponeurosis (Blazevich, 2006). Fusiform muscles typically have longer fascicle lengths than pennate muscles when expressed relative to muscle length (Langenderfer et al., 2004; Murray et al., 2000; Ward et al., 2009), theoretically allowing a greater contraction speed due to the

summation of serial sarcomere shortening (Gans and Gaunt, 1991). On the other hand, fascicle angulation in pennate muscles allows the placement of more fascicles into a given area of aponeurosis/muscle volume, leading to a greater number of parallel sarcomeres and thus a greater muscle maximal strength capacity (Gans and Gaunt, 1991; Lieber and Fridén, 2000).

Nonetheless, the rate at which muscle strength can be expressed is also crucial to daily living and sports activities (Maffiuletti et al., 2016; Rodríguez-Rosell et al., 2018). Explosive strength is often quantified as the rate of torque development (RTD) during an explosive maximal voluntary contraction (MVC) (Maffiuletti et al., 2016). RTD can be calculated within "early" ( $\leq 100$  ms) and "late" ( $\geq 200$  ms) time periods after contraction onset (Andersen and Aagaard, 2006; Maffiuletti et al.,

**Abbreviations:** BB, Biceps brachii; EF, Elbow flexors; EMD, Electromechanical delay; EMG, Electromyographic; EMG<sub>50</sub>, EMG RMS in the 50-ms immediately before the torque onset; FA, Fascicle angles; KE, Knee extensors; MVC, Maximal voluntary contraction; nRTD<sub>200</sub>, Normalized RTD<sub>200</sub>; RTD<sub>50</sub>, Normalized RTD<sub>50</sub>; RMS, Root mean square; RTD, Rate of torque development; RTD<sub>200</sub>, RTD measured at 200ms from the contraction onset (late); RTD<sub>50</sub>, RTD measured at 50ms from the contraction onset (early); VL, Vastus lateralis.

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2016), with early RTD being mainly influenced by the rate of neural activation (Cossich and Maffiuletti, 2020; Del Vecchio et al., 2019; Folland et al., 2014) while late RTD is associated with maximal strength capacity (Andersen and Aagaard, 2006; Cossich and Maffiuletti, 2020) and probably influenced by similar neuromuscular factors, such as muscle size (Blazevich, 2006; Maden-Wilkinson et al., 2020).

Although an association between RTD and muscle architecture has been proposed (Spector et al., 1980), few studies have been conducted *in vivo* in humans, and these studies have addressed different architectural variables (Coratella et al., 2020; Cossich and Maffiuletti, 2020; Stock et al., 2017; Wagle et al., 2017; Zaras et al., 2016). With respect to muscle size, Coratella et al. (2020) reported a significant correlation between vastus intermedius thickness and RTD to 100 and 250 ms from contraction onset ( $r = 0.55\text{--}0.69$ ) but not for torque measured over shorter time intervals. Similarly, Cossich and Maffiuletti (2020) observed a moderate correlation ( $r = \sim 0.50$ ) between the summed thicknesses of vastus lateralis and intermedius and the late RTD. These results and others (Stock et al., 2017; Wagle et al., 2017; Zaras et al., 2016) suggest that muscle size is an important variable influencing late RTD, and may be a factor contributing to the strong association between MVC torque and late RTD (Andersen and Aagaard, 2006). With regard to fascicle length, Zaras et al. (2016) found positive correlations between vastus lateralis fascicle length and both early and late knee extensor RTD only after a period of strength training, whilst Blazevich et al. (2009a) observed a negative correlation between changes in the early RTD and the shift of the knee extensor moment-angle relationship after strength training, which was attributed to an increase in fascicle length possibly reducing RTD through an increase in series elasticity (Edman and Josephson, 2007). Regarding fascicle angle, several studies have observed no correlation between RTD and either vastus lateralis (Coratella et al., 2020; Zaras et al., 2016) or vastus intermedius angle (Coratella et al., 2020), yet Wagle et al. (2017) reported a positive correlation between vastus lateralis fascicle angle, measured with the subject in standing position, and both early and late RTDs. The latter findings are consistent with data showing greater force production during a brief twitch contraction in the nearly-parallel fibred cat soleus than pennate gastrocnemius muscle (Spector et al., 1980). Collectively, these results reveal a lack of consistency in the relationships between muscle architectural variables and RTD in the muscles studied, leading to conclusions that architecture may have minimal effect on RTD *in vivo* in humans (Maffiuletti et al., 2016).

Other factors are known to strongly influence RTD, such as the rate of voluntary muscle activation (Cossich and Maffiuletti, 2020; Del Vecchio et al., 2019; Duchateau and Baudry, 2014; Folland et al., 2014), muscle-tendon stiffness (Bojsen-Møller et al., 2005; Monte and Zignoli, 2021; Watsford et al., 2010), and muscle fiber type (Andersen et al., 2010; Korhonen et al., 2006). Thus, these factors need to be considered within any experimental model assessing the muscle architecture-RTD relationship. As the mechanical effect of muscle architecture on RTD is unknown, the present study compared RTD produced by the predominately fusiform elbow flexor muscles and highly pennate knee extensors. The mean architecture varies considerably between these groups, whilst measurements of muscle activation rate (e.g., using electromyography) and muscle-tendon unit series stiffness (estimated by electromechanical delay - EMD) can be performed, and significant information relating to muscle fiber type already exists (Bojsen-Møller et al., 2005). Thus, it may be possible to delineate the specific effects of muscle architecture by accounting for the multiple other differences between these groups. We also selected biceps brachii and vastus lateralis for further architectural measurement in order to quantify differences in fascicle angle in our cohort. We hypothesized that the knee extensors would produce faster absolute early and late RTDs due to the high correlation between RTD and maximum strength (Andersen and Aagaard, 2006; Folland et al., 2014). However, when normalized to maximal strength the RTD would be higher in the EF due its fusiform fascicle arrangement. These outcomes were not expected to be explicable by differences in muscle

activation rate, muscle-tendon unit stiffness (i.e., EMD) or reported fiber type.

## 2. Methods

### 2.1. Participants

Seventeen physically active men (mean  $\pm$  SD:  $28.4 \pm 6.2$  years old; body mass:  $78.4 \pm 10.0$  kg; height:  $176.2 \pm 5.2$  cm) volunteered for the current investigation. All participants were engaged in a moderate or high level of physical activity as classified by the International Physical Active Questionnaire (Lee et al., 2011) ( $5655 \pm 4322$  min/week). None of the subjects were involved in specific strength/power training using the elbow and knee joints. The exclusion criteria included a history of neuromuscular disorder and/or orthopedic surgery. The research was approved by the local Ethics Committee and all participants gave the written informed consent.

### 2.2. Experimental protocol

All procedures were performed in a single session lasting approximately 60 min. Participants were asked to complete maximal voluntary isokinetic and explosive isometric contractions of the elbow flexors (EF) and knee extensors (KE). From the isometric efforts, MVC peak torque, RTD measured within short (50 ms; RTD<sub>50</sub>) and longer (200 ms; RTD<sub>200</sub>) time intervals from contraction onset, and electromyography (EMG) activity in the early muscle activation phase (50 ms before the contraction onset; EMG<sub>50</sub>) was recorded. Subsequently, biceps brachii (BB) and vastus lateralis (VL) fascicle angles (FA) were measured from ultrasonography images captured in a resting state. All measurements were conducted unilaterally on the dominant side, which was self-defined as the preferred writing hand and kicking leg (16 right and 1 left).

### 2.3. Knee extensor and elbow flexor strength measurements

KE and EF peak torques ( $T_{\text{peak}}$ ) and the peak torque angles (Angle<sub>peak</sub>) were obtained during a concentric isokinetic test performed at  $30^\circ/\text{s}$  (HUMAC NORM II, CSMI, USA). The participants were seated with hips flexed at  $\sim 85^\circ$  for KE and whilst laying prone with the shoulder abducted at  $\sim 45^\circ$  for EF. In both tests, the joint was aligned with the dynamometer axis of rotation, and KE and EF were tested in a randomized order. For each test, participants performed a warm-up/familiarization set comprising five progressive intensity repetitions at  $30^\circ/\text{s}$  (20, 40, 60, 80, and 100% of subjective maximal effort). The test comprised five maximal elbow or knee extension/flexion repetitions performed with strong verbal encouragement. Angle<sub>peak</sub> was recorded from the repetition with the highest  $T_{\text{peak}}$ , and this angle was used for subsequent isometric explosive assessment. A slow isokinetic velocity was chosen to approach the mechanical characteristics of an isometric contraction yet allow the optimum angle to be determined without repeated maximal tests across multiple joint angles. After 3 min of rest, explosive isometric MVC testing was performed on the same joint. Before the test, a familiarization set of three progressive submaximal isometric contractions were performed (50, 80, and 100% of subjective maximal effort). After 30 s of rest, the participants performed three maximal explosive isometric contractions lasting  $\sim 3$  s. Participants were instructed to perform the contraction "as fast and hard as possible" and to keep the maximum effort whenever the verbal instruction given by the tester persisted (Cossich and Maffiuletti, 2020; Laett et al., 2021). To minimize the dampening effect between the shin and the lever arm, and simultaneously minimize potential shin pain, a standard hard soccer shin protector was used during KE. A minimum rest of 30 s was provided between trials. Torque signals were acquired by an external analog-to-digital converter (EMG 830c, EMG System do Brasil, Brazil) at a 1-kHz sampling frequency and recorded.

## 2.4. Superficial electromyogram signal acquisition

The surface EMG from VL, rectus femoris (RF), and vastus medialis (VM) were acquired during the KE MVCs, whilst BB EMG was acquired during the EF MVCs. A standard device for biological signal recording (EMG 830c - EMG System do Brasil, Brazil) was used. The Ag-AgCl electrodes (RedDot, 3 M Corp, EUA) were set by the same evaluator after skin shaving, cleaning, and abrasion with soaked cotton with 70° alcohol. A bipolar configuration with 2-cm interelectrode distance as used, following standard recommendations (Hermens et al., 2000). The reference electrode was placed over the lateral humeral condyle during KE and over the ulnar styloid process during EF acquisitions. EMG signals were amplified (gain: 1000), band-pass filtered (20–500 Hz), recorded at 1-kHz sampling frequency, and synchronized with the torque signal.

## 2.5. Torque and EMG data processing

The torque and EMG signals were processed by a custom-built routine developed in Matlab 2014 (Mathworks Inc., USA). The torque signals were filtered using a fourth-order, low-pass, zero-lag Butterworth filter with 50-Hz cut-off frequency (Thompson, 2019). This cut-off frequency was sufficient to smooth the signal without shifting the estimated point of contraction onset (Cossich and Maffiuletti, 2020; Laett et al., 2021). Contraction onset was defined by a fixed torque threshold of 1 Nm and set visually by the same evaluator with the help of a dashed line created by the analysis software (Cossich and Maffiuletti, 2020). The torque signals were systematically corrected for the passive torque using the average torque produced at the transducer during a baseline resting period of 500 ms. Only the contraction with the highest instantaneous value (MVC torque) was retained for analysis. RTD was calculated as the slope of the torque-time relations for the first 50 and 200 ms (RTD<sub>50</sub> and RTD<sub>200</sub>, respectively) from torque onset (Fig. 1C and D). The RTD measurements were expressed in both absolute and normalized values (nRTD<sub>50</sub> and nRTD<sub>200</sub>), with normalized data being set relative to the MVC peak torque.

EMG onset was determined as the point at which the raw signal

increased more than three standard deviations above baseline (an averaged 500-ms window) with the muscle relaxed and visually expected by the same evaluator and did not return for > 3 s (Tenan et al., 2017). After the onset determination, the signals were filtered to reduce signal noise (Mello et al., 2007). The early EMG voluntary activity was subsequently calculated as the root mean square (RMS) EMG in the 50-ms window immediately before the torque onset (EMG<sub>-50</sub>) as described by Cossich and Maffiuletti (2020) (Fig. 1C and D); this variable showed the strongest correlation with RTD variables in pilot testing. The EMG<sub>-50</sub> values were normalized by the RMS EMG value obtained during a 500-ms period around the point of peak torque (250 ms before to 250 ms after), accounting for variability in EMG amplitude between muscles and subjects (Del Vecchio et al., 2019). For KE muscles, EMG<sub>-50</sub> was calculated using the mean of VL, RF, and VM values.

The EMD was defined as the time elapsed between the EMG onset in the first active muscle and the torque onset. For EF this was the time between EMG onset in BB and detectable torque, whilst for KE only the longest EMD was calculated (i.e. from first EMG onset of any muscle to torque onset) (Fig. 1C and D).

## 2.6. Vastus lateralis and biceps brachii architecture assessment

Ultrasound images were obtained using a 7.5-MHz, 40-mm linear array probe with standard equipment (SDD900, ALOKA, Japan) in B-mode. The angle of the fascicle relative to the aponeurosis (fascicle angle; FA) was measured from images obtained with subjects lying supine in anatomical position. VL images were acquired at half the distance between the greater trochanter and the superior edge of the patella (Blazevich et al., 2006). BB images were acquired from the distal attachment – at this portion both BB head works as a single functional and anatomical structure – where the internal aponeurosis of the biceps tendon was clearly visible (Erskine et al., 2014). The probe was aligned to the fascicle plane. VL FA was defined as the angle formed between the muscle fascicle and deep aponeurosis, and BB FA was defined as the angle formed between the final portion of the fascicle and the internal aponeurosis (Blazevich et al., 2006; Erskine et al., 2014) (Fig. 1A and B). FA measurements were made using ImageJ 1.51 software (National

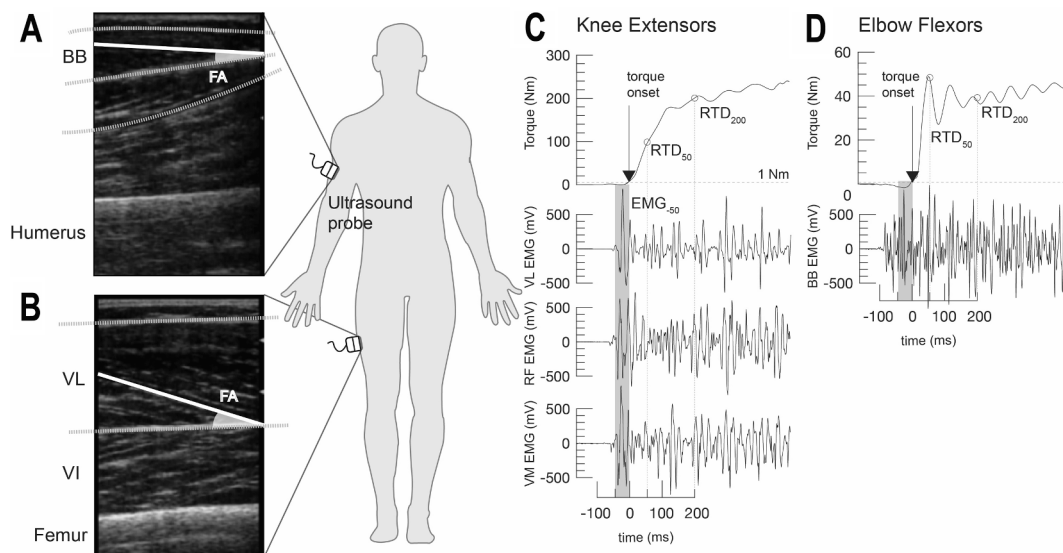


**Fig. 1.** Example of raw data collected on one participant. A) Biceps brachii (BB) ultrasound image acquired at the distal portion of the muscle. Aponeuroses are shown by dashed lines, a visible fascicle is highlighted by the white line, and the shaded angles highlight the fascicle angle (FA). B) Representative image of vastus lateralis (VL) acquired at half the distance from the greater trochanter to the superior border of the patella. C) and D) In the upper row, representative torque signals are acquired during explosive maximal voluntary knee extensor and elbow flexor contractions (MVC). The torque signal was used to measure both peak torque and rate of torque development at 50 ms (RTD<sub>50</sub>) and 200 ms (RTD<sub>200</sub>) from contraction onset (indicated by the arrow). Below each torque signal, a representative electromyogram signal (EMG) from vastus lateralis (VL), rectus femoris (RF), and vastus medialis (VM) was acquired during knee extension and biceps brachii (BB) during elbow flexion is shown. The RMS EMG amplitude in the 50 ms preceding torque onset (shaded area) was used to quantify ‘rapid’ muscle activation (EMG<sub>-50</sub>).

Institutes of Health, Bethesda, Maryland), with three measurements made of a clearly visible fascicle by the same investigator and the average then computed ( $ICC_{2,1} = 0.94$ ).

## 2.7. Statistical analyses

Values are reported as mean  $\pm$  SD. All variables were evaluated using the Shapiro-Wilk test and showed a normal distribution ( $p < 0.05$ ). The absolute and normalized RTD values were evaluated by separate mixed ANCOVA (within-factor: time interval [early: 50 ms and late: 200 ms], between-factor: muscle groups [KE and EF], covariates: EMG<sub>50</sub> and EMD). If sphericity could not be assumed, then the correction of Greenhouse-Geisser was applied. Follow-up independent t-tests were used for comparisons between KE and EF of the studied variables. The relationship between RTD and EMG<sub>50</sub> was examined by Pearson's correlation coefficient and linear regression analysis. Correlation coefficients were arbitrarily considered as negligible (0.00–0.09), weak (0.10–0.39), moderate (0.40–0.69), strong (0.70–0.89), and very strong (0.90–1.00) (Schober et al., 2018). The effect size was assessed by  $\eta_p^2$  and Cohen's  $d$ , and classified as small (0.01), medium (0.06), or large (0.14) (Cohen, 1988). All statistical procedures were made with SPSS (v.23 IBM SPSS Inc., Chicago, IL, USA). Statistical significance was adopted at the  $p \leq 0.05$  level.

## 3. Results

KE  $T_{peak}$  and  $Angle_{peak}$  were  $246.9 \pm 38.7$  Nm and  $64.5 \pm 6.6^\circ$ , respectively, whilst EF KE  $T_{peak}$  and  $Angle_{peak}$  were  $60.8 \pm 16.8$  Nm and  $79.5 \pm 14.9^\circ$ , respectively. MVC peak torque was significantly higher in KE (Table 1). After controlling for EMG<sub>50</sub> and EMD there was a significant difference within the RTD early and late for both absolute ( $F(1,30) = 5.06$ ,  $p = 0.03$ ,  $\eta_p^2 = 0.14$ ) and normalized ( $F(1,30) = 7.17$ ,  $p = 0.01$ ,  $\eta_p^2 = 0.19$ ) values. Also, there was a significant effect for muscle group on both absolute ( $F(1,30) = 62.5$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.68$ ) and normalized RTD ( $F(1,30) = 5.4$ ,  $p < 0.027$ ,  $\eta_p^2 = 0.15$ ). Follow-up analyses demonstrated that both absolute RTD<sub>50</sub> and RTD<sub>200</sub> were significantly higher in KE (Table 1). However, when normalized, nRTD<sub>50</sub> was significantly higher in EF than KE while no differences were observed for nRTD<sub>200</sub> (Table 1). No significant differences were observed in EMG<sub>50</sub> or EMD between KE and EF (Table 1). FA was significantly smaller in BB ( $7.0 \pm 3.6^\circ$ ) than VL ( $16.7 \pm 3.1^\circ$ ,  $p < 0.001$ ,  $d = 2.8$ ).

There were significant moderate and strong correlations between

EMG<sub>50</sub> and nRTD<sub>50</sub> in KE ( $r = 0.53$ ,  $R^2 = 0.28$ ,  $p = 0.03$ , 95% CI = [0.07, 0.80]) and EF ( $r = 0.73$ ,  $R^2 = 0.55$ ,  $p < 0.001$ , 95% CI = [0.39, 0.90]), respectively. However, no significant correlations were found between EMG<sub>50</sub> and nRTD<sub>200</sub> in either KE ( $r = 0.32$ ,  $R^2 = 0.10$ ,  $p = 0.21$ , 95% CI = [-0.19, 0.69]) or EF ( $r = 0.06$ ,  $R^2 = 0.004$ ,  $p = 0.82$ , 95% CI = [-0.43, 0.53]) (Fig. 2).

## 4. Discussion

The aim of the present study was to investigate the effect of muscle architecture on rate of torque development (RTD) by comparing the predominately-fusiform elbow flexor (EF) and highly-pennate knee extensor (KE) muscles, which have similar fiber type profiles, whilst controlling for the effects of potential confounding variables such as maximum muscle force capacity, muscle length (joint angle), rate of muscle activation (amplitude of the early EMG response), and musculotendinous unit series stiffness (estimated as electromechanical delay [EMD]) (Bojsen-Møller et al., 2005). We observed KE (Andersen and Aagaard, 2006; Blazeovich et al., 2009a) and EF (Follmer et al., 2017; Philippou et al., 2012) RTD values that were similar to previous investigations, confirming that KE produce a faster absolute RTD (RTD<sub>50</sub> and RTD<sub>200</sub>), in line with its higher peak force capacity, but that EF produce a faster early RTD when normalized to maximum strength (MVC peak torque). Thus, in accordance with our hypothesis, EF was observed to have a faster intrinsic force production capacity, and this could not be explained by differences in fiber type or estimates of activation rate or series stiffness. In line with previous results in cat plantar flexors (Spector et al., 1980), we conclude that the largely fusiform architecture of the human biceps brachii gives the elbow flexors an advantage for fast force production relative to the highly pennate knee extensor muscles. Muscle architecture therefore appears to influence a muscle's rate of force production *in vivo*.

The influence of muscle architecture on RTD had been suggested in several studies (Blazeovich et al., 2009a; Stock et al., 2017; Wagle et al., 2017; Zaras et al., 2016). Although the positive correlation between muscle thickness – and thus muscle mass – and RTD is a recurrent observation (Coratella et al., 2020; Cossich and Maffiuletti, 2020; Stock et al., 2017; Wagle et al., 2017; Zaras et al., 2016), the influence of fascicle angle and length, i.e. the fascicle orientation or muscle design, on RTD remains unclear. It was previously suggested that pennate muscles develop force more rapidly (Maffiuletti et al., 2016), based on two factors: a higher muscle physiological cross-sectional area (Blazeovich, 2006; Gans and Gaunt, 1991) and higher architectural gear ratio (Azizi et al., 2008; Azizi and Roberts, 2014). The former strongly influences the maximal strength capacity of a muscle, increasing RTD if the time to reach a relative force level is constant (Coratella et al., 2020; Cossich and Maffiuletti, 2020; Maden-Wilkinson et al., 2020), and the latter allows for an increased muscle shortening velocity (Azizi et al., 2008; Eng and Roberts, 2018), which should stretch series elastic component more rapidly and thus promote force transfer. It should be mentioned that the velocity enhancement produced by architectural gearing has largely been studied during isotonic contractions (Azizi et al., 2008; Azizi and Roberts, 2014), with a lower gear (reduced muscle length to fascicle length change ratio) occurring with higher-load, low-speed contractions (Azizi et al., 2008; Azizi and Roberts, 2014), although recent studies have also shown a reduction in gear in isometric contractions in chronic stroke patients (Son and Rymer, 2020) and positive correlations between plantar flexor peak RTD and muscle gearing (Monte and Zignoli, 2021). A drawback of pennation, however, is that only part of the produced force by each fiber in pennate muscles is delivered to the tendon (Blazeovich et al., 2009a; Gans and Gaunt, 1991; Ikegawa et al., 2008; Kawakami et al., 1995). On the other hand, forces produced by fibers in fusiform muscles transfer forces directly in line with the tendon and the longer relative fiber lengths allow a higher speed of contraction to stretch in-series connective tissues (Blazeovich, 2006; Gans and Gaunt, 1991; Lieber and Fridén, 2000), perhaps

**Table 1**

MVC torque, RTD, rate of muscle activation (EMG<sub>50</sub>), and EMD of knee extensors and elbow flexors.

| Variable                          | KE                 | EF                | p-value                     | d-cohen |
|-----------------------------------|--------------------|-------------------|-----------------------------|---------|
| MVC peak torque (Nm)              | 271.6 $\pm$ 50.6   | 65.9 $\pm$ 11.7   | <b>&lt;</b><br><b>0.001</b> | 5.6     |
| RTD <sub>50</sub> (Nm/s)          | 1345.7 $\pm$ 619.5 | 626.4 $\pm$ 492.0 | <b>&lt;</b><br><b>0.001</b> | 1.3     |
| RTD <sub>200</sub> (Nm/s)         | 1019.5 $\pm$ 189.9 | 239.2 $\pm$ 56.6  | <b>&lt;</b><br><b>0.001</b> | 5.6     |
| nRTD <sub>50</sub> (%MVC torque)  | 5.1 $\pm$ 2.2      | 9.1 $\pm$ 6.5     | <b>0.02</b>                 | 0.8     |
| nRTD <sub>200</sub> (%MVC torque) | 3.7 $\pm$ 0.4      | 3.6 $\pm$ 0.6     | 0.50                        | 0.2     |
| EMG <sub>50</sub> (%max)          | 0.84 $\pm$ 0.41    | 0.78 $\pm$ 0.51   | 0.67                        | 0.2     |
| EMD (ms)                          | 75.1 $\pm$ 24.7    | 80.5 $\pm$ 27.9   | 0.55                        | 0.2     |

Values described as mean  $\pm$  SD. MVC torque: maximal voluntary contraction torque; RTD: absolute rate of torque development; nRTD: normalized rate of torque development; EMG: electromyogram amplitude; EMD: electromechanical delay; subscript numbers indicate the time elapsed in milliseconds from torque onset (RTD) or before torque onset (EMG). KE: knee extensors; EF: elbow flexors (EF). Significant differences are highlighted in bold.

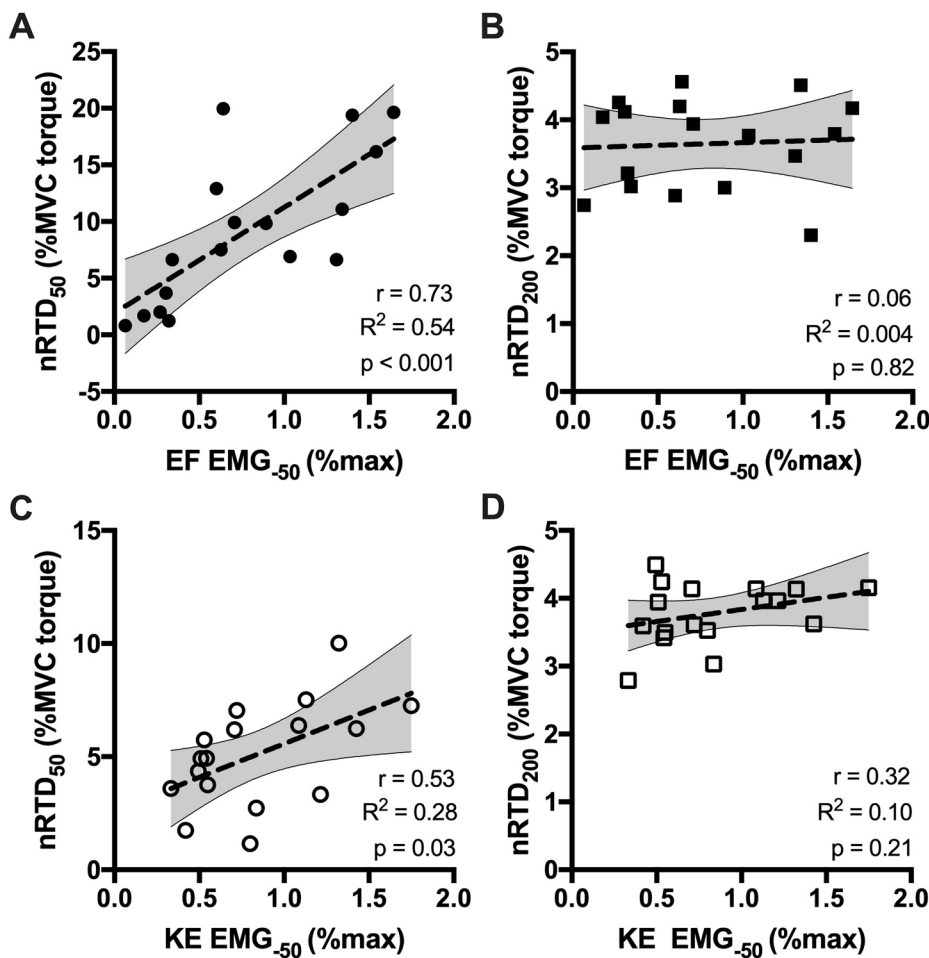


**Fig. 2.** Scatterplots of the normalized rate of torque development (nRTD) during knee extension (KE) and elbow flexion (EF) against the muscle activity observed in the 50 ms before torque onset (EMG<sub>50</sub>). Subscript RTD numbers indicate the time elapsed in milliseconds from the torque onset. (A) EF EMG<sub>50</sub> against EF nRTD<sub>50</sub>, (B) EF EMG<sub>50</sub> against EF nRTD<sub>200</sub>, (C) KE EMG<sub>50</sub> against KE nRTD<sub>50</sub>, and (D) KE EMG<sub>50</sub> against KE nRTD<sub>200</sub>. Early-phase RTD is represented circles and later-phase RTD by squares. Closed symbols represent EF and open symbols represent KE. The gray area represents 95% CIs of the linear regressions.

allowing a faster RTD.

There is a very strong correlation between MVC torque and RTD (Andersen and Aagaard, 2006; Folland et al., 2014), especially for RTD developed to longer time points after the onset of contraction. In the present study, KE MVC torque was ~4-fold greater than EF MVC peak torque – thus, if the intrinsic rate of force production were the same, the absolute RTD should be much faster in KE. The substantially greater force capacity in KE was sufficient to allow a faster absolute RTD when measured to both shorter (50 ms) and longer (200 ms) time intervals than EF, despite EF having a faster intrinsic force development capacity. It should be kept in mind that the process of normalization to MVC peak torque not only accounts for differences in muscle size but also other factors that influence force such as the joint moment arm (Blazeovich et al., 2009b). Thus, to investigate the effect of muscle architecture on intrinsic force production rates, normalization to MVC peak torque appears to be good practice, as proposed elsewhere (Maffiuletti et al., 2016). It should be highlighted that a majority of the studies previously investigating relationships between muscle architecture and RTD analyzed only the absolute RTD (Coratella et al., 2020; Methenitis et al., 2019; Wagle et al., 2017), so important effects of architecture on the rate of force development may have been missed.

We measured vastus lateralis and biceps brachii fascicle angles to confirm the previously-documented differences in muscle design (Blazeovich et al., 2006). As expected, biceps brachii demonstrated a smaller angles than vastus lateralis (Lieber and Fridén, 2000; Nelson et al., 2016). Although, theoretically, fusiform muscles have no fiber angle, a small fascicle inclination is often observed in the distal portion allowing fiber attachment onto the distal aponeurosis (Asakawa et al., 2002), explaining our observed value ~7°. Although vastus lateralis and biceps

brachii are each one of several muscles acting across their respective joints, they are largely reflective of the designs of their synergist muscles (Blazeovich et al., 2006; Langenderfer et al., 2004; Murray et al., 2000), and the provision of data will allow comparisons to be made between the current study and future studies on these muscle groups.

It can be argued that fiber, or fascicle, length might also influence RTD through its effects on series elastic stiffness (Blazeovich et al., 2009a; Edman and Josephson, 2007). As vastus lateralis and biceps brachii fascicle lengths are similar (Blazeovich et al., 2006; Langenderfer et al., 2004; Murray et al., 2000), the possible effects of differences in in-series stiffness on RTD should theoretically be small. Thus, it is most likely that fascicle angle, rather than length, was the key factor influencing the intrinsic rate of force development differences observed between the muscle groups. However, some effect of fascicle length cannot be dismissed since this parameter varies greatly between muscles and between regions within muscles, and the fascicle length-to-muscle length ratios also differ between the muscle groups. As the effect of fascicle length on RTD remains unclear (Blazeovich et al., 2009a; Maffiuletti et al., 2016), future research is needed to more explicitly test the effect of fascicle length on RTD.

Besides muscle architecture, fiber type proportions (Andersen et al., 2010), muscle-tendon stiffness (Bojsen-Møller et al., 2005), and the rate of voluntary muscle activation are considered to influence RTD. Despite notable inter-individual and inter-study variability, both vastus lateralis and biceps brachii appear have similar type II muscle fiber contents (Methenitis et al., 2019, 2016; Pontén and Stål, 2007; Staron et al., 2000) (see supplementary material for details), although it should be clarified that fiber type was not directly assessed in the present study. Additionally, we did not observe any differences in EMD or the rate of

voluntary muscle activation (EMG<sub>50</sub>; the EMG amplitude average in the 50 ms before contraction onset) between KE and EF, suggesting that series elastic stiffness and activation rate should not have underpinned differences in RTD (Bojsen-Møller et al., 2005; Cossich and Maffiuletti, 2020). Nonetheless, future studies may use alternative methods of quantifying these factors to ensure that the choice of measurement method does not impact the conclusions drawn. Of final interest was that the voluntary muscle activation rate was able to explain the early (nRTD<sub>50</sub>) but not later RTD (nRTD<sub>200</sub>) in both KE and EF, corroborating previous observations (Del Vecchio et al., 2019; Folland et al., 2014). However, although little previous evidence suggests that the later RTD is strongly influenced by the rate of muscle activation (see Maffiuletti et al., 2016 for review), it cannot be discounted that EMG measured to other time intervals might have shown greater associations with RTD; an effect of activation rate cannot, therefore, be completely discounted. With consideration of these limitations and in the absence of other explanations, differences in muscle architecture, and particularly fascicle angle, appear to best explain the differences in the intrinsic rate of force production between the knee extensor and elbow flexor muscle groups.

In conclusion, the present results demonstrate that the human knee extensors produce force much faster than the elbow flexors, which can be largely attributed to their greater maximal strength capacity. However, when RTD is normalized to maximum force, a faster early RTD in EF was revealed, indicating a faster intrinsic force production capacity. Since we controlled several variables well known to influence RTD, and (1) RTD was tested at the same relative position on the angle-torque relationship, (2) the muscles have similar fascicle lengths, (3) the muscles have similar fiber type proportions, (4) the early rate of muscle activation did not differ between the muscle groups, and (5) no differences in EMD, used as an indicator of series muscle-tendon unit stiffness, were detected between muscle groups, we conclude that the fusiform architecture of EF may allow a faster intrinsic force production capacity in the early rise in force of an isometric contraction. Nonetheless, these results should be considered as the first, indirect evidence of an effect of muscle architectural design on RTD, and further studies are warranted that more directly test the effects of various anatomical and physiological variables.

#### CRediT authorship contribution statement

**Victor R.A. Cossich:** Conceptualization, Methodology, Data curation, Software, Writing - original draft, Writing - review & editing. **Conrado T. Laett:** Data curation, Writing - original draft, Writing - review & editing. **Ubiratã F. Gavilão:** Data curation, Writing - original draft, Writing - review & editing. **Anthony J. Blazevich:** Conceptualization, Methodology, Writing - review & editing. **Carlos G. de Oliveira:** Conceptualization, Methodology, Software, Writing - review & editing

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary material

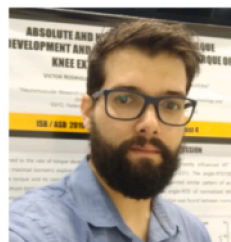
Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jelekin.2021.102570>.

[org/10.1016/j.jelekin.2021.102570](https://doi.org/10.1016/j.jelekin.2021.102570).

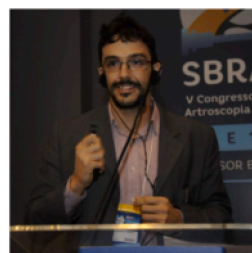
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