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Elyse Hucteau, Marc Jubeau, Christophe Cornu, Thomas Cattagni. Is there an intermuscular relationship in voluntary activation capacities and contractile kinetics?. *European Journal of Applied Physiology*, 2020, 120 (2), pp.513-526. 10.1007/s00421-019-04299-z . hal-04081468

HAL Id: hal-04081468

<https://hal.science/hal-04081468v1>

Submitted on 25 Apr 2023

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Is there an intermuscular relationship in voluntary activation capacities and contractile kinetics?

Elyse Hucteau¹ · Marc Jubeau¹ · Christophe Cornu¹ · Thomas Cattagni¹ 

Abstract

Purpose The force-generating capacities of human skeletal muscles are interrelated, highlighting a common construct of limb strength. This study aimed to further determine whether there is an intermuscular relationship in maximal voluntary activation capacities and contractile kinetics of human muscles.

Methods Twenty-six young healthy individuals participated in this study. Isometric maximal voluntary contraction (MVC) torque, voluntary activation level (VAL), and doublet twitch contractile kinetics (contraction time and half-relaxation time) evoked by a paired supramaximal peripheral nerve stimulation at 100 Hz were obtained in elbow flexors, knee extensors, plantar flexors and dorsiflexors of the dominant limb.

Results Peak MVC torque had significant positive correlations between all muscle group pairs (all P values < 0.01). A significant positive correlation for VAL was found only between knee extensors and plantar flexors ($r = 0.60$, $P < 0.01$). There were no significant correlations between all muscle group pairs for doublet twitch contraction time and doublet twitch half-relaxation time.

Discussion These results show that there is a partial common construct of maximal voluntary activation capacities that only concerns muscle groups that have incomplete activation during MVC (i.e., knee extensors and plantar flexors). This suggests that the common construct of MVC strength between these two muscle groups is partly influenced by neural mechanisms. The lack of intermuscular relationship of contractile kinetics showed that there is no common construct of muscle contractile kinetics, as assessed in vivo by investigating the time-course of evoked doublet twitch contractions.

Keywords Maximal voluntary contraction · Voluntary activation · Twitch · Plantar flexors · Dorsiflexors · Knee extensors · Elbow flexors

Abbreviations

MVC Maximal voluntary contraction

VAL Voluntary activation level

Introduction

Maximal voluntary contraction (MVC) performance is known to widely vary among human skeletal muscles (Behm et al. 2002). Despite this variability, there is a positive relationship between the strength measures of various muscle groups for both upper and/or lower limbs in young or old healthy individuals and also in clinical populations [see Bohannon et al. (2008) for review]. Bohannon et al. (2012) reported in healthy individuals aged from 18 to 85 years that isometric grip and knee extension MVC strengths are strongly correlated, reflecting, according to these authors, a common construct of limb MVC strength. In the unaffected side of individuals with hemiparetic stroke, Takahashi et al. (2017) also found significant positive correlations (r values ranged between 0.51 and 0.90) between each pair of muscle groups that they assessed, including hand-grip muscles, shoulder flexors and extensors, elbow flexors and

Communicated by Toshio Moritani.

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extensors, hip flexors, knee extensors and dorsiflexors. To the best of our knowledge, the mechanisms underlying the common construct of limb MVC strength in humans have never been addressed.

MVC strength is known to be related to numerous factors, such as specific muscle size, architecture, contractile properties, activation, moment arm and to be associated with total muscle/lean body mass (Reed et al. 1991; Gonzalez et al. 1997; Ryan et al. 2011; Miyatake et al. 2012; Chen et al. 2013; Baxter and Piazza 2014; Akagi et al. 2018). The fact that the MVC strength of a given muscle group is highly related to its specific size (Baxter and Piazza 2014; Akagi et al. 2018), and also to total muscle/lean body mass (Reed et al. 1991; Miyatake et al. 2012; Chen et al. 2013) suggests that the common construct of limb MVC strength mainly results from a homogenous distribution of muscle tissue quantity within human limbs. Vikne et al. (2012) also demonstrated a consistent distribution of muscle quality within human limbs. They found an intermuscular relationship of human muscle fibre type proportions. This suggests that human muscles may share a common construct in their contractile kinetics, which remains to be clarified. The contractile kinetics of several muscle groups have been widely examined in vivo by evoking a single or a doublet supramaximal stimulation of motor nerve at rest and analysing some properties of the twitch torque/force signal, such as twitch contraction time and twitch half-relaxation time (Merton 1954; Fitch and McComas 1985; Allen et al. 1995; Behm and St-Pierre 1997; Behrens et al. 2016). In the last years, it has been observed that the analysis of a twitch resulting from a doublet stimulation (100 Hz frequency) at a supramaximal intensity, rather than a twitch resulting from a single stimulation at a comparable intensity, was a better estimate of muscle function and quantity (Ryan et al. 2011; Mau-Moeller et al. 2015; Behrens et al. 2016). The study of contraction time and half-relaxation time of a doublet twitch in different human muscles can be used to identify whether human muscles share a common construct in their contractile kinetics.

Although MVC strength depends mainly on muscle quantity and quality in healthy populations, it can be also influenced by the level of muscle activation during MVC effort, called voluntary activation level (VAL) (Merton 1954; Strojnik and Komi 1998; Behm et al. 2002; Klass et al. 2005; Cattagni et al. 2018). The common construct of limb MVC strength could also be related to neural mechanisms. Since the works of Merton (1954), VAL has been studied in several muscle groups in healthy young individuals using the interpolated twitch technique. During isometric action, VAL is maximal or almost maximal for dorsiflexors [(Lanza et al. 2004; Klass et al. 2005; Chung et al. 2007); plantarflexion ranged between 10 and 35°; 0°: neutral ankle position], but submaximal for knee extensors [(Cannon et al. 2007; Suetta et al. 2009; Neyroud et al.

2013a; Kluka et al. 2015); knee flexion ranged between 65 and 90°; 0°: leg extension] and plantar flexors [(Behm et al. 2002; Akagi et al. 2018; Merlet et al. 2018); plantarflexion: 0°]. The capacity to maximally activate elbow flexors is still debated with some authors finding an almost full activation for them during isometric MVC effort [(Klein et al. 2001; Behm et al. 2002) elbow flexion ranged between 90 and 100°; 180°: elbow extension], whereas other authors have reported incomplete activation (Allen et al. 1994; Bilodeau et al. 2001; Neyroud et al. 2013a). Overall, although VAL can be also influenced by contraction mode and muscle length (or joint angle) (Lanza et al. 2017; Doguet et al. 2017; Behrens et al. 2019), these observations showed that VAL is muscle-dependent. It, however, remains to determine whether the VALs of human muscles are interrelated. In other words, it is still unknown if an individual with a low VAL in a given muscle group also have a low VAL in other muscle groups.

Some findings corroborate a possible between-muscle relationship for VAL in humans. It has been demonstrated that fatiguing exercises focused on one muscle group induce neural alterations of that muscle group, and also of other ipsilateral muscles (Kennedy et al. 2013; Šambaher et al. 2016; Aboodarda et al. 2017). For instance, Kennedy et al. (2013) reported that forearm fatigue protocols induced a decrease in MVC torque resulting from reduced VAL of the non-fatigued plantar flexor muscles. Recent work of Ben Othman et al. (2018, 2019) also showed that eight-week unilateral resistance training on a lower limb can improve the maximal strength of the ipsilateral upper limb. These authors suggested that this cross-muscle transfer was the result of neural adaptations leading to increased muscle activation (i.e., VAL) of ipsilateral upper limb muscles during MVC.

The current study aimed to determine whether, as for MVC strength, there is a common construct of VAL and contractile kinetics among human muscles. To that end, we assessed MVC torque, VAL and twitch contractile properties of four muscle groups of the lower (knee extensors, dorsiflexors and plantar flexors) and upper (elbow flexors) limb in young healthy adults. We expected to find positive between-muscle group correlations for MVC torque, VAL, doublet twitch peak torque, doublet twitch contraction time and doublet twitch half-relaxation time. This would display for the first time the existence of an intermuscular relationship in: (1) VAL, (2) contractile kinetics and confirm an intermuscular relationship of MVC strength in young healthy adults.

Methods

Participants

Twenty-six healthy participants (9 women and 17 men, 22 ± 5 years, 174 ± 10 cm, 67 ± 10 kg), aged between 18

and 38 years old, volunteered for this experiment. None of the participants had injuries on either the upper or lower limb. The physical activity score of the sample was 9.5 ± 1.2 (ranging from 7.0 to 12.2), i.e., a moderate physical activity level. Information was obtained by interview using the Baecke Physical Activity Questionnaire in French, where 3 is the lowest score and 15 is the highest score (Vol et al. 2011). Written informed consent was obtained after participants were informed of the experimental protocol and potential discomfort of the current investigation. The study protocol was approved by our local ethics committee and conformed with the Declaration of Helsinki (last modified in 2013).

Experimental protocol

Neuromuscular assessment was performed in a random order for elbow flexors, knee extensors, plantar flexors and dorsiflexors in the dominant limb. The dominant limb was determined by asking the participants which hand was used for writing (i.e., dominant arm) and which leg was used to kick a ball (i.e., dominant leg). The optimum nerve stimulation site and intensity were first determined for each muscle group. Two paired stimuli (doublet at supramaximal intensity, i.e., 120% of optimal stimulation intensity) at 100 Hz were delivered at rest, with a 5 s interval between each stimulation(s), to examine the muscle contractile properties (i.e., doublet twitch peak torque, contraction time and half-relaxation time). Two minutes after a standardized warm-up (three contractions at 30%, 60%, and 90% of the estimated MVC torque), the participants were asked to perform three 4 s isometric MVCs. A 2 min rest period was respected between each MVC. Doublets at 100 Hz were applied both during (superimposed doublet) and 3 s after (potentiated doublet) each MVC to assess VAL (see below). For all attempts, strong verbal encouragements were given.

Torque recordings

Torque values for evoked and voluntary contractions were collected using an isokinetic dynamometer (Biodex, Shirley, NY, USA). The output signal from the dynamometer was collected at 2000 Hz using a Biopac acquisition system (MP35, BIOPAC System Inc., Goleta, USA).

Knee extensors

Participants were tested in a seated position with the hip and knee aligned in the frontal axis. The hip angle was fixed at 80° and the knee joint at 70° (0°—full extension for both joints), corresponding to the mean optimum knee angle for knee extensors (Newman et al. 2003). The lateral epicondyle of the femur was aligned with the axis of rotation of the dynamometer. The lower leg was attached to the lever

arm right above the ankle. Trunk and thighs were securely strapped to the dynamometer and participants were asked to cross their arms on their chest during contractions.

Plantar flexors

Participants were tested in a seated position with the hip angle at 80°, knee angle at 0° and ankle angle with 15° of dorsiflexion (0°—neutral ankle position), about the optimum joint configuration to produce the highest plantar-flexion torque (Sale et al. 1982; Landin et al. 2015). The lateral malleolus was aligned with the axis of rotation of the dynamometer. The foot, trunk and thighs were securely strapped to the footplate or the seat of the dynamometer and participants were asked to cross their arms on their chest during contractions.

Dorsiflexors

Participants were tested in a seated position with the hip angle at 80°, knee angle at 0° and ankle angle with 15° of plantarflexion, corresponding to the optimum ankle angle for dorsiflexors in terms of force production (Marsh et al. 1981). The lateral malleolus was aligned with the axis of rotation of the dynamometer. The foot, trunk and thighs were securely strapped to the footplate or the seat of the dynamometer and participants were asked to cross their arms on their chest during contractions.

Elbow flexors

Participants were tested in a seated position with a hip angle of 80°. For the dominant arm, the elbow was positioned to lean on a pad and the medial epicondyle of the humerus was aligned with the rotation axis of the dynamometer. The wrist was securely strapped into the lever arm. Shoulder and elbow were aligned along the front axis and the elbow joint was fixed at 80° (0°—full extension), corresponding to the optimum angle for elbow flexors (Leedham and Dowling 1995). The untested arm was positioned on the ipsilateral thigh and participants' trunks and thighs were securely attached to the dynamometer to limit extraneous movement during testing procedures.

Electrical nerve stimulation

A high-voltage (400 V) Digitimer stimulator (Model DS7-AH, Digitimer Ltd., Hertfordshire, UK) was used to generate single and paired (100 Hz frequency) electrical stimulations (rectangular pulses of 1 ms duration). For elbow flexors, knee extensors and plantar flexors, a hand-held cathode ball (0.5 cm-diameter) was used to determine the optimum cathode position, namely the site where the greatest resting

single twitch torque was evoked at 10 mA. For dorsiflexors, the bipolar surface stimulating electrode was placed in the site where the greatest resting single twitch torque was evoked at 10 mA. Then, for each muscle group, a recruitment curve of the resting single twitch was performed to determine the optimum stimulation intensity by progressively increasing current intensity from 10 mA until achieving maximal single twitch peak torque. Maximal single twitch peak torque was considered to be reached when no improvement in peak torque was observed between two stimulation intensities (Behm et al. 2002). A supramaximal stimulation intensity (i.e., 120% of the last stimulation intensity used in the recruitment curve of the resting single twitch) was used during the experiment to guarantee complete recruitment of motor units (Neyroud et al. 2013b).

Knee extensors

Electrical stimulations were applied to the femoral nerve to evoke knee extensor contraction. In agreement with previous studies the cathode (1 cm diameter, Kendall Medi-Trace™, Canada) was positioned over the inguinal space on the femoral nerve, and the anode (89×50 mm, Chattanooga Medical Supply Inc.) in the gluteal fold (Neyroud et al. 2013a; Doguet et al. 2017) (Fig. 1).

Plantar flexors

Electrical stimulations were applied to the tibial nerve to evoke plantar flexor contraction. In agreement with previous studies, the cathode (1 cm diameter, Kendall Medi-Trace™, Canada) was located in the popliteal fossa and the anode (130×80 mm, Chattanooga Medical Supply Inc.) over the anterior surface of the knee (Cattagni et al. 2017; Akagi et al. 2018; Merlet et al. 2018) (Fig. 1).

Dorsiflexors

Electrical stimulations were applied to the peroneal nerve to evoke dorsiflexor contraction. In agreement with previous studies, a bipolar surface stimulating electrode (8 mm diameter, Technomed medical accessories, Netherlands) was positioned just above the head of the fibula on the anterior part of the peroneal nerve (Meunier et al. 1990; Behm et al. 2002; Chung et al. 2007) (Fig. 1).

Elbow flexors

Electrical stimulations were applied to the brachial plexus to evoke elbow flexor contraction. In agreement with previous

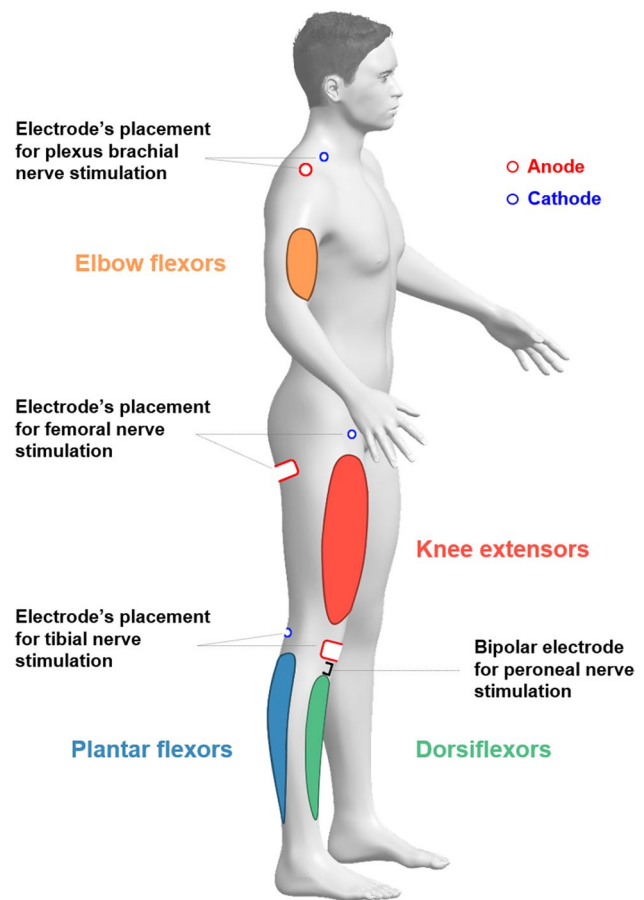


Fig. 1 Overview of muscles assessed and placement of stimulation electrodes

studies, the cathode (1 cm diameter, Kendall Medi-Trace™, Canada) was placed over the brachial plexus in the supra clavicular fossa and the anode (5 cm diameter, Chattanooga Medical Supply Inc.) over the acromion (Neyroud et al. 2013a; Šambaher et al. 2016) (Fig. 1).

Data analysis

Maximal voluntary torque and voluntary activation

For each muscle group, MVC torque was considered as the highest peak torque value measured over three trials. From the MVC trial with the highest peak torque, VAL was quantified by measuring the amplitudes of the superimposed doublet twitch peak torque and the potentiated doublet twitch peak torque (Fig. 2b). VAL was estimated according to the following formula, including the Strojnik and Komi (1998) correction:

$$\text{VAL} = \left[1 - \frac{\text{Superimposed doublet twitch torque} \times \frac{\text{Torque}_{\text{at stimulation}}}{\text{MVC torque}}}{\text{Potentiated doublet twitch torque}} \right] \times 100.$$

Contractile properties

For each muscle, the following parameters of resting doublet twitch contraction were calculated: peak torque, which is the amplitude between baseline signal and the highest torque value of the doublet twitch; contraction time, which is the time from start of the contraction (determined visually) to doublet twitch peak torque; half-relaxation time, which is the time from twitch peak torque to 50% decline in doublet twitch peak torque (Fig. 2a). For each parameter of resting twitch contraction, an average of the two mechanical responses was calculated.

Statistical analysis

All statistical tests were performed with Statistica 10 (StatSoft Inc., Tulsa, Oklahoma, USA). The Shapiro–Wilk test was used to check for the normality of the data. Since a non-Gaussian distribution was observed for most data, non-parametric tests were used. One-way Friedman analysis of variance was used to compare the MVC torque, VAL and doublet twitch contractile properties (peak torque, contraction time and half-relaxation time) between the four muscle groups tested (knee extensors, plantar flexors, elbow flexors and dorsiflexors). The χ^2 statistical value, the total sample size (n), the degree of Freedom (df) with $df = k - 1$ where k is the number of groups, the probability value (P) and the coefficient of concordance (Kendall's W), which ranges from 0 (no agreement) to 1 (complete agreement), were calculated

for each Friedman test. Post-hoc analyses using the Wilcoxon signed-rank test were conducted when a main effect was found. The non-parametric Spearman rank correlation was used to assess the degree of association between each pair of muscle groups for MVC torque, VAL, doublet twitch peak torque, doublet twitch contraction time and doublet twitch half-relaxation time. A correlation coefficient (r) between 0.9 and 1 indicated a very high positive correlation, between 0.7 and 0.9 indicated a high positive correlation, between 0.5 and 0.7 indicated a moderate positive correlation, and between 0.3 and 0.5 indicated a low positive correlation (Mukaka 2012). A Bonferroni correction was applied for all the statistical analyses. Consequently, the cumulative or family-wise error rate was below 0.05 (Field 2009), resulting in a significance level set at $P < 0.0125$.

Results

Between-muscle comparisons of neuromuscular properties

All data and statistical analyses concerning MVC torque, VAL and doublet twitch contractile properties for the overall sample are presented in Table 1. One-way Friedman analysis of variance revealed a significant muscle effect for all variables tested: MVC torque [χ^2 ($n = 26$, $df = 3$) = 72.78, $P < 0.0001$, Kendall's $W = 0.93$], VAL [χ^2 ($n = 26$, $df = 3$) = 57.65, $P < 0.0001$, Kendall's $W = 0.74$], doublet twitch peak torque [χ^2 ($n = 26$, $df = 3$) = 75.69,

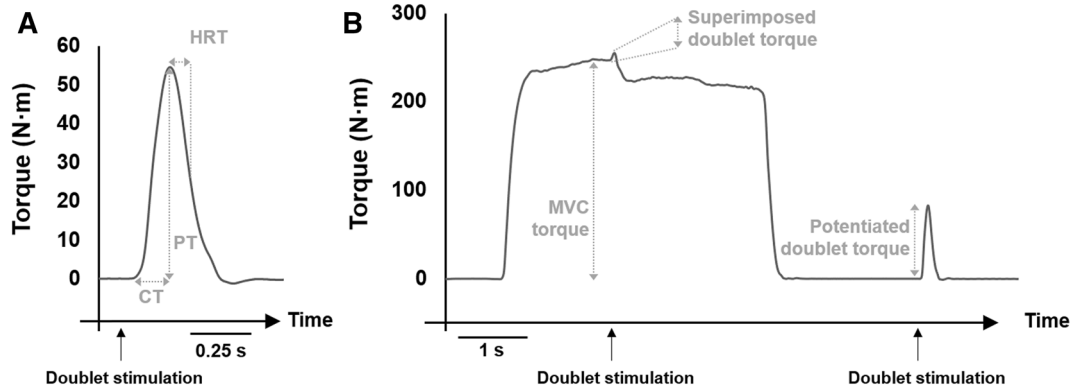


Fig. 2 Typical raw data traces of knee extensor torque during an evoked doublet twitch contraction at rest (a) and an isometric maximal voluntary contraction (MVC) associated with doublet stimulations (b). *CT* doublet twitch contraction time, *HRT* doublet twitch half-relaxation time

Table 1 Neuromuscular characteristics of knee extensor, plantar flexor, dorsiflexor and elbow flexor muscles

	Knee extensors	Plantar flexors	Dorsiflexors	Elbow flexors
MVC torque, N·m	202.9 ± 69.6* ^{§†}	142.9 ± 50.7 ^{§†}	35.9 ± 6.7 [†]	51.6 ± 14.7
VAL, %	84.1 ± 8.9 ^{§†}	87.6 ± 12.2 ^{§†}	99.7 ± 0.8	99.3 ± 2.0
PT, N·m	54.0 ± 13.7* ^{§†}	40.6 ± 7.9 ^{§†}	6.0 ± 2.1 [†]	10.9 ± 3.2
CT, ms	128.8 ± 8.2* [†]	178.2 ± 12.6 ^{§†}	137.0 ± 15.4 [†]	102.4 ± 6.8
HRT, ms	103.4 ± 31.1 [†]	113.1 ± 17.6 [†]	103.2 ± 17.5 [†]	78.1 ± 9.1

Data are presented as mean ± SD

MVC maximal voluntary contraction, VAL voluntary activation level, PT peak torque of doublet twitch, CT contraction time of doublet twitch, HRT half-relaxation time of doublet twitch

*Significant difference from plantar flexors, $P < 0.01$

[§]Significant difference from dorsiflexors, $P < 0.01$

[†]Significant difference from elbow flexors, $P < 0.01$

$P < 0.0001$, Kendall's $W = 0.97$], doublet twitch contraction time [χ^2 ($n = 26$, $df = 3$) = 69.00, $P < 0.0001$, Kendall's $W = 0.88$] and doublet twitch half-relaxation time [χ^2 ($n = 26$, $df = 3$) = 38.17, $P < 0.0001$, Kendall's $W = 0.49$].

The MVC torques of the muscle groups tested are all significantly different from each other ($P < 0.0001$). From the strongest to the weakest, the muscle groups were ranged as follows: knee extensors > plantar flexors > elbow flexors > dorsiflexors.

VAL was significantly higher ($P < 0.001$) in dorsiflexors and elbow flexors than in knee extensors and plantar flexors. No statistical differences for VAL were found between elbow flexors and dorsiflexors ($P = 0.79$), as well as between knee extensors and plantar flexors ($P = 0.09$).

The doublet twitch peak torque of the muscle groups tested are all significantly different from each other ($P < 0.0001$). From the strongest to the weakest, the muscle groups were ranged as follows: knee extensors > plantar flexors > elbow flexors > dorsiflexors.

Doublet twitch contraction time was significantly greater in plantar flexors than in dorsiflexors ($P < 0.0001$), knee extensors ($P < 0.0001$) and elbow flexors ($P < 0.0001$). It was also significantly greater for knee extensors ($P < 0.0001$) and dorsiflexors ($P < 0.0001$) than for elbow flexors. No significant difference in doublet twitch contraction time was found between knee extensors and dorsiflexors ($P = 0.03$).

Doublet twitch half-relaxation time was significantly greater in knee extensors ($P < 0.001$), plantar flexors ($P < 0.0001$) and dorsiflexors ($P < 0.0001$) than in elbow flexors. No significant differences were observed between plantar flexors, dorsiflexors and knee extensors.

Between-muscle correlations

Significant moderate-to-strong positive significant correlations were found for MVC torque between each pair of muscle groups ($0.54 < r$ values < 0.80 ; $0.0001 < P$ values < 0.005) (Fig. 3). A significant moderate positive correlation was

observed between the VAL of the knee extensors and that of the plantar flexors ($r = 0.60$; $P < 0.01$) (Fig. 4a). No other significant correlations for VAL were found between the other pairs of muscle groups ($0.03 < P$ values < 0.82) (Fig. 4b–f). Moderate positive correlations were observed between the doublet twitch peak torques of knee extensors and plantar flexors ($r = 0.68$; $P < 0.001$), knee extensors and elbow flexors ($r = 0.58$; $P < 0.01$) and dorsiflexors and elbow flexors ($r = 0.51$; $P < 0.01$) (Table 2). No other significant correlations for doublet twitch peak torque were revealed between the other pairs of muscle groups ($0.02 < P$ values < 0.67) (Table 2). No significant correlations between muscle groups were found for doublet twitch contraction time ($0.09 < P$ values < 0.45 ; Table 3) and doublet twitch half-relaxation time ($0.07 < P$ values < 0.58 ; Table 4).

Discussion

The main aim of this study was to determine whether as for MVC strength, there is a common construct of VAL and contractile kinetics among human muscles. The positive correlations found for MVC torque between each muscle groups that we assessed (i.e., knee extensors, plantar flexors, dorsiflexors and elbow flexors) first confirmed a common construct of limb MVC strength. However, between-muscle correlations for doublet twitch peak torque were only found between knee extensors and plantar flexors, knee extensors and elbow flexors, and dorsiflexors and elbow flexors. Unlike our assumptions, the results only revealed a positive relationship between the VALs of knee extensors and plantar flexors. In other words, individuals with the lowest (or the highest) VALs for knee extensors were those with the lowest (or the highest) VALs for plantar flexors. This study therefore highlighted a partial common construct of limb VAL that only concerned muscle groups with incomplete activation during MVC effort. Finally, the lack of correlation between muscle groups for doublet twitch contraction

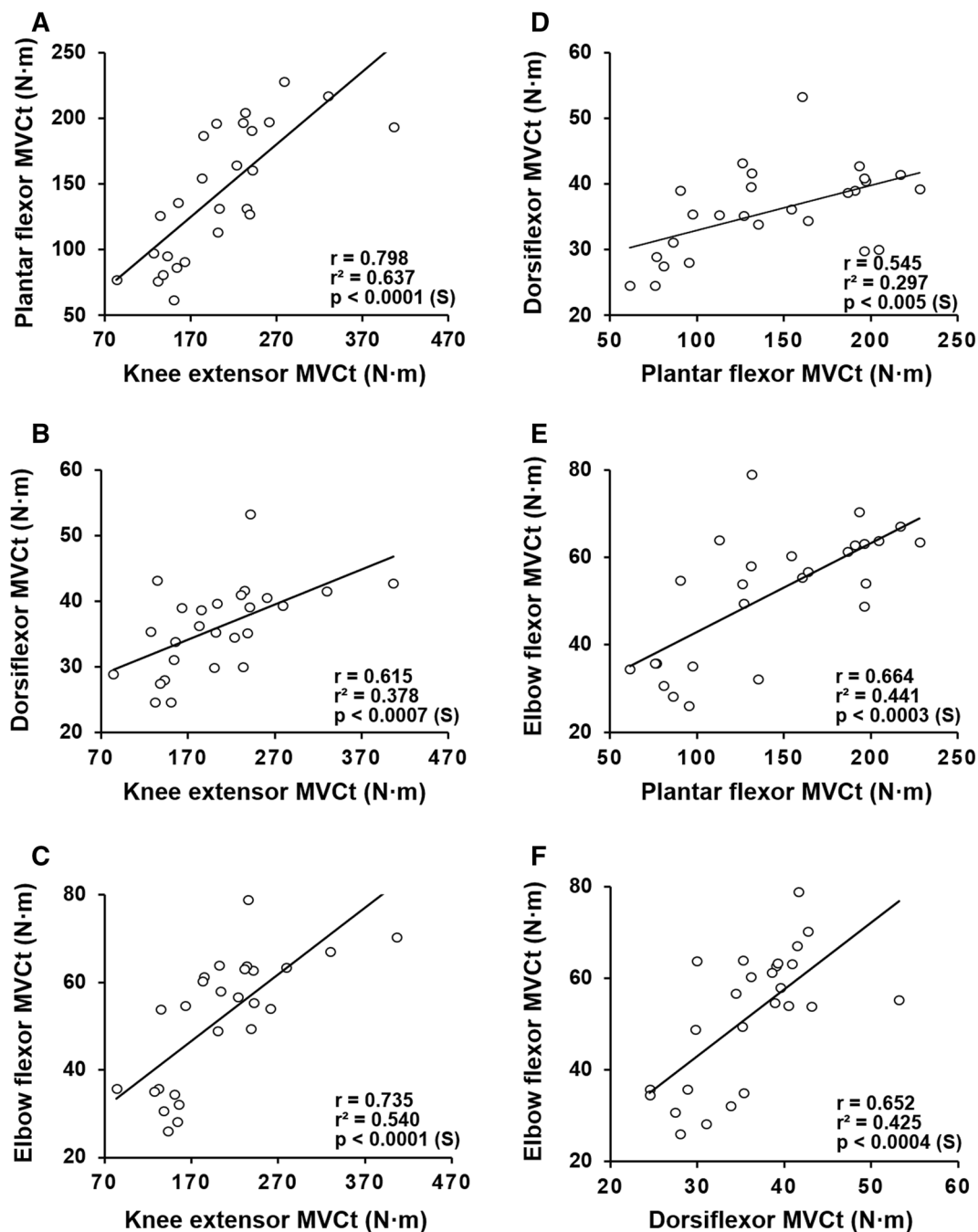


Fig. 3 Between-muscle correlations for maximal voluntary contraction torque (MVCT). S significant correlation

time and half-relaxation time showed that there is no common construct of twitch contractile kinetics among human muscles.

A common construct of limb strength in young healthy people

The present results revealed moderate-to-high positive correlations between the MVC torques of the muscle groups

we assessed in young healthy people. This indicated that individuals with the highest (or the lowest) MVC torque for a given muscle group are also those with the highest (or the lowest) MVC torque for the other muscle groups. The relationships between MVC torque or strength of different human muscles have been frequently investigated to establish if the assessment of MVC torque or strength of few muscles (one or two) can be used to estimate the global muscle strength of an individual [see Bohannon et al. (2008)

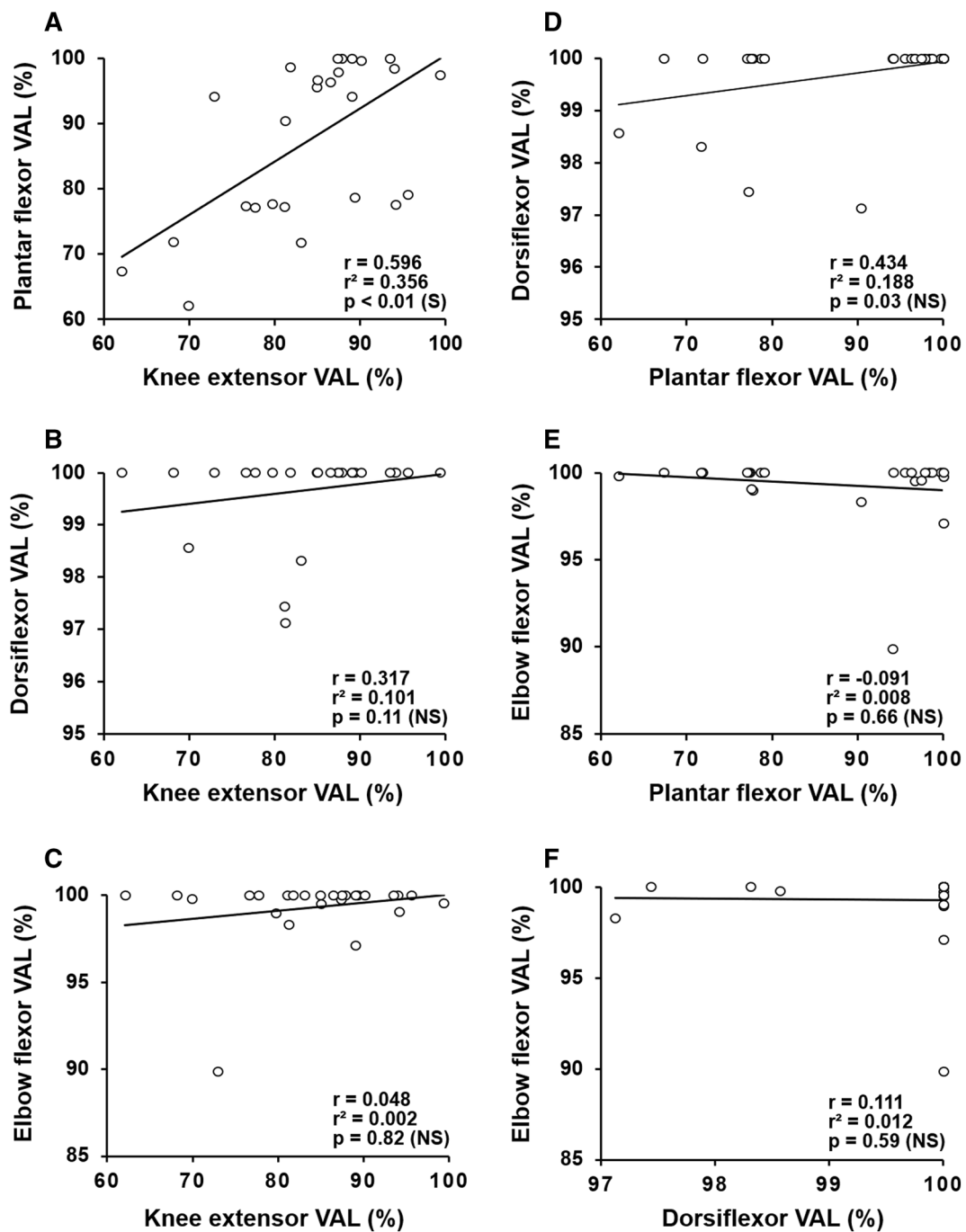


Fig. 4 Between-muscle correlations for voluntary activation level (VAL) during maximal voluntary contraction. *NS* not significant, *S* significant correlation, *VAL* voluntary activation level

for review]. Since hand-grip muscle strength can be used easily in a clinical context and requires low-cost tools to perform the assessment, most studies aimed to determine if this test is representative of the MVC strength of other muscle groups. The isometric hand-grip muscle strength was found to be well correlated with the isometric MVC strengths of upper and lower muscles in healthy adolescents

(Singla and Hussain 2018), young and older adults (Samuel and Rowe 2012; Bohannon 2012; Bohannon et al. 2012), as well as in patients with stroke (Takahashi et al. 2017) or Duchenne muscular dystrophy (Fowler and Gardner 1967). These previous results therefore validated that an assessment of the hand-grip muscle strength can be used in a clinical context to provide an approximate picture of the overall

Table 2 Between-muscle Spearman correlation for the doublet twitch peak torque

	Knee extensors	Plantar flexors	Dorsiflexors	Elbow flexors
Knee extensors	1			
Plantar flexors	0.68**	1		
Dorsiflexors	0.25	0.09	1	
Elbow flexors	0.58*	0.46	0.51*	1

*Significant difference, $P < 0.01$

**Significant difference, $P < 0.001$

Table 3 Between-muscle Spearman correlation for the doublet twitch contraction time

	Knee extensors	Plantar flexors	Dorsiflexors	Elbow flexors
Knee extensors	1			
Plantar flexors	0.20	1		
Dorsiflexors	0.22	0.23	1	
Elbow flexors	-0.33	-0.26	-0.16	1

Table 4 Between-muscle Spearman correlation for the doublet twitch half-relaxation time

	Knee extensors	Plantar flexors	Dorsiflexors	Elbow flexors
Knee extensors	1			
Plantar flexors	-0.18	1		
Dorsiflexors	0.31	0.11	1	
Elbow flexors	0.36	-0.26	0.25	1

muscle strength of an individual. Between-muscle correlations for other muscle groups have been mainly observed in pathologic populations or in healthy older people (Fowler and Gardner 1967; Rantanen et al. 1994; Bohannon 2008; Takahashi et al. 2017). For instance, Rantanen et al. (1994) reported in 295 75-year-old individuals (104 men and 191 women) moderate positive correlations (r values ranging between 0.52 and 0.64 for men and between 0.51 and 0.67 for women) between the isometric MVC strengths of the muscle groups (or action) they assessed, including hand-grip muscles, elbow flexors, hip flexors and extensors, and knee extensors. They reported a correlation between the MVC strengths of elbow flexors and knee extensors less strong than what we found between the MVC torques of these same muscle groups (r values: 0.54 vs. 0.73, respectively). Takahashi et al. (2017) found in the non-paretic side of 31 individuals with chronic stroke (~74-year-old; 19 men and 12 women) positive correlations between the isometric MVC strengths of the elbow flexors and knee extensors ($r=0.64$), elbow flexors and dorsiflexors ($r=0.77$), and knee extensors and dorsiflexors ($r=0.57$). These correlations were close to what we observed for MVC torque in healthy young participants (i.e., r values = 0.73, 0.65 and 0.61, respectively). The significant positive correlations between MVC torque or strength of several muscle groups in various populations highlights the robustness of the common construct of limb

MVC strength. In this study, we did not assess the intrinsic force-generating capacity of each muscle group but their respective MVC torque, which is obviously influenced by muscle intrinsic force-generating capacity but also by other factors, such as lever arm (or moment arm) length, tendon stiffness, pennation angle and VAL (Lieber and Fridén 2000; Baxter and Piazza 2014). We assumed that all these factors may have underestimated the power of the between-muscle correlations in strength in this study. Finally, the strongest between-muscle group relationship ($r=0.80$) for MVC torque was found between plantar flexors and knee extensors. As discussed below, our results supported that this strong relationship might be due to neural mechanisms.

Since MVC torque is, in part, related to muscle size (Baxter and Piazza 2014) and it was previously reported that doublet twitch torque is moderately-to-highly correlated with muscle size (Ryan et al. 2011; Mau-Moeller et al. 2015; Behrens et al. 2016), it could be expected between-muscle group correlations for evoked peak torque. However, only correlations between knee extensors and plantar flexors, knee extensors and elbow flexors, and dorsiflexors and elbows flexors were found. This may suggest that the distribution of muscle quantity between human muscles is not always consistent within an individual. Nevertheless, the relationship between twitch peak torque and muscle size has been established only for plantar flexors and knee extensors (Ryan et al. 2011;

Mau-Moeller et al. 2015; Behrens et al. 2016) but not for elbow flexors and dorsiflexors. Furthermore, twitch peak torque is not only related to muscle size or force-generating capacity but also to other factors, such as muscle length, Ca^{2+} sensitivity and muscle–tendon stiffness (Mayfield et al. 2016) that can also influence between-muscle correlations in twitch peak torque. Therefore, the present results cannot be used to support the hypothesis that there is (or not) between-muscle relationships in muscle size in humans. Further studies using accurate assessments of muscle size (e.g., muscle volumes from magnetic resonance imagery) should be done to determine between-muscle relationships in muscle size for whole human body.

What can explain the presence or absence of a common construct of voluntary activation level among human muscles?

The positive relationship between the VALs of the knee extensors and plantar flexors indicates that the higher the VAL of the knee extensors, the higher it is for the plantar flexors. Only the VALs of plantar flexors was correlated with the VALs of knee extensors, while no other correlation was found, suggesting a unique neural link between these muscles. Indeed, plantar flexors and knee extensors are synergist for most daily life activities such as gait, running, cycling, a sit-to-stand movement or vertical jump (Meunier et al. 1994; Khemlani et al. 1999; Ivanenko et al. 2004; d'Avella and Bizzi 2005; Wakefield and Horn 2008). During these tasks, these muscles are often activated simultaneously under the control of descending cortical circuits, but also the specific spinal networks that connect them, such as in recurrent inhibition from the quadriceps to soleus (Meunier et al. 1990) or soleus to quadriceps (Iles and Pardoe 1999), and heteronymous Ia facilitation from the quadriceps to soleus (Morita et al. 1995). It is therefore consistent to find such a relationship between the VALs of knee extensors and plantar flexors even if the neural mechanisms (supra-spinal vs. spinal level) underlying this relationship remains to be investigated. Nevertheless, because submaximal voluntary activation has been associated with lower cortical activation during MVC (Darling and Butler 2013), it can be expected that there is a potential relationship between the level of cortical activation of knee extensors and plantar flexors in our sample.

A possible explanation for the lack of correlations between the VALs of each pair of muscle groups including dorsiflexors and/or elbow flexors is a potential ceiling effect associated with the poor variability of VAL. Indeed, we found that the VALs of elbow flexors ($99.3 \pm 2.0\%$; complete activation for 17/26 of the participants) and dorsiflexors ($99.7 \pm 0.8\%$; complete activation for 22/26 of

the participants) were maximal or nearly maximal. This means that for most individuals only muscle groups having a submaximal VAL may have a common construct of maximal voluntary activation capacities. This suggests that VAL appears not to be a mechanism involved in the common construct of limb MVC strength in human muscles where VAL is maximal or almost maximal.

In contrast, the relationship between the VALs of plantar flexors and knee extensors indicates that VAL is a mechanism involved in the common construct of limb MVC strength between these two muscle groups for which VAL is not maximal.

What can explain the absence of a common construct of contractile kinetics among human muscles?

The present study failed to observe any between-muscle correlation for twitch contraction time and half-relaxation time, suggesting a lack of common construct of twitch contractile kinetics among human muscles. Because muscle contractile kinetics depend on muscle fiber type (Buchthal and Schmalbruch 1970), this result is not in agreement with a previous study showing an across-muscle phenotype with respect to fibre-type proportions (Vikne et al. 2012). Twitch contractile kinetics are known to be related to the efficacy of the excitation–contraction process, which includes intracellular calcium movements (Baylor and Hollingworth 2003, 2012). Twitch contraction time is mainly related to development of the sarcoplasmic reticulum, Ca^{2+} release and sequestration rate, and with Ca^{2+} concentration in the interfibrillar area (Salviati et al. 1982; Baylor and Hollingworth 2003, 2012). Twitch relaxation time is mainly related to the efficiency of sarcoplasmic reticulum for re-uptake of Ca^{2+} (Westerblad et al. 1997). In this investigation, twitch contractile kinetics were not directly assessed on isolated muscle fibre as performed in latter studies. Between-muscle correlations in contractile kinetics can therefore be biased by force transmission factors, such as muscle–tendon compliance. For instance, differences in muscle–tendon compliance (or series elastic element) may alter twitch contractile properties (Mayfield et al. 2016). In the present study, participants have been tested with joint angles representing the mean optimum force production angles for each tested muscle group reported in samples of previous studies (Marsh et al. 1981; Sale et al. 1982; Leedham and Dowling 1995; Newman et al. 2003). However, the lack of correlation might in part be due to individual force–length characteristics of the investigated muscle groups, which can modulate the characteristics of evoked muscle contraction. Because of these biases, the results of the present study cannot be used to definitively conclude on the absence of a common construct of limb contractile kinetics.

Perspectives

As mentioned above, the lack of common construct of VAL for muscle groups having a VAL maximal or near maximal may be due to a ceiling effect. The muscle strength generated during the first 50–75 ms of a very fast isometric contraction is another approach to assess maximal voluntary activation capacities. This method, associated with electromyographic recordings, can be used to characterize the neural determinants of the rate of torque/force development (Maffiuletti et al. 2016). It has the advantage of not including a ceiling effect and should be used in further studies to determine if there is a common construct of maximal human muscle activation capacities during very fast contractions.

This study showed that a common construct of VAL among human muscles having incomplete activation is present in healthy young people. In some healthy older people (Bilodeau et al. 2001; Jakobi and Rice 2002; Cattagni et al. 2018) or clinical populations, such as individuals with multiple sclerosis or chronic stroke people (Rice et al. 1992; Bowden et al. 2014), the VAL of several muscles is affected. It may be worthwhile to investigate in these populations if VAL is homogeneously affected across different muscle groups and therefore determine if there is also a common construct of muscle VAL in such populations. If so, this means that clinical interventions carried out to improve maximal activation capacities of one muscle group in those populations could also benefit other muscle groups, in terms of maximal activation capacities.

Study limitations

In this study, we chose to assess and compare the neuromuscular characteristics for only knee extensors, plantar flexors, dorsiflexors and elbow flexors because they have different motor functions and they can be easily investigated using the interpolated twitch technique (Bilodeau et al. 2001; Behm et al. 2002; Morse et al. 2004; Neyroud et al. 2013a). As previously reported (Behm et al. 2002), we observed that the order of the muscle groups from the strongest to the weakest is knee extensors, plantar flexors, elbow flexors and dorsiflexors. The results also showed that the VAL of elbow flexors ($99.3 \pm 2.0\%$) and dorsiflexors ($99.7 \pm 0.8\%$) were significantly greater than those of the knee extensors ($84.1 \pm 8.9\%$) and plantar flexors ($87.6 \pm 12.2\%$). We cannot exclude that concomitant stimulation of antagonist muscles could occur during electrical nerve stimulation, especially on small muscle groups such as elbow flexors, potentially overestimating VAL (Shield and Zhou 2004). However, our VAL values were close to those reported in other works for knee extensors, dorsiflexors and elbow flexors (Gandevia et al. 1998; Klein et al. 2001; Chung et al. 2007; Neyroud et al. 2013a; Kluka et al. 2015), but slightly below what is

commonly observed for plantar flexors at comparable ankle angles, i.e., 88–97% (Behm et al. 2002; Akagi et al. 2018; Merlet et al. 2018). It is worth noting that we did not include a familiarization session prior the main experimental session that may possibly explain why we observed a low VAL for the plantar flexors. Nevertheless, previous studies reported higher plantar flexor VAL in comparable samples while no familiarization sessions have also been performed (Behm et al. 2002; Akagi et al. 2018; Merlet et al. 2018).

In addition, we only tested our participants during isometric contractions. The between-muscle correlations that we have found for MVC torque only concern isometric contraction. Nevertheless, since isometric and isokinetic torque or strength of a given muscle group are known to be correlated (Knapik and Ramos 1980; Spiteri et al. 2014), we can also expect between-muscle correlations in isokinetic MVC torque. As previously mentioned, participants have been tested with fixed joint angles representing the mean optimum strength or torque production angles for each tested muscle group, according to previous reports (Marsh et al. 1981; Sale et al. 1982; Leedham and Dowling 1995; Newman et al. 2003). They have not been tested in the individual force–length characteristics of their investigated muscle groups. Because joint angle (or muscle length) was probably not optimum for some muscle groups of participants, this could have affected the power of the between-muscle correlations in MVC torque.

Conclusion

While the common construct of limb strength involves most human muscles, the current study demonstrated that there is also a common construct of maximal voluntary activation capacities for human muscles that have an incomplete activation during MVC effort (i.e., plantar flexors and knee extensors). However, the results of this study did not support any intermuscular relationship in contractile kinetics, as assessed in vivo by investigating the time-course of evoked twitch contractions.

Author contributions TC, MJ and CC conceived and designed research. EH and TC conducted experiments. EH analyzed data. EH and TC wrote the manuscript. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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