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RESEARCH ARTICLE

Do individual differences in the distribution of activation between synergist muscles reflect individual strategies?

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Abstract

Individual differences in the distribution of activation between synergist muscles have been reported during a wide variety of tasks. Whether these differences represent actual individual strategies is unknown. The aims of this study were to: (i) test the between-day reliability of the distribution of activation between synergist muscles, (ii) to determine the robustness of these strategies between tasks, and to (iii) describe the inter-individual variability of activation strategies in a large sample size. Eighty-five volunteers performed a series of single-joint isometric tasks with their dominant leg [knee extension and plantarflexion at 25% of maximal voluntary contraction (MVC)] and locomotor tasks (pedalling and walking). Of these participants, 62 performed a second experimental session that included the isometric tasks. Myoelectrical activity of six lower limb muscles (the three superficial heads of the quadriceps and the three heads of the triceps surae) was measured using surface electromyography (EMG) and normalized to that measured during MVC. When considering isometric contractions, distribution of normalized EMG amplitude among synergist muscles, considered here as activation strategies, was highly variable between individuals ($15.8\% < CV < 42.7\%$) and robust across days ($0.57 < ICC < 0.82$). In addition, individual strategies observed during simple single-joint tasks were correlated with those observed during locomotor tasks [$0.37 < r < 0.76$ for quadriceps ($n = 83$); $0.30 < r < 0.66$ for triceps surae ($n = 82$); all $P < 0.001$]. Our results provide evidence that people who bias their activation to a particular muscle do so during multiple tasks. Even though inter-individual variability of EMG signals has been well described, it is often considered noise which complicates the interpretation of data. This study provides evidence that variability results from actual differences in activation strategies.

Keywords Electromyography · Muscle coordination · Pedalling · Gait

Introduction

Human movement results from the coordination of multiple muscles. Given the redundant nature of our motor control system (Valero-Cuevas et al. 2015), even simplest tasks can be achieved by different muscle activation strategies. This leads to the assumption that each individual uses their own unique coordination strategy (Hug and Tucker 2017).

Surface electromyography (EMG) remains the most common technique used to provide insight into muscle activation strategies. Inter-individual variability of EMG signals has been observed during a wide variety of tasks, from multi-joint tasks [e.g., gait (Ahn et al. 2011; Ivanenko et al. 2002; Winter and Yack 1987); pedalling (De Marchis et al. 2013; Hug et al. 2010)] to simple isometric single-joint tasks [e.g., plantarflexion (Masood et al. 2014) and knee extension (Hug et al. 2015)]. For example, the distribution of activation between the lateral (GL) and medial (GM) head of the gastrocnemius during gait varied greatly between individuals, with seven out of the ten participants activating their GM more than their GL, and the other three participants activating their GM and GL nearly equally (Ahn et al. 2011). Such large individual

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differences have also been observed during more controlled tasks, such as isometric knee extensions where the number of participants using greater activation of the lateral head of the quadriceps (VL) being almost equal to those using greater activation of the medial head (VM) (Hug et al. 2015). It is important to understand the origin of such inter-individual variability, and the mechanical impact of individual patterns on the soft tissues and joint structures (Alessandro et al. 2018). However, we believe that a necessary first step is to provide evidence that these individual differences in activation reflect the existence of actual individual strategies rather than random variability.

To confidently interpret these inter-individual differences as evidence of individual muscle activation strategies, it is necessary to address the following considerations. First, individual differences in activation strategy should persist over time. Second, they should be robust between tasks. Third, these differences should be reported on a large sample size, previous experiments being typically conducted with fewer than 20–25 participants [12 and 22 healthy controls in Masood et al. (2014) and Hug et al. (2015), respectively].

With these considerations in mind, the aims of this study were: (i) to test the between-day reliability of the distribution of activation between synergist muscles, (ii) to determine the robustness of these strategies between tasks, and (iii) to describe the inter-individual variability of activation strategies in a large sample size. To address these aims, we considered muscle activation strategies as the distribution of normalized EMG amplitude among synergist muscles within two muscle groups from the lower limb (quadriceps and triceps surae muscle groups). We tested the between-day reliability and described activation strategies measured during well-controlled isometric tasks, and compared the activation strategies used during isometric tasks to those used during gait and submaximal pedalling.

Methods

Participants

Eighty-five healthy volunteers (55 males and 30 females; Table 1) participated in this study. Participants had no history of lower leg pain that had limited function within the 2 months prior to testing. All participants were between 18 and 43 years. The ethics committee "CPP Ouest V" approved the study (n°CPP-MIP-010) and all procedures adhered to the Declaration of Helsinki. Participants provided informed written consent. Each participant completed the International Physical Activity Questionnaire [IPAQ; evaluation tool of physical activity (Craig et al. 2003)].

Table 1 Demographic and anthropometric data for the tested population

	Males ($n=55$)	Females ($n=30$)
Age	24.3 ± 5.3	23.4 ± 5.4
Height (cm)	179.9 ± 6.9	165.2 ± 5.6
Body mass (kg)	72.2 ± 7.8	57.0 ± 5.8
MVC knee extension torque (Nm)	282.2 ± 65.0	188.9 ± 36.9
MVC plantarflexion torque (Nm)	161.2 ± 27.8	123.0 ± 18.1
Physical activity (MET-min/week)	5568 ± 4874	4387 ± 2618
Left footed	8 (14.5%)	7 (23.3%)

Maximal Voluntary Contraction (MVC) torque was measured during isometric contractions. Physical activity was estimated using the International Physical Activity Questionnaire (IPAQ; Craig et al. 2003)

Experimental design

The experimental session consisted in a series of single-joint isometric tasks performed with the dominant leg [knee extension and plantarflexion at 25% of maximal voluntary contraction (MVC)] and multi-joint submaximal tasks (pedalling at 150 Watts and walking on a treadmill at 0.83 m/s). These tasks were performed in a randomized order. From the 85 participants, 62 participated in a second experimental session 11 ± 12 days (range 1–58 days) after the first session. This second session included both the submaximal knee extension and plantarflexion tasks and data were used to assess the between-day reliability of the activation strategies during well-controlled tasks. A series of maximal isometric tasks was performed at the beginning of each session for normalization of the surface EMG signal and for determination of the target torque for the submaximal isometric tasks.

Myoelectrical activity

Myoelectrical activity was collected using surface EMG from two muscle groups of the dominant leg: rectus femoris (RF), vastus lateralis (VL), and vastus medialis (VM) for the quadriceps; gastrocnemius medialis (GM), gastrocnemius lateralis (GL), and soleus (SOL) for the triceps surae. For each muscle, a pair of self-adhesive Ag/AgCl electrodes (diameter of the recording area: 5 mm; Kendall Medi-Trace™, Canada) was attached to the skin with an inter-electrode distance of 20 mm (center-to-center) at the site recommended by SENIAM (Hermens et al. 2000). This location was refined using B-mode ultrasound (Aixplorer, Supersonic Imagine, France), such that the electrodes were placed longitudinally with respect to the muscle fascicle alignment (for VM, VL, GM, and GL), and

away from the border of neighbouring muscles. The electrode locations were intentionally not marked on the skin, such that variability of the electrode placement, which is a possible cause of inter-individual variability of EMG signals, would not contribute to the between-individual variability observed in this study. Prior to electrode application, the skin was shaved and cleaned with alcohol. Electrode cables were well secured to the skin with a tubular elastic bandage (tg®fix, Lohmann & Rauscher International, GmbH & Co. KG, Germany) to minimize movement artefacts. EMG signals were band-pass filtered (8–500 Hz) and pre-amplified close to the electrodes (375×) and digitized at a sampling rate of 1000 Hz using an EMG acquisition system (ME6000, Mega Electronics Ltd, Finland).

Experimental protocol

Isometric contractions

Participants performed a series of isometric knee extension and plantarflexion tasks while seating on an isokinetic dynamometer (Con-Trex, CMV AG, Dübendorf, Switzerland) with their hip flexed at 70° (0° = hip fully extended). For the knee extension tasks, the knee was positioned at 80° of flexion (0° = knee fully extended) and the shank was fixed to the dynamometer with inextensible strap. For the plantarflexion task, the knee was fully extended; the ankle was positioned at 0° (the foot perpendicular to the shank). Two inextensible straps were used to immobilize their torso. For each task, participants first performed a standardized warm-up, which included a series of 20 isokinetic contractions with a progressive increase in contraction intensity and 4 submaximal contractions at 60, 70, 80, and 90% of their subjective maximal contraction for 3–4 s, with 1 min rest between each contraction. This warm-up was followed by three maximal isometric voluntary contractions for 3 s, with 90 s rest between each contraction. Then, the experimental task involved matching submaximal target torque set at 25% of MVC during two short (≈ 10–15 s) isometric contractions with 20–30 s rest between each repetition. This target force level was presented on a feedback screen.

Pedalling

The pedalling task was performed on an electronically braked cycloergometer (Excalibur Sport; Lode, Groningen, The Netherlands) equipped with standard cranks (170 mm) and clipless pedals. The saddle height was standardized, such that it was at the same level as the greater trochanter of the participants during standing. Participants were instructed to maintain their seated position throughout the task. After familiarization with the cycloergometer, participants were asked to pedal at 150 W at 80 rpm for 1 min. A Transistor–Transistor Logic (TTL) pulse indicated the top dead center of the right pedal (highest position of the pedal) and was recorded on the EMG acquisition system, such that the crank position and the EMG data were synchronized.

Gait

To minimize perturbations induced by the external environment and to ensure that all the participants adopted the same walking speed, the experiments were conducted on a treadmill (Cardiotread, Cardioline, Trento, Italy). Participants walked barefoot and familiarized with the treadmill before the start of the experimental task, which consisted in walking at 0.83 m/s for 1 min. A force-sensitive resistor (FSR; FSR151AS) was taped under the heel of the dominant leg to detect the onset of the foot contact, i.e., the onset of the stance phase. These signals were recorded on the acquisition system used for EMG, such that the foot pressure and the EMG data were synchronized.

Data analysis

All mechanical and EMG data were processed using MATLAB (The Mathworks, Nathicks, USA). Raw EMG signals were first band-pass filtered (20–495 Hz) with a second-order Butterworth filter and a notch filter at 50 Hz was applied. Then, EMG signals were inspected for noise or artefact. At this stage, data were discarded for isometric plantarflexion (one participant; technical problems), pedalling (one participant; movement artefacts), and gait (two participants; movement artefacts).

Maximal torque and maximal EMG amplitude

Torque signals from the isometric tasks were low-pass filtered at 10 Hz. Maximal MVC torque was determined for both the three maximal knee extensions and the three maximal plantarflexions as the maximal torque measured over a 500-ms time window. To determine the maximal EMG amplitude, the root mean square (RMS) of the EMG signal was calculated over a moving time window of 500 ms and the maximal value was considered as the maximal activation level.

Submaximal EMG amplitude

During the isometric torque-matched tasks performed at 25% of MVC, the RMS EMG amplitude was calculated over 5 s at the middle of the force plateau. These values were averaged between the two contractions, such that one representative value was further considered.

For the pedalling task, the raw EMG signal was first rectified. After excluding the first 20 cycles, we selected the

first 15 consecutives cycles free of any artefacts. Each of these cycles was then interpolated to 200 time points and an ensemble-averaged cycle was obtained. The RMS EMG amplitude was calculated between − 5.5 and 44.4% of cycle, which corresponded to the downstroke phase [340°–160°; (Brochner Nielsen et al. 2017)]. EMG was considered during this phase as it represents the main phase of activity for both the knee extensors and the plantarflexors (Hug and Dorel 2009).

A similar procedure was used for gait, where 15 consecutive strides identified using the foot-sensible resistor sensors (onset of pressure) were ensemble-averaged. As activation of the quadriceps muscles is low during walking at low speed (< 5% of RMS EMG_{max} in our study), it was difficult to distinguish between noise and EMG for some participants. As such, only the muscles from the triceps surae were considered. The RMS EMG amplitude was calculated between 0 and 65% of cycle, which corresponded to the stance phase (Hebenstreit et al. 2015) during which these muscles are active (Schmitz et al. 2009).

For each submaximal task, the EMG amplitude was normalized to that determined during the maximal isometric task. This procedure was important to make between-muscles and between-days comparisons, but did not affect the relationship between tasks assessed from the first experimental session. We considered the activation contribution of each muscle to a given muscle group through the calculation of the activation ratio:

$$\frac{\text{Muscle } (i)}{\text{Muscle Group}} \text{ ratio } (\%) = \frac{\text{RMS EMG muscle } (i)}{\text{RMS EMG Muscle 1} + \text{Muscle 2} + \text{Muscle 3}} \times 100, \quad (1)$$

where (*i*) represents an individual muscle from the synergistic group considered.

For each muscle group, we also considered the activation ratio between the two muscles that share the same function (i.e., VL/VM as monoarticular knee extensors; GM/GL as biarticular plantarflexors).

Statistics

Statistical analyses were performed in Statistica v7.0 (Statsoft, Tulsa, OK, USA). All data are reported as mean ± SD. A Student *t* test was used to compare age and physical activity level between males and females. To test the robustness of the activation strategies during the isometric tasks, the between-day reliability of the EMG data was assessed using the intra-class correlation coefficient (ICC) and the standard error of measurement (SEM) as recommended by Hopkins (2000). ICC values were calculated as a measure of between-day reliability with values less than 0.4, between 0.4 and 0.6, between 0.6 and 0.75, and greater than 0.75 as poor, fair, good, and excellent agreement, respectively (Cicchetti et al. 2006). The inter-individual variability of the distribution of the activation ratios (VL/VM, RF/Quad, VL/Quad, VM/Quad; GM/GL, GM/TS, GL/TS, and SOL/TS) was then assessed using descriptive statistics [standard deviation (SD), coefficient of variation (CV), range, and interquartile range (IQR)]. As the previous studies reported sex difference in activation strategies (Hewett et al. 2005), separate repeated-measures analyses of variance (ANOVA) were performed for each activation ratio to determine the difference between males and females [between subject factor: sex (males vs. females); within-subject factor: task (knee extension or plantarflexion, pedalling, and gait)]. Post hoc analyses were performed using the Bonferroni test. The level of significance was set at $P < 0.05$. To determine the relationship between tasks (isometric tasks, gait, and pedalling), we calculated the Pearson's correlation coefficient. To provide insights into possible explanations for individual differences, we tested the relationship between each activation ratio and potential explanatory factors (physical activity level and MVC torque).

Results

Submaximal isometric tasks

Between-day reliability

Individual examples of raw EMG signals are depicted in Fig. 1. For the isometric knee extensions performed at 25% of MVC, the between-day reliability of the normalized RF, VL, and VM RMS EMG amplitude was fair to good (ICC > 0.50 and SEM < 3.5% of MVC; Table 2). Similarly, the reliability of the activation ratios was fair to good (ICC > 0.57 and SEM < 4.7%; Table 2). Even though the ICC value for RF RMS EMG and VL/VM ratio was interpreted as fair, the SEM values remained relatively low. For the isometric plantarflexions performed at 25% of MVC, the between-day reliability of the normalized GM, GL, and SOL RMS EMG amplitude was good to excellent (ICC > 0.64 and SEM < 3.4% of RMS EMG_{max}; Table 2). Similarly, the reliability of the activation ratios was good to excellent (ICC > 0.65 and SEM < 6.4%; Table 2). This overall fair-to-excellent reliability obtained on 62 participants suggests that activation strategies are robust between days.

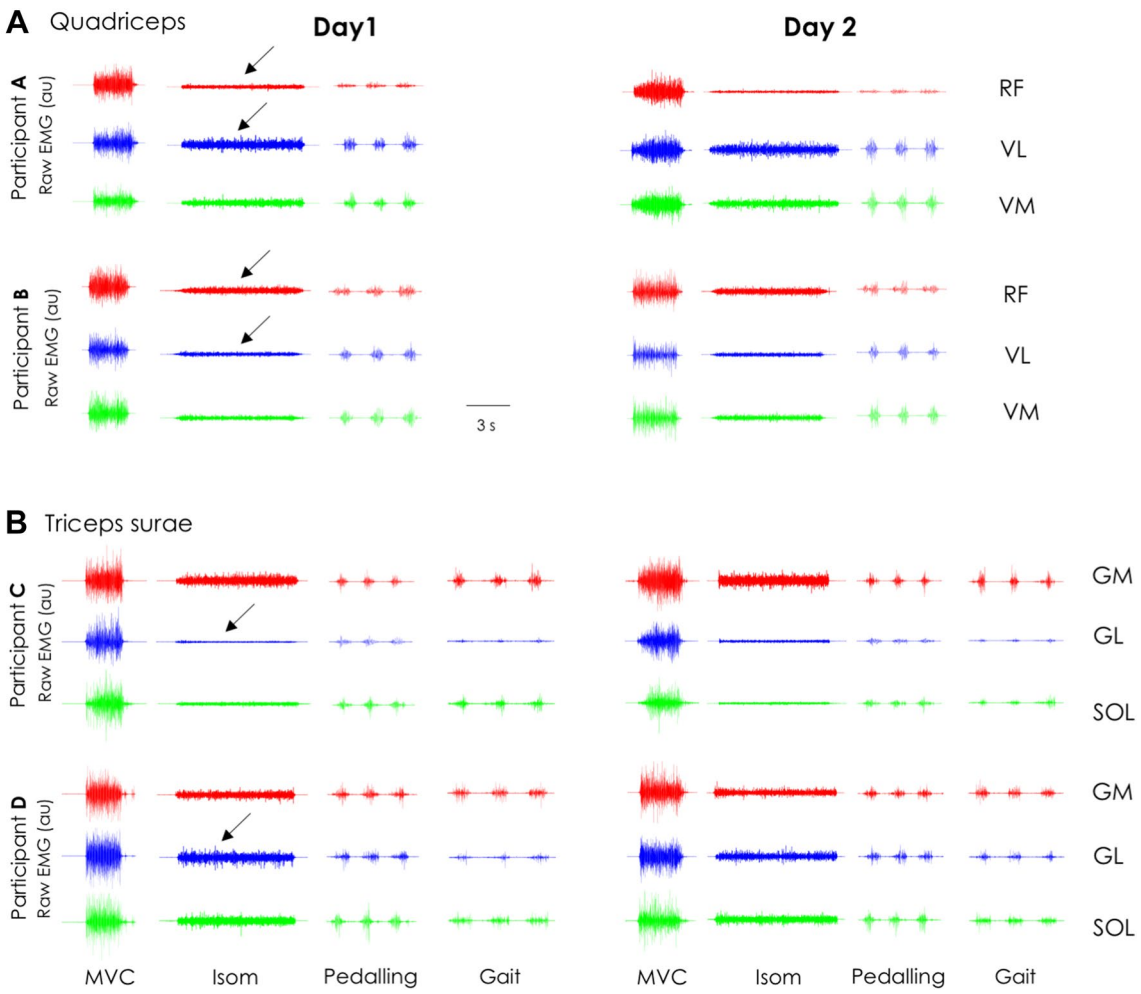

Fig. 1 Individual examples of the raw surface electromyographic signals. Representative raw electromyographic signal (EMG, arbitrary unit) of each head of the quadriceps (panel A: rectus femoris, RF; vastus lateralis, VL; vastus medialis, VM) and triceps surae (panel B: gastrocnemius medialis, GM; gastrocnemius lateralis, GL; soleus, SOL). EMG activity was measured during maximal voluntary contraction (MVC), isometric submaximal contractions performed at 25% of MVC (Isom), pedalling, and gait. Arrows show the inter-individual differences (e.g., Participant A: VL-biased; Participant C: GM-biased); the two columns (Day 1 and Day 2) illustrate the between-day consistencies

Table 2 Between-day reliability of muscle activation (RMS EMG) and activation ratios measured during the submaximal isometric force-matched tasks at 25% of MVC

$n=62$	RF RMS EMG	VL RMS EMG	VM RMS EMG	VL/VM	RF/Quad	VL/Quad	VM/Quad
ICC (90% CI)	0.50 (0.33–0.64)	0.63 (0.48–0.74)	0.62 (0.48–0.74)	0.57 (0.41–0.70)	0.71 (0.58–0.80)	0.61 (0.46–0.73)	0.64 (0.50–0.75)
SEM	3.4	3.5	3.4	4.7	4.4	4.1	3.8
$n=62$	GM RMS EMG	GL RMS EMG	SOL RMS EMG	GM/GL	GM/TS	GL/TS	SOL/TS
ICC (90% CI)	0.73 (0.61–0.81)	0.64 (0.50–0.75)	0.77 (0.67–0.84)	0.73 (0.62–0.81)	0.82 (0.74–0.88)	0.65 (0.50–0.75)	0.74 (0.63–0.82)
SEM	3.4	3.2	3.3	6.4	4.7	5.2	5.5

ICC intra-class coefficient of correlation, *SEM* standard error of measurement (expressed in % of RMS EMG_{max} for RMS EMG values and as % for the ratios), *RF* rectus femoris, *VL* vastus lateralis, *VM* vastus medialis, *Quad* quadriceps, *GM* gastrocnemius medialis, *GL* gastrocnemius lateralis, *SOL* soleus, *TS* triceps surae

Individual differences

Individual differences in activation strategies during the well-controlled single-joint tasks were assessed. During the isometric knee extensions at 25% of MVC, the mean EMG amplitude was 15.0 ± 4.6, 18.3 ± 5.7, and 17.6 ± 5.1% of RMS EMG_{max} for RF, VL, and VM, respectively. The mean ratio of EMG amplitude was 50.8 ± 8.0% (range 32.4–69.9%; IQR = 9.9; CV = 15.8%) for VL/VM, 29.7 ± 7.5% (range 14.9–57.1%; IQR = 9.8; CV = 25.3%) for RF/Quad, 35.8 ± 7.1% (range 21.3–58.2%; IQR = 11.0; CV = 19.8%) for VL/Quad, and 34.5 ± 6.4% (range 15.4–51.0%; IQR = 8.7; CV = 18.5%) for VM/Quad. As indicated by ranges, IQR, and CV, there was large variability between individuals (Fig. 2). For example, when considering the VL/VM ratio, there were an almost equal number of participants demonstrating greater VL RMS EMG than those with greater VM RMS EMG.

During the isometric plantarflexions at 25% of MVC, the mean EMG amplitude was 21.3 ± 6.2, 11.3 ± 5.8, and 18.3 ± 7.0% of RMS EMG_{max} for GM, GL, and SOL, respectively. The mean ratio of EMG amplitude was 66.2 ± 13.1% (range 35.5–89.6%; IQR = 19.2; CV = 19.8%) for GM/GL, 42.3 ± 10.5% (range 9.3–65.3%; IQR = 13.1; CV = 24.7%) for GM/TS, 21.7 ± 9.3% (range 5.0–46.7%; IQR = 14.0; CV = 42.7%) for GL/TS, and 36.0 ± 11.1% (range 16.6–78.9%; IQR = 13.8; CV = 30.8%) for SOL/TS. As observed for the quadriceps muscle group, range, IQR, and CV showed large variability between individuals (Fig. 3). Nine of the 84 participants activated their GL more than GM; the remaining participants activated their GM more than GL, with GM/GL ratios ranging from 50.0 to 89.6%.

There was no significant correlation between any of the activation ratios and MVC torque or IPAQ results (all *r* values < 0.18). This suggests that the activation strategies do not depend on muscle strength or physical activity level.

Relationship between isometric contractions and locomotor tasks

During pedalling, the mean EMG amplitude was 9.1 ± 5.0, 22.7 ± 9.5, and 25.1 ± 10.2% of RMS EMG_{max} for RF, VL, and VM, respectively; and 17.3 ± 5.7, 15.2 ± 6.1, and 19.8 ± 8.6% of RMS EMG_{max} for GM, GL, and SOL, respectively. During gait, the mean EMG amplitude was 14.4 ± 4.4, 7.7 ± 3.0, 14.9 ± 5.7% of RMS EMG_{max} for GM, GL, and SOL, respectively. Mean activation ratios are depicted in Table 3.

When considering the quadriceps muscle heads, there was a main effect of sex only for RF/Quad ($P = 0.003$), which was lower for males than females, regardless of the task. There was a main effect of task for each ratio (all *P* values < 0.0001). There was no significant sex × task interaction (all *P* values > 0.081), except for the VM/Quad activation ratio ($P = 0.041$). When the *post hoc* analysis was performed on VM/Quad, no significant differences

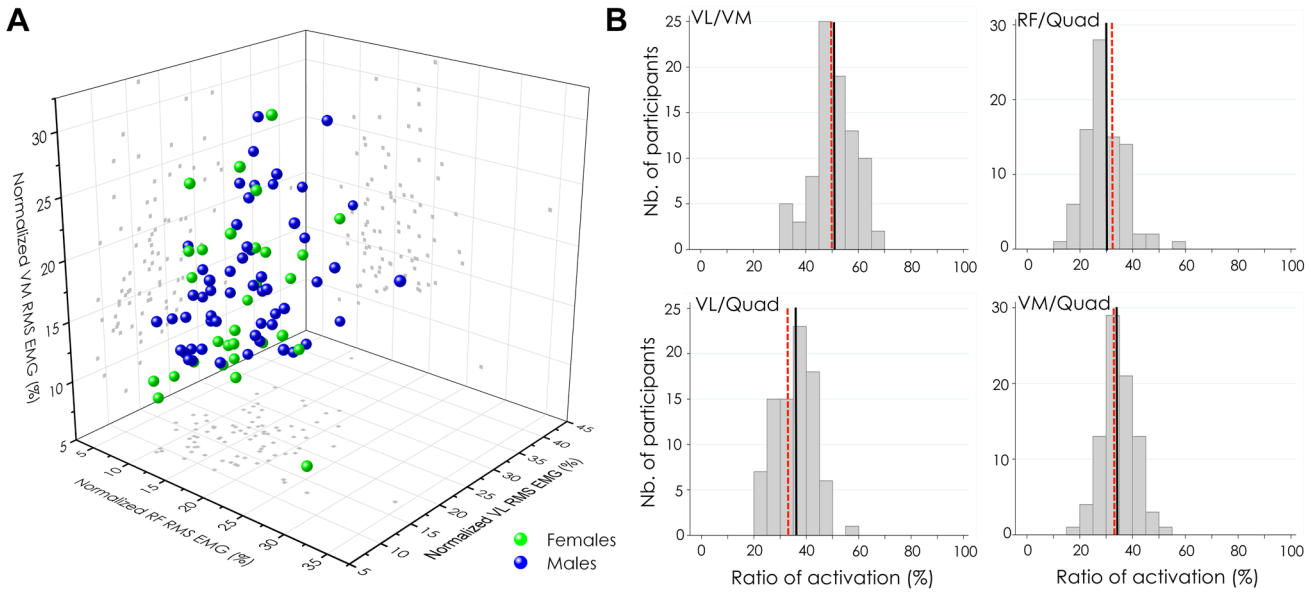

Fig. 2 Variability of activation strategies during the isometric knee extension task. **a** Normalized EMG amplitude for each muscle head. The spread of the dots within this 3-D space confirms that strategies to distribute activation among the synergist muscles are individual-specific. **b** Group distribution of the ratio of activation (RMS EMG). The red vertical line indicates a balanced activation among the synergist muscles (i.e., 50% and 33% when two muscles and three muscles were considered, respectively). The dashed vertical line indicates the mean value. *RF* rectus femoris, *VL* vastus lateralis, *VM* vastus medialis, *Quad* quadriceps

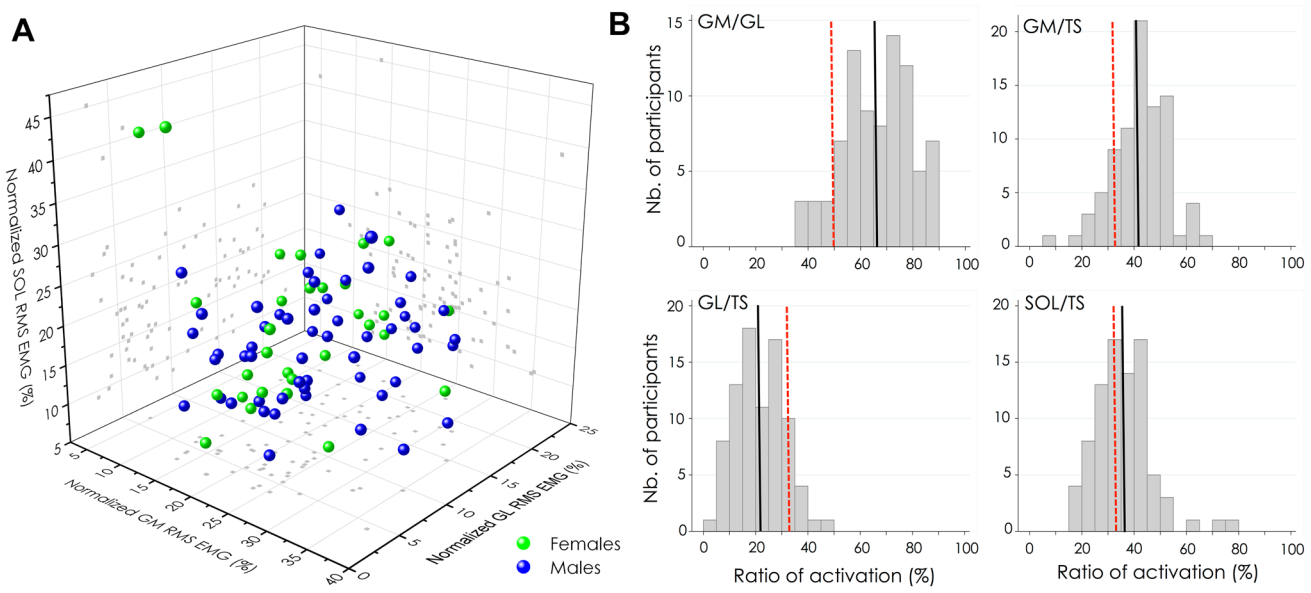

Fig. 3 Variability of activation strategies during the isometric plantarflexion task. **a** Normalized EMG amplitude for each muscle head. The spread of the dots within this 3-D space confirms that strategies to distribute activation among the synergist muscles are individual-specific. **b** Group distribution of the ratio of activation (RMS EMG). The red vertical line indicates a balanced activation among the synergist muscles (i.e., 50% and 33% when two muscles and three muscles were considered, respectively). The dashed vertical line indicates the mean value. *GM* gastrocnemius medialis, *GL* gastrocnemius lateralis, *SOL* soleus, *TS* triceps surae

Table 3 Correlation of the activation ratios between tasks

	VL/VM	RF/Quad	VL/Quad	VM/Quad	GM/GL	GM/TS	GL/TS	SOL/TS
Isom vs. Pedalling	0.76	0.37	0.72	0.60	0.37	0.21	0.41	0.30
Isom vs. Gait					0.55	0.43	0.61	0.43
Pedalling vs. Gait					0.43	0.47	0.47	0.66

All the correlations were significant, with effect sizes ranging from moderate to large, except that of GM/TS between Isom and pedalling ($P = 0.058$)

RF rectus femoris, VL vastus lateralis, *VM* vastus medialis, *Quad* quadriceps, *GM* gastrocnemius medialis, *GL* gastrocnemius lateralis, *SOL* soleus, *TS* triceps surae, *Isom* isometric

were observed between males and females (all P values > 0.225), but significant differences were observed between tasks (all P values < 0.001). For the sake of clarity, all these results are reported in Table 4.

When considering the heads of the *triceps surae*, we observed a main effect of sex for GM/GL ($P = 0.027$) but not for the other ratios (all P values > 0.074). There was a main effect of task for all the ratios (all P values < 0.023). We observed a significant sex × task interaction for GM/GL, GM/TS, and SOL/TS (all P values < 0.03), but not for GL/TS ($P = 0.558$). *Post hoc* analysis showed that neither GM/TS nor SOL/TS were significantly different between males and females, for any of the tasks (all P values > 0.051). However, GM/GL activation ratio was higher for males (68.8 ± 11.9%) than females (61.7 ± 14.1%) during isometric plantarflexion ($P = 0.039$), while no difference was found during pedalling ($P = 0.655$) and gait ($P = 1$). For the sake of clarity, all these results are reported in Table 4.

Each ratio of activation measured during pedalling was positively correlated to that measured during the isometric knee extension for quadriceps muscles ($n = 84$; $0.37 < r < 0.76$; all P values < 0.001; Table 3). Similar significant correlations were observed between pedalling and isometric plantarflexion for triceps surae ($n = 83$; $0.30 < r < 0.41$; all P values < 0.001; Table 3), except for GM/TS ($P = 0.058$). Notably, the coefficients of correlation were lower for the triceps surae muscles than for the quadriceps muscles. When considering the triceps surae, each ratio of activation measured during gait was positively correlated to that measured during the isometric plantarflexion ($n = 82$; $0.43 < r < 0.61$; all P values < 0.001; Table 3) or pedalling ($n = 82$; $0.43 < r < 0.66$; all P values < 0.001; Table 3). Overall, it signifies that

Table 4 Between-task comparison of activation strategies

	VL/VM		RF/Quad		VL/Quad		VM/Quad	
	Males	Females	Males	Females	Males	Females	Males	Females
A. Quadriceps								
Isom	51.3 ± 7.1	50.0 ± 9.5	28.6 ± 7.3	31.6 ± 7.6	36.8 ± 6.8	34.1 ± 7.4	34.7 ± 5.5	34.3 ± 7.8
Pedalling	46.9 ± 8.1	48.1 ± 11.2	14.0 ± 7.1	19.1 ± 3.9	40.4 ± 8.2	38.9 ± 9.0	45.6 ± 7.7[a]	42.0 ± 9.7[a]
	Main effect task ($P < 0.001$; Isom > Ped)		Main effect sex ($P = 0.003$; F > M) Main effect task ($P < 0.001$; Isom > Ped)		Main effect task ($P < 0.001$; Isom < Ped)		Sex × task interaction ($P = 0.041$)	
	GM/GL		GM/TS		GL/TS		SOL/TS	
	Males	Females	Males	Females	Males	Females	Males	Females
B. Triceps surae								
Isom	68.8 ± 11.9	61.7 ± 14.1[c]	44.2 ± 8.9	38.8 ± 12.1	20.5 ± 8.6	24.0 ± 10.2	35.3 ± 9.6	37.2 ± 13.4
Pedalling	55.6 ± 8.6[a]	50.7 ± 8.6[a]	34.9 ± 6.5[a]	30.8 ± 6.4[a]	28.1 ± 7.3	30.1 ± 6.9	37.0 ± 8.8	39.1 ± 8.5
Gait	65.8 ± 8.9[b]	65.1 ± 8.1[b]	38.2 ± 6.6[a]	41.2 ± 7.1[b]	20.1 ± 6.3	22.1 ± 5.8	41.7 ± 7.8[a,b]	36.7 ± 7.6
	Sex × task interaction ($P = 0.030$)		Sex × task interaction ($P < 0.001$)		Main effect Task ($P < 0.001$ Ped > Isom and Gait)		Sex × task interaction ($P = 0.003$)	

The distribution of activation among synergist muscles was estimated using the calculation of activation ratio

RF rectus femoris, *VL* vastus lateralis, *VM* vastus medialis, *Quad* quadriceps, *GM* gastrocnemius medialis, *GL* gastrocnemius lateralis, *SOL* soleus, *TS* triceps surae, *Isom* isometric

[a]Different compared to isometric

[b]Different compared to pedalling

[c]Difference between males and females

even though between-tasks differences in activation ratios logically exist at the group level (Table 4), individual-specific strategies are retained between tasks.

Discussion

This study has three main findings. First, the distribution of normalized EMG amplitude among synergist muscles is robust between days, allowing us to consider that it represents an individual muscle activation strategy. Second, these strategies vary greatly between individuals. Third, distribution of EMG amplitude is correlated between tasks, providing evidence that people who bias their activation to a particular muscle do so during multiple motor tasks. Even though inter-individual variability of EMG signals has been well described in the literature, it is often considered noise which complicates the interpretation of data. This study provides evidence that inter-individual variability results from actual differences in activation strategies. It is our contention that consideration of this inter-individual variability is important to expand our knowledge of the role of muscle coordination in the development of musculoskeletal disorders.

Important considerations to interpret individual differences in EMG amplitude

There are three important considerations when interpreting inter-individual differences in EMG amplitude as an evidence of individual-specific motor strategies. The first is to test the consistency of EMG data across days. Our results, obtained from a subgroup of 62 participants, demonstrate a fair-to-good reliability for the quadriceps muscles and a good-to-excellent reliability for the triceps surae muscles. Even though the quadriceps muscles exhibited lower ICC values than the triceps surae muscles, SEM values were similar between muscle groups, which suggest that the lower ICC values were likely explained by the smaller variance of the quadriceps muscles rather than a lower reliability. Despite the overall good reliability, between-day variability inevitably exists. Importantly, this between-day variability may not be (entirely) explained by variability of the activation strategies between days as methodological factors may also affect EMG amplitude [e.g., electrode placement, normalization procedure, and skin impedance; reviewed in Farina et al. (2004)]. In contrast to the previous work (Hug et al. 2015), we intentionally did not mark the electrode locations, such that day-to-day variability of the electrode placement could contribute to a possible difference in the

observed motor behaviour between days. It was important to not exclude this source of between-day variability as electrode placement might explain, at least in part, the inter-individual variability of the EMG signals. It is important to note that other factors such as crosstalk and signal cancellation may affect the relationship between EMG amplitude and muscle activation (Farina et al. 2004). To limit crosstalk, we followed the SENIAM recommendations and we used B-mode ultrasound to place the electrodes away from the muscle borders. To limit the influence of signal cancellation, we normalized the EMG amplitude to that measured during MVC (Keenan et al. 2005).

The second important consideration relates to the interpretation of the distribution of EMG amplitude as a neural strategy. Even though the ratio of VL/VM EMG amplitude observed from the group data (50.8 ± 8.0%) is in accordance with the recent results suggesting a balanced or common neural drive between these muscles (Martinez Valdes et al. 2018; Laine et al. 2015), it is well understood that EMG amplitude only provides a crude index of neural drive, i.e., the number of motor neuron action potentials (Dideriksen et al. 2011; Enoka and Duchateau 2015). EMG amplitude is more closely related to muscle activation, which relates to the number of muscle fibre action potentials (Dideriksen et al. 2011; Enoka and Duchateau 2015). Note that the relationship between neural drive and muscle activation depends on the size of the motor units, i.e., the number of muscle fibres within each active motor unit. In the absence of a difference in muscle fibre electrical properties between muscles (muscle fibre conduction velocity and size of the motor unit action potentials), between-muscle difference in EMG amplitude can be interpreted as between-muscle difference in activation (Enoka and Duchateau 2015; Farina et al. 2010). First, there is no evidence that fibre conduction velocity differs between synergist muscles during non-fatiguing contractions performed at a low intensity, as were performed in our study. This is because slow-twitch muscle fibres are likely preferentially recruited during such tasks (Henneman et al. 1965). Second, the difference in the size of the motor units action potential, if any, might have been minimized by the normalization procedure (Martinez-Valdes et al. 2018). With these considerations in mind, we interpreted the inter-individual differences in the distribution of normalized EMG amplitude across synergist muscles as differences in muscle activation strategies rather than differences in neural strategies.

Individual-specific muscle activation strategies

The vast majority of studies on muscle coordination report values averaged from a group of individuals, making it impossible to appreciate the individual differences in the activation strategies that inevitably exist. Here, a large inter-individual variability of the activation ratios was observed during the submaximal single-joint tasks (Figs. 2, 3), the magnitude of which exceeded the within-participant variability assessed between two different days. To the best of our knowledge, the significance of inter-individual variability has received a little attention in the literature. Pal et al. (2012) reported a wide range of VL/VM activation ratios in people with patellofemoral pain during gait, but different methodologies for EMG normalization and ratio calculation preclude comparison with our data. Other work reported a similar individual variability in the activation ratios for quadriceps (Hug et al. 2015) or triceps surae muscles (Ahn et al. 2011; Masood et al. 2014), but they were conducted on relatively small sample sizes (between 8 and 22 individuals). The novelty of the present study is to describe these individual differences in a larger sample size ($n = 85$) and to demonstrate the robustness of the distribution of EMG amplitude between muscles across time, allowing us to consider that it represents a true individual-specific activation strategy. Furthermore, even though the distribution of activation was significantly different between some (but not all) tasks, a significant correlation of the activation ratios between tasks was observed. Differences in muscle function imposed by the different mechanical constraints (isometric vs. dynamic contractions) might have involved different neuronal circuits (Kurtzer et al. 2005; Shadmehr 2016), leading to the observed differences between tasks. However, the existence of significant correlation between tasks indicates that a participant who exhibits an activation strategy biased toward a specific muscle will exhibit this strategy regardless of the task (at least within the tasks considered here in). Overall, these results provide strong evidence for the individuality principle (Ting et al. 2015), i.e., individuals exhibit different activation strategies, evidenced here as different distribution of activation across synergist muscles. Importantly, these strategies may evolve as a result of changes within the musculoskeletal systems due to training/disuse (e.g., muscle typology and muscle volume), or the presence of musculoskeletal pain (Hodges and Tucker 2011). The extent to which individual features (or signatures) are retained throughout this adaptation process is unknown.

Despite not being the main outcome of this study, differences in the mean activation ratios were observed between tasks, and between males and females. We believe that the interpretation of these differences requires the consideration of the relative contraction intensity (in percentage of maximal intensity), which may differ between tasks or between males and females during gait and pedalling. Indeed, the distribution of activation logically depends on the contraction intensity, with the contribution of synergist muscles being more balanced at higher contraction intensities that require near-complete or complete activation (Hug et al. 2015; Pincivero and Coelho 2000). However, because differences

in contraction intensity remained of small amplitude, they are unlikely to fully explain the observed between-task and between-sex differences. Note that the sex difference observed for some, but not all, activation ratios is in accordance with the previous studies reporting between-sex difference in activation strategies (Hewett et al. 2005). The origin of these differences remains unclear.

Origin of individual muscle activation strategies

Interestingly, the inter-individual variability of the distribution of EMG amplitude was observed even during well-controlled tasks, such as the single-joint isometric contractions, and the pedalling task. Here, we argue that this consistency provides evidence that they reflect true difference in activation strategies rather than different kinetics/kinematics strategies. Yet, the origin of these individual differences is unknown. They can be discussed in regards to the current motor control theories. The optimal feedback control theory (Todorov 2004) proposed that motor patterns are selected, such that movement costs (e.g., smoothness, activation, jerk, and energy) are constantly minimized. Within this framework, it is possible that each individual optimizes a different cost and/or that optimizing the same cost(s) requires different activation strategies across individuals because of individual characteristics (e.g. anatomy, muscle morphology, muscle moment arm, and neural constraints). An alternative motor control theory, the good-enough theory, proposes that a hierarchy of sensorimotor networks gradually adapt through trial-and-error learning to produce effective movements which are good enough to achieve the task goal (Loeb 2012). It is, therefore, possible that individuals develop different good-enough muscle activation strategies through motor exploration, experience, and training, leading to habitual rather than optimal strategies (De Rugy et al. 2012). Here, we did not find any association between the level of physical activity and the activation strategies. However, the IPAQ questionnaire only evaluates general physical activity. It is possible that past and present experience with specific motor skills (i.e., motor history) might have participated to shape individual strategies. Retrospective studies on large cohorts or longitudinal studies performed at different lifespans are needed to address this question. An alternative explanation of our results is that the distribution of muscle activation, but not that of neural drive differs between participants, as recently suggested from data averaged over a group of participants (Martinez Valdes et al. 2018). In this case, it would mean that individual muscle activation strategies would originate from peripheral features rather than differences in neural drive. Further works with advanced EMG decomposition techniques are needed to unravel the origin of the inter-individual variability of activation strategies as described in the present study.

Consequences of individual muscle activation strategies

Although the origin of the individual differences in muscle activation strategies is unknown, we believe that they may have important functional consequences. First, muscle activation strategies might impact muscle performance. Prilutsky and Zatsiorsky (2002) suggested that fatigue may be minimized by more equal stress distribution (and thus activation) among muscles with similar typology. In other words, if activation is not equally shared between synergist muscles throughout a fatiguing task, fatigue would develop sooner in the most activated muscle, which would, therefore, be the weakest link. As such, Avrillon et al. (2018) reported a significant negative correlation between the imbalance of activation across the hamstring muscles and the time to exhaustion during a submaximal force-matched task, i.e., the larger the imbalance of activation across muscles, the lower the muscle endurance performance.

Second, each individual muscle activation strategy may have specific mechanical effect on the musculoskeletal system (Hug and Tucker 2017). As muscle activation is not systematically adjusted to balance forces between the synergist muscles of differing force-generating capacities, it is likely to lead to a force imbalance between these muscles (Crouzier et al. 2018; Hug et al. 2015). Importantly, the magnitude of this force imbalance may vary greatly between participants. Even though the mechanical effect of this force imbalance on non-muscular structures is unknown, it is possible that some activation strategies put some individuals at more risk of developing musculoskeletal disorders (Hug and Tucker 2017).

Conclusion

Although it is well known that muscle activation can vary between individuals, these differences have been very rarely considered as relevant information to expand our knowledge on motor control. By showing their robustness, our results strongly provide evidence that these differences reflect the existence of individual activation strategies. Further works with advanced EMG decomposition techniques are needed to unravel the origin of the observed inter-individual variability of the activation strategies as described in the present study.

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Compliance with ethical standards

Conflict of interest The authors have no financial conflicts of interest to disclose.

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