J Neurophysiol 111: 768–776, 2014.
First published November 20, 2013; doi:10.1152/jn.00595.2013.

Effect of vastus lateralis fatigue on load sharing between quadriceps femoris muscles during isometric knee extensions

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Submitted 22 August 2013; accepted in final form 15 November 2013

Bouillard K, Jubeau M, Nordez A, Hug F. Effect of vastus lateralis fatigue on load sharing between quadriceps femoris muscles during isometric knee extensions. *J Neurophysiol* 111: 768–776, 2014. First published November 20, 2013; doi:10.1152/jn.00595.2013.—The present study aimed to investigate the effects of selective fatigue (i.e., one muscle of the quadriceps) on load sharing strategies during submaximal knee extensions. Shear wave elastography was used to measure muscle shear elastic modulus, as this is considered to be an index of individual muscle force. Sixteen participants attended two experimental sessions that each involved six 10-s knee extensions at 20% of maximal voluntary contraction (MVC) followed by a sustained submaximal isometric knee extension at 20% of MVC, until task failure (Tlim). Between the 10-s contractions and Tlim, participants were required to rest (5 min) for the control session or underwent 5 min of electromyostimulation (EMS) on vastus lateralis (EMS session). Compared with the control session, vastus lateralis shear elastic modulus values were significantly lower after EMS considering both the start of Tlim (54.6 ± 11.8 vs. 68.4 ± 19.2 kPa; $P = 0.011$) and the entire Tlim contraction (59.0 ± 14.0 vs. 74.4 ± 20.3 kPa; $P = 0.019$). However, no significant differences were observed for the other recorded muscles (vastus medialis and rectus femoris; both $P = 1$), i.e., different patterns of changes were found between participants. In conclusion, this study demonstrates that prefatiguing a single agonist muscle does not lead to a consistent redistribution of load sharing among the quadriceps muscles between individuals. These results suggest that the central nervous system does not use a common principle among individuals to control load sharing when neuromuscular fatigue occurs.

elastography; muscle coordination; electromyostimulation; supersonic shear imaging; shear wave elastography

THE REDUNDANCY of the musculoskeletal system implies vast degrees of freedom. Consequently, a given joint moment can be produced by an infinite number of muscle force combinations. The question of how the central nervous system (CNS) manages load sharing between muscles is central to the understanding of motor control (Erdemir et al. 2007), for design of robotic and prosthetic systems that mimic or restore human movement (Veeger et al. 2004) and for the improvement of rehabilitation programs (Fox 1975; Zory et al. 2005).

Modeling approaches (e.g., Erdemir et al. 2007; Tsirakos et al. 1997) and/or experimental techniques such as electromyography (EMG) (e.g., Buchanan et al. 1986; Praagman et al. 2010; Zhang et al. 2003) have been proposed to study load sharing strategies. However, because of the lack of experimental techniques, the validity of the biomechanical models cannot be established (Dennerlein et al. 1998; Erdemir et al. 2007). Although EMG can be used to study the neural control of muscle coordination during both isometric and dynamic contractions (d'Avella et al. 2003; Bizzi and Cheung 2013), it cannot be used to accurately predict muscle force (Disselhorst-Klug et al. 2009). First, during dynamic contractions, muscle length change distorts the relationship between activity and force. Consequently, the same force can be achieved at different activation levels if the muscle operates at different lengths (Altenburg et al. 2009). Second, surface and fine-wire EMG signals do not provide any information about passive force that also depends on the muscle length. Finally, this inability to use EMG to accurately estimate muscle force is confounded further during fatiguing tasks, where the presence of neuromuscular fatigue impairs the relationship between surface EMG activity and force (Dideriksen et al. 2011; Edwards and Lippold 1956; Enoka and Stuart 1992; De Luca 1984), leading to unacceptable errors. For instance, an error of ≈20% of the maximal voluntary contraction (MVC) was observed when muscle force was estimated from the EMG during an isometric fatiguing contraction performed at 40% of MVC (Bouillard et al. 2012a). These limitations may explain the lack of reliable information regarding the effect of neuromuscular fatigue on load sharing strategies.

A strong linear relationship exists between muscle shear elastic modulus measured by a shear wave elastographic technique (supersonic shear imaging, SSI) and individual muscle force (Bouillard et al. 2011), and this relationship is not altered by fatigue (Bouillard et al. 2012a). Consequently, SSI can be used to quantify relative changes in force for an individual muscle during isometric fatiguing contractions (Bouillard et al. 2012a). Taking advantage of this experimental technique, Bouillard et al. (2012a) reported evidence of changes in load sharing among the knee extensors during a sustained isometric fatiguing contraction. However, this was not observed in all participants, and when it was observed participants did not exhibit the same strategies, i.e., compensations did not systematically occur between the same muscles. The origin of these differences remains unclear. It is possible that participants performed the task differently (different load sharing across muscles), and thus fatigue was distributed differently among the quadriceps muscles. This would mean that people would adopt a compensation strategy specific to fatigue location [i.e., muscle(s) where the fatigue predominantly occurred]. One approach to test this assumption is to selectively fatigue one

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muscle. This can be achieved by electrically stimulating a muscle as previously described elsewhere (Akima et al. 2002).

Therefore, the aim of the present study was to investigate the effects of selective fatigue (i.e., one muscle of the quadriceps muscles) on load sharing strategies during submaximal knee extensions. First, we quantified changes in load sharing among the knee extensors during a submaximal isometric contraction after vastus lateralis (VL) was selectively fatigued with electromyostimulation (EMS). Second, we investigated the effect of prefatiguing VL on the changes of load sharing that occurred throughout a sustained contraction performed until task failure. Shear wave elastography was used to measure muscle shear elastic modulus, as this is considered to be an index of individual muscle force (Bouillard et al. 2011, 2012a, 2012b). We hypothesized that *1*) localized fatigue on VL would induce a systematic decrease in the force produced by this muscle, compensated by an increase in the force produced by the other extensors, and *2*) fatigue on VL would lead to similar changes in load sharing between individuals during the sustained fatiguing contraction, suggesting a common compensation strategy.

MATERIALS AND METHODS

Participants/Ethical Approval

Sixteen healthy volunteers (24.6 ± 2.6 yr, 180.0 ± 6.7 cm, 73.9 ± 9.8 kg; 15 men, 1 woman) participated in this study. Participants were informed of the possible risk and discomfort associated with the experimental procedures prior to giving their written consent to participate. The experimental design of this study was approved by the local Ethical Committee (Nantes) and was carried out in accordance with the Declaration of Helsinki.

Measurements

Dynamometer. Participants sat on an isokinetic dynamometer (Biodex System 3 Research, Biodex Medical), with their trunk and right leg flexed at 85° and 80°, respectively (0° being full extension of trunk or knee). The axis of the dynamometer was aligned with the approximate axis of rotation of the knee. The torso, the waist, and the left thigh were strapped to the dynamometer chair to minimize changes in body position throughout the experiment. The torque signal from the Biodex ergometer was digitized at a sampling rate of 200 Hz with an analog-to-digital converter (Bagnoli 16, Delsys).

Electromyostimulation. Transcutaneous EMS was applied to VL with the intent of fatiguing this muscle. VL was preferred among the quadriceps muscles because of its volume and location, both of which contribute to its selective activation by EMS. Two rectangular electrodes (5 × 5 cm for the distal electrode and 5 × 10 cm for the proximal electrode; Compex, Annecy-le-vieux, France) were placed 5 cm proximal to the superior aspect of the patella and 10 cm distal to the greater trochanter (Akima et al. 2002). The correct location of the electrodes over VL was verified by ultrasonographic images (B mode). A constant-current stimulator (DS7A, Digitimer, Letchworth Garden City, UK) coupled with a train/delay generator (DG2A, Digitimer) was used to deliver trains of pulses at the frequency of 50 Hz (pulse duration = 500 μs). Each evoked a contraction that lasted 3 s, followed by 2-s rest. The EMS fatigue protocol lasted 5 min (i.e., 60 evoked contractions). Current intensity was set to induce a torque of 20% of MVC. Because fatigue induced a progressive decrease in evoked torque during the 5-min protocol, the current intensity was regularly increased to match 20% of MVC as much as possible, within the limits of the maximal intensity that could be tolerated by the subject. A MVC was performed immediately after the EMS protocol to verify the presence of fatigue.

Shear elastic modulus. An Aixplorer ultrasound scanner (version 4.2, Supersonic Imagine, Aix en Provence, France) coupled with a linear transducer array (4–15 MHz; SuperLinear 15-4, Vermon, Tours, France) was used in the SSI mode (musculo-skeletal preset). The method used to obtain the shear wave speed (V_s) has been described in detail previously (Bercoff et al. 2004; Tanter et al. 2008). Then, assuming a linear elastic behavior (Bercoff et al. 2004; Catheline et al. 2004), the muscle shear elastic modulus (μ) was calculated as follows:

$$\mu = \rho V_s^2 \tag{1}$$

where ρ is the density of muscle (1,000 kg/m^3). Maps of the shear elastic modulus were obtained at 1 Hz with a spatial resolution of 1 × 1 mm.

Three quadriceps muscles were studied: VL, vastus medialis (VM), and rectus femoris (RF). Note that the vastus intermedius muscle (VI) was not recorded. Because VI is located deeper than VM, VL, and RF, shear elastic modulus of this muscle cannot be measured with the same presets of the ultrasound scanner, and consequently it was not possible to record this muscle along with the other three. In addition, the quality of the elasticity maps obtained for VI during pilot studies was not satisfactory. After the participants were positioned on the ergometer, the B-mode ultrasound image was used to determine the optimal transducer location for each muscle: a region with a muscle thickness of at least 1.5 cm, avoiding hypoechoic regions related to dense connective tissues. The probe was aligned to the muscle fiber direction for vastus muscles (VL and VM) or to the shortening direction for RF (Blazevich et al. 2006). These locations were marked on the skin with a waterproof marker. Then shear elasticity maps were chosen to be as large as possible, depending on the muscle depth/thickness (~1.5 × 1.5 cm), to obtain a representative averaged shear elastic modulus value. As contractions were isometric, negligible movements of the muscles relative to the skin were not expected or observed.

Protocol

Participants performed two experimental sessions (control and EMS sessions) in a randomized order ~6 days apart (Fig. 1). After a standardized warm-up, the subjects performed two maximal isometric voluntary knee extensions for 3 s, separated by 2 min to allow recovery. The maximum torque was considered as the best performance (MVC). They then performed six 10-s knee extensions at 20% of MVC determined for the current session (30-s rest between contractions). Torque feedback was provided on a monitor placed in front of the participants. During each contraction, the shear elastic modulus of one of the knee extensors (VL, VM, or RF) was measured in a

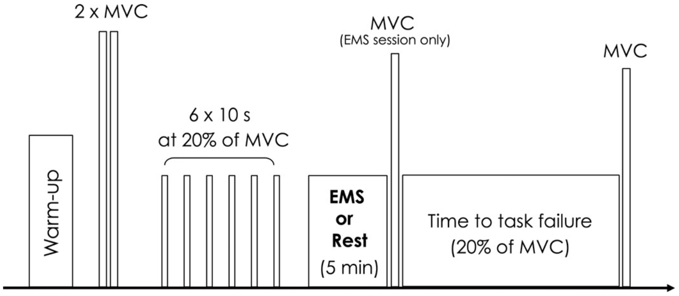


Fig. 1. Experimental design. Participants performed 6 isometric 10-s knee extensions at 20% of maximal voluntary contraction (MVC). They then rested for 5 min (Control session) or underwent an electromyostimulation (EMS) protocol aimed at selectively fatiguing the vastus lateralis (VL) (EMS session). Immediately after, they were asked to produce 20% of MVC until task failure (Tlim).

random order, so that each muscle was studied twice to evaluate repeatability of the modulus measurement. Participants were then required to rest (5 min) for the control session or underwent 5 min of EMS on VL for EMS session. Immediately after this, the participants performed a sustained submaximal isometric knee extension in which 20% of MVC was maintained, until task failure (limit time to task failure, Tlim). Verbal encouragements were given to the participant throughout the Tlim. Task failure (exhaustion) was defined as the instant when the torque produced decreased by >5% from the required target for >5 s, and the investigator stopped the contraction at this time point. During this contraction, the ultrasound transducer was alternatively placed over the three muscles (VL, VM, and RF) for 10-s periods. This fatiguing task was immediately followed by a MVC to verify that a decrease in MVC occurred, confirming the presence of neuromuscular fatigue.

Data Analysis

All data were processed with MATLAB (MathWorks, Natick, MA). For each of the contractions (except MVC), torque was averaged over each second.

Movies of shear elastic modulus maps were exported from the software (version 4.2, Supersonic Imagine) in "mp4" format and sequenced in "jpeg" format. Image processing converted the colored map into shear elastic modulus values. A region of interest (ROI) was defined for each movie as the largest rectangular muscular region available that avoided aponeuroses, tendon, and bone (Fig. 2). In light of previous work (Bouillard et al. 2012a), the saturation level of the device (266 kPa) was not expected to be reached. However, we checked that the saturation level was never reached for any ROI of any participant. This criterion was completed for all the analyzed maps.

Maps of the shear elastic modulus were obtained at 1 Hz. Values were averaged across the ROI and between the consecutive images to provide a representative value per contraction, i.e., one value for each of the 10-s contractions performed before the intervention (5-min EMS or 5-min rest period). During the sustained fatiguing contraction, the probe was alternatively moved from one muscle to another until the end of the contraction. For each measurement (corresponding to one muscle), five consecutive elasticity maps were obtained and averaged to obtain one representative value for each time point. Considering the time to relocate the transducer during the Tlim, one value for each of the three muscles (i.e., 3 successive probe locations) was obtained every 20–25 s. The total number of values obtained for each muscle depended on the duration of the exercise, and thus on the participant (e.g., for a time to task failure of ≈300 s, ≈9 time points were obtained for each muscle). The first value obtained for each muscle during the Tlim was referenced under the "start-Tlim" modulus, and the last value was referenced under the "end-Tlim" modulus. For the Tlim contraction, an average shear elastic modulus value was also calculated for each muscle over four time windows, dividing the Tlim into four equal sections, i.e., 0–25%, 25–50%, 50–75%, and 75–100% of Tlim. For each window, all mean modulus values obtained for a given muscle were averaged. Thus, for each muscle, changes in modulus were summarized by four values over the entire Tlim. Fewer than four measurements per muscle were available for three participants during the Tlim; therefore these subjects were excluded from this latter analysis and only the start-Tlim and end-Tlim values were considered.

Statistical Analysis

Data distributions consistently passed the Kolmogorov-Smirnov normality test (Statistica V10, Statsoft, Maison-Alfort, France), and thus the values are reported as means ± SD. As one participant did not carefully maintain the target torque during Tlim, his data were excluded from the analysis. Thus results refer to 15 participants. The level of significance was set as $P < 0.05$.

The intrasession repeatability of the shear elastic modulus was assessed for each muscle between the two measurements obtained during the 10-s contractions of the control session by calculating intraclass correlation coefficient (ICC) and standard error of measurement (SEM) (Hopkins 2000).

To verify that EMS induced neuromuscular fatigue, MVC values measured before and after EMS were compared with a paired *t*-test. A repeated-measures ANOVA [random factor: 15 subjects; between-

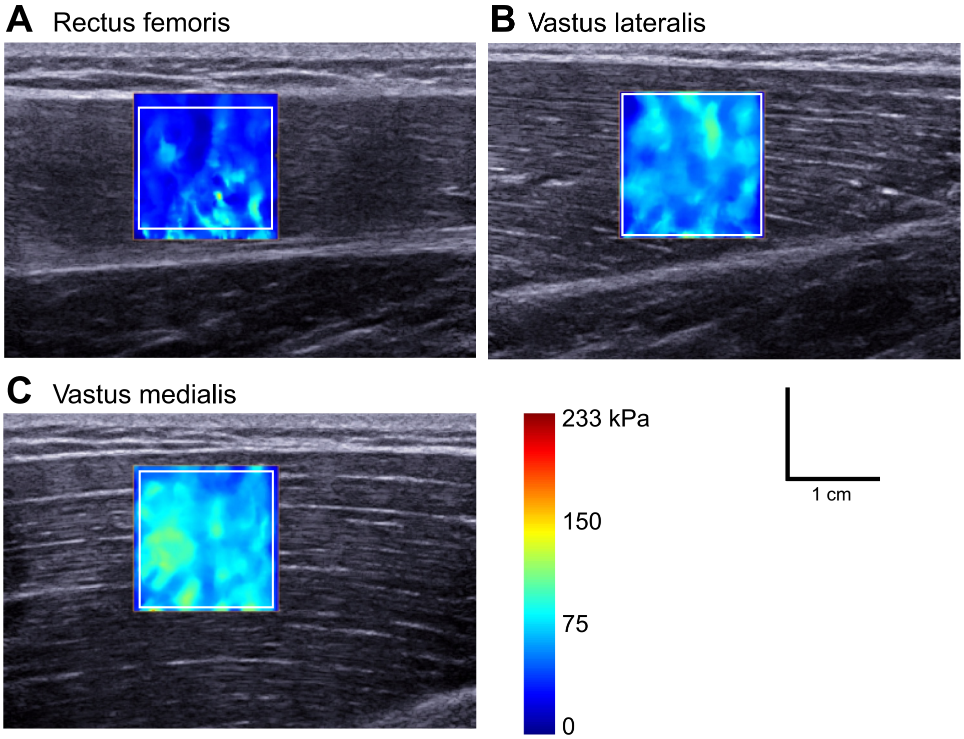


Fig. 2. Typical maps of shear elastic modulus. The colored region represents the shear elasticity map for the 3 muscles (blue being soft and red being stiff). To obtain a representative value, the shear elastic modulus (in kPa) was averaged over the greatest muscular area (white rectangles), avoiding hypoechoic regions and aponeurosis.

subject factors: session (control and EMS) and time (first and last MVC performed after the warm-up and after Tlim, respectively)] was performed to determine whether MVC was altered throughout the protocol and whether it was different between the two sessions. To determine the effect of EMS (VL fatigue) on Tlim duration, a paired *t*-test was used to compare the duration between the two sessions.

To determine whether localized VL fatigue altered the sharing load during nonfatiguing exercise (*hypothesis 1*), we performed a repeated-measures ANOVA [random factor: 15 subjects; between-subject factors: muscle (VM, VL, and RF), session (control and EMS), and time (10-s contractions and start-Tlim)]. The same ANOVA was performed on torque values to ensure that the produced torque did not change between and within the sessions. A repeated-measures ANOVA [random factor: 12 subjects; between-subject factors: muscle (VM, VL, and RF), session (control and EMS session), and time (0–25%, 25–50%, 50–75%, and 75–100% of Tlim)] was performed to determine the effect of localized VL fatigue on torque and shear elastic modulus during the sustained contraction (*hypothesis 2*). To account for the multiple comparisons, post hoc analyses were performed by the Bonferroni method (adjusted *P* values provided by the statistical software are provided in RESULTS).

In addition to these statistical analyses, data were displayed pictorially to evaluate changes in shear modulus for each muscle and each participant, as performed in previous studies when high interindividual variability was observed (Hodges et al. 2013). Changes were analyzed within each session between the 10-s contractions and start-Tlim and between start-Tlim and end-Tlim. For each muscle, the modulus values were defined as increased or decreased if they changed by >SEM value determined from the 10-s contractions of the control session (repeatability data, see above). Data are presented descriptively for this analysis.

RESULTS

Performance

Performance data (MVC and time to task failure) are depicted in Table 1. EMS induced a significant decrease ($-17.6 \pm 14.2\%$; $P < 0.001$) in MVC torque, confirming that the EMS protocol induced fatigue. In addition, Tlim was significantly shorter ($-14.3 \pm 20.9\%$; $P = 0.023$) during the EMS session compared with the control session.

When considering the MVC torque values obtained at the beginning (after warm-up) and at the end (after Tlim) of each session, a significant decrease in MVC torque was found ($-28.8 \pm 14.0\%$; $P < 0.001$). Neither a main effect of "session" ($P = 0.45$) nor a "time × session" interaction ($P = 0.08$) was reported.

Neither a significant main effect of "session" ($P = 0.289$) and "time" ($P = 0.145$) nor a significant "time × session" interaction ($P = 0.817$) was found on target torque values during 10-s contractions and start-Tlim. Similarly, neither a significant effect of "session" ($P = 0.529$) nor a significant "time × session" interaction ($P = 0.116$) was found on target torque values during Tlim. However, we found a main effect of "time" ($P < 0.001$), showing that the target torque was slightly lower at 75–100% of Tlim compared with 0–25% ($-4.1 \pm 4.5\%$ of target torque). Because of the criterion used to stop the Tlim (i.e., decrease in torque by >5% from the required target), this slight but significant effect of time was expected.

Table 1. *Performance data*

	Control Session	EMS Session
MVC-pre, N·m	268.9 ± 68.2	273.9 ± 67.3
MVC-post EMS, N·m		226.2 ± 72.7
MVC-end Tlim, N·m	210.0 ± 67.0	188.0 ± 63.4
Tlim duration, s	328 ± 261	275 ± 212

Values are means ± SD. MVC-pre, maximal torque reached during the maximal voluntary contractions (MVCs) performed at the beginning of the protocol; MVC-post EMS, maximal torque reached during MVC performed immediately after electromyostimulation (EMS) protocol; EMS-end Tlim, maximal torque reached during MVC performed immediately after the limit time to task failure (Tlim).

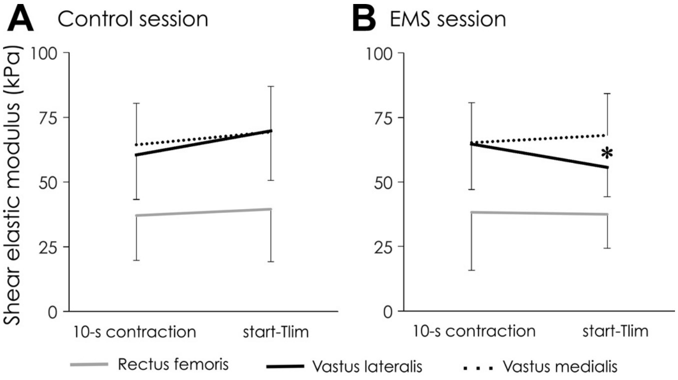


Fig. 3. Shear elastic modulus values obtained during the 10-s contraction and start-Tlim for control (*A*) and EMS (*B*) sessions. Asterisk indicates that the shear elastic modulus of VL was significantly lower during start-Tlim for the EMS session compared with the control session ($P = 0.011$). No significant differences were observed for vastus medialis (VM) or rectus femoris (RF).

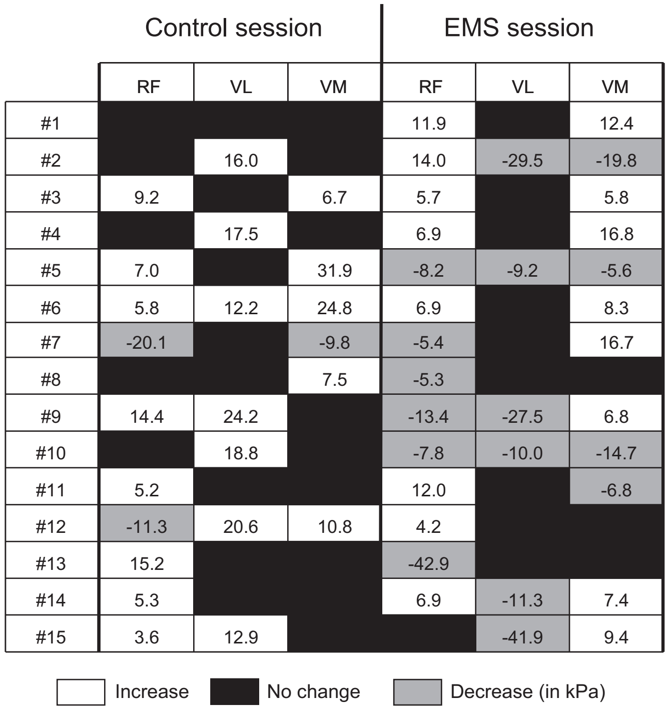
Repeatability of Shear Elastic Modulus

For each muscle, the repeatability of the shear elastic modulus values was assessed between the two 10-s contractions of the control session. ICC values were high (0.962, 0.873, and 0.872 for RF, VL, and VM, respectively), and SEM values were relatively low (3.4, 6.7, and 5.5 kPa for RF, VL, and VM, respectively).

Effect of VL Fatigue on Shear Elastic Modulus During Nonfatiguing Contractions

To test the effect of VL fatigue on load sharing during nonfatiguing contractions, we compared the shear elastic modulus values of the 10-s contractions and start-Tlim (Fig. 3). Note that start-Tlim corresponds to the first value obtained for each muscle at the beginning of the Tlim. Except for VL during the EMS session, negligible fatigue was expected for this start-Tlim value. Neither a main effect of "time" ($P = 0.153$) nor a main effect of "session" ($P = 0.583$) was found on the shear elastic modulus values. However, a significant "time × session × muscle" interaction was found ($P = 0.031$). More precisely, while the VL shear elastic modulus measured during the 10-s contractions was not different between the sessions ($P = 1.00$; 59.5 ± 17.0 and 62.8 ± 18.8 kPa for control and EMS sessions, respectively), the VL elastic modulus measured during start-Tlim was significantly lower ($P = 0.011$) for the EMS session (54.6 ± 11.8 kPa) compared with the control session (68.4 ± 19.2 kPa). No significant differences were observed for VM and RF.

Figure 4 provides a visual summary of the changes in shear elastic modulus for the three muscles of all participants between the 10-s contraction and start-Tlim. During the control session, seven participants exhibited an increase in VL elastic



	Control session			EMS session		
	RF	VL	VM	RF	VL	VM
#1	■	■	■	11.9	■	12.4
#2	■	16.0	■	14.0	-29.5	-19.8
#3	9.2	■	6.7	5.7	■	5.8
#4	■	17.5	■	6.9	■	16.8
#5	7.0	■	31.9	-8.2	-9.2	-5.6
#6	5.8	12.2	24.8	6.9	■	8.3
#7	-20.1	■	-9.8	-5.4	■	16.7
#8	■	■	7.5	-5.3	■	■
#9	14.4	24.2	■	-13.4	-27.5	6.8
#10	■	18.8	■	-7.8	-10.0	-14.7
#11	5.2	■	■	12.0	■	-6.8
#12	-11.3	20.6	10.8	4.2	■	■
#13	15.2	■	■	-42.9	■	■
#14	5.3	■	■	6.9	-11.3	7.4
#15	3.6	12.9	■	■	-41.9	9.4

□ Increase ■ No change ▨ Decrease (in kPa)

Fig. 4. Individual changes in shear elastic modulus (in kPa) between the 10-s contraction and start-Tlim. For each muscle, the modulus values were defined as increased (white) or decreased (gray) if they changed by > standard error of measurement (SEM) determined from the 10-s contractions of the control session (i.e., 3.4, 6.7, and 5.5 kPa for RF, VL, and VM, respectively). Otherwise, the modulus was considered constant (black). While 7 participants exhibited an increase of the VL shear elastic modulus during the control session (the others exhibited no change), 6 participants exhibited a decrease of the VL shear elastic modulus during the EMS session.

modulus by >6.7 kPa (corresponding to the repeatability—SEM—of the shear elastic modulus values calculated between the two 10-s contractions). The opposite was observed during the EMS session, as none of the participants exhibited an increase in VL modulus and 6 of the 15 participants exhibited a decrease. This latter result was associated with *1*) an increase in the VM modulus for two of these six participants (*participants 9* and *15*), *2*) an increase in the RF modulus for one participant (*participant 2*), and *3*) an increase in both VM and RF modulus for one participant (*participant 14*). These results suggest compensation between quadriceps muscles (changes in load sharing) during the EMS session for these participants. Note that *participants 5* and *10* exhibited a decrease for each of the three recorded muscles during the EMS session. As torque was maintained at constant level, this decrease was likely compensated by the nonrecorded synergist muscle (VI).

Effect of VL Fatigue on Shear Elastic Modulus Throughout Fatiguing Contraction (Tlim)

A significant ($P = 0.039$) "session" × "time" interaction was found on the shear elastic modulus values recorded during the Tlim (Fig. 5). Post hoc analysis revealed that shear elastic modulus values were significantly higher at 50–75% ($P = 0.0037$) and 75–100% ($P < 0.0001$) of Tlim compared with 0–25% during the control session. During the EMS session, the increase in shear elastic modulus occurred earlier, as 25–50% ($P = 0.0006$), 50–75% ($P < 0.0001$), and 75–100% ($P < 0.0001$) were all significantly different from 0–25% of Tlim. No significant interaction that included both "time" and "muscle" factors was found, indicating that these changes were similar among the three muscles. However, a significant ($P < 0.01$) "muscle × session" interaction was found, showing that VL shear elastic modulus values (averaged across the Tlim) were significantly lower during Tlim for the EMS session compared with the control session ($P = 0.019$; 74.4 ± 20.3 and 59.4 ± 14.0 kPa for control and EMS sessions, respectively).

Figure 6 provides a visual summary of the changes observed between start-Tlim and end-Tlim. Regarding the changes in load sharing, no systematic strategy was observed, confirming the results of the statistical analysis. This does not mean that no changes in load sharing occurred during the Tlim but that these changes were not systematic between individuals. For example, Fig. 6 shows opposite changes in shear elastic modulus values between muscles in six participants during the control session (*participants 2*, *3*, *5*, *8*, *9*, and *13*) and seven participants during the EMS session (*participants 1*, *2*, *3*, *5*, *7*, *9*, and *14*). Although this suggests that compensations occurred, these compensations did not systematically occur between the same muscles. Second, in contrast to what was observed for the nonfatiguing contractions, no clear differences appeared between the sessions, confirming that selectively fatiguing one muscle did not induce a consistent compensation strategy between individuals.

DISCUSSION

The present study shows that when fatigue was induced in one of the quadriceps muscles (VL) lower shear elastic modulus values (indicative of a lower force production) were measured in this muscle during a subsequent submaximal

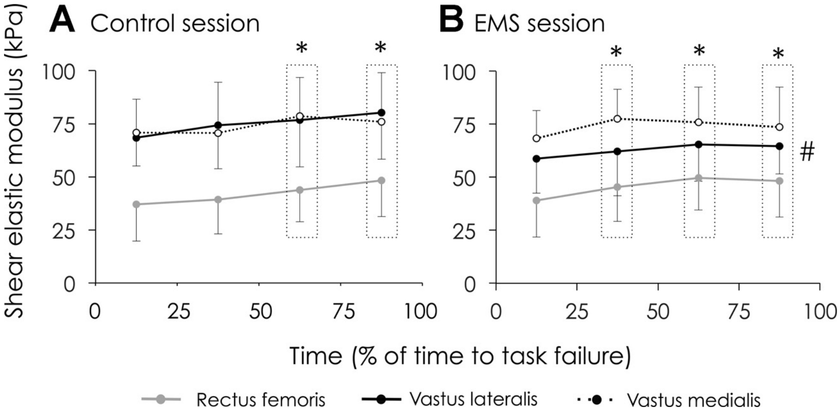


Fig. 5. Shear elastic modulus values during the Tlim for control (*A*) and EMS (*B*) sessions. A significant session × time interaction was found, showing that the shear elastic modulus increased during the Tlim (for all muscles). A significant muscle × session interaction was found, showing that VL shear elastic modulus (throughout the Tlim) values were lower during the EMS compared with the control session. *Difference from 0–25% (without any difference between the muscles); #difference in VL shear elastic modulus between the 2 sessions (considering the whole Tlim).

	Control session			EMS session		
	RF	**VL**	**VM**	**RF**	**VL**	**VM**
#1	■	8.6	28.5	-9.6	12.4	18.3
#2	-10.3	24.1	17.7	22.8	-11.3	■
#3	50.3	-17.9	-13.5	34.5	8.4	-22.4
#4	63.8	18.9	■	27.9	■	■
#5	16.2	■	-9.2	13.0	37.7	-10.4
#6	■	19.8	26.1	16.3	■	26.0
#7	13.9	18.8	32.8	14.1	23.6	-24.1
#8	-3.8	9.1	15.2	4.7	16.4	8.4
#9	-11.8	7.2	-6.8	-7.8	■	50.8
#10	21.1	13.6	■	25.8	6.8	25.9
#11	15.7	23.8	■	24.6	15.8	12.5
#12	-16.6	-15.6	-14.5	-21.3	-8.9	-7.6
#13	-27.6	41.7	■	7.1	11.2	7.4
#14	5.9	9.2	■	-4.1	21.9	■
#15	■	24.4	27.9	■	16.8	35.5

☐ Increase ■ No change ▨ Decrease (in kPa)

Fig. 6. Individual changes in shear elastic modulus (in kPa) between start-Tlim and end-Tlim. For each muscle, the modulus values were defined as increased (white) or decreased (gray) if they changed by >SEM determined from the 10-s contractions of the control session (i.e., 3.4, 6.7, and 5.5 kPa for RF, VL, and VM, respectively). Otherwise, the modulus was considered constant (black). Although these results suggest some compensation strategies, they did not systematically occur between the same muscles.

isometric torque-matched task. However, no systematic compensation was observed, i.e., different patterns of changes were found for the other recorded muscles (VM and RF) between participants. Finally, despite a similar location of fatigue (VL) at the beginning of the sustained fatiguing contractions, participants did not exhibit a similar compensation strategy throughout the sustained fatiguing contraction. Taken together these results suggest that the CNS does not use a common principle among individuals to control load sharing when neuromuscular fatigue occurs.

Methodological Considerations

The present results require consideration of several methodological aspects. First, both the decrease in MVC after EMS and the shorter Tlim during the EMS session confirmed that EMS was effective in inducing neuromuscular fatigue. Zory et al. (2005) demonstrated that a similar EMS protocol performed on knee extensor muscles does not induce central fatigue, allowing us to consider the force-generating capacity of the nonstimulated muscles as being unaffected in our study. This is particularly important, as it is well known that central fatigue can cross over into nonexercised muscles (Kennedy et al. 2013). Nevertheless, as discussed by Akima et al. (2002), even if electrodes were placed to selectively induce fatigue in VL, VI could have also been partially stimulated and thus fatigued. However, even if VI was stimulated along with VL, it should be much less fatigued, and it does not prevent us from testing the hypothesis of consistent change in load sharing through RF and VM shear elastic modulus changes. Unfortunately, as justified in MATERIALS AND METHODS, VI could not be measured.

Second, although we cannot provide evidence that VL did not recover during the Tlim, the significant decrease in MVC torque measured after the EMS protocol (−17.6 ± 14.2%) associated with a shorter Tlim duration during the EMS session (−28.8 ± 14.0%) makes us confident that the EMS-induced fatigue did persist during the whole Tlim. Finally, it is important to note that the shear elastic modulus values cannot be considered as a direct estimation of muscle force (in N) but instead represent an accurate and reliable quantification of changes in muscle force, and thus in load sharing (Bouillard et al. 2011, 2012a). In other words, it was not possible to quantify the contributions of each muscle to the knee extension torque produced, but these measurements did allow us to precisely quantify the changes in these contributions over time.

Changes in Load Sharing

Using magnetic resonance imaging (MRI), Akima et al. (2002) reported an increase in the transverse relaxation time (T2, reflecting metabolic changes) of VM and RF after submaximal dynamic knee extensions when VL was previously fatigued by an EMS protocol. However, direct comparison with our results is not straightforward, as changes in T2 are indirectly related to muscle activation and consequently to muscle force (Adams et al. 1992). In addition, metabolic changes induced long-lasting changes in T2 (Green and Wilson 2000), limiting the use of MRI for the determination of change in load sharing across time. In the present study, VL shear elastic modulus was significantly lower during start-Tlim of the EMS session compared with the control session (i.e., −16.0 ± 21.4%), suggesting that the force produced by VL was lower during this session. As the knee extension torque was not different between the sessions, this decrease in VL force was likely compensated by other synergist muscles (RF, VM, and VI). However, no systematic compensations were observed. In addition, this absence of systematic compensations could explain the fact that no significant changes were observed between the 10-s contraction and the start-Tlim of the EMS session. However, this does not mean that no compensation occurred but rather that these compensations differed between participants. For instance, among the six participants exhibiting a decrease (by more than SEM determined during the control session) in VL modulus between the 10-s contraction and start-Tlim (Fig. 4), four participants showed a concomitant increase in the modulus of VM and/or RF. The two other participants (*5* and *10*) exhibited a decrease in the modulus of the three measured muscles, suggesting compensation with VI. It is important to note that, although care was taken to minimize changes in body position throughout the experiment (see MATERIALS AND METHODS), we cannot exclude the contribution of the hip extensors to the knee extension torque produced, as previously reported by Nozaki et al. (2005). This is particularly important, as the elastographic measurements and the stimulation electrodes did not allow us to strap the right thigh. It is therefore possible that the decrease in VL modulus observed between the sessions was partly compensated by an increase in hip extensor force. However, even if this occurred, it does not prevent us from testing our hypotheses and it raises interesting neurophysiological perspectives as discussed below.

The significant decrease in VL modulus between the sessions but the absence of change within the EMS session may be explained by the increasing trend between the 10-s contractions and start-Tlim observed during the control session (Fig. 3). In this way, seven participants exhibited an increase between the 10-s contraction and start-Tlim during the control session but none of them exhibited any increase during the EMS session (instead, 6 decreased).

With the use of surface EMG (and thus an indirect measure), alternate muscle activity between synergist muscles has been reported during sustained isometric knee extensions (Akima et al. 2002; Kouzaki et al. 2002), suggesting that neuromuscular fatigue can affect load sharing. However, these changes were only observed during low-level contractions (≤5% of MVC) that do not require the activation of all the synergist muscles at the same time, which may facilitate the occurrence of such strategies. In the present study, although VL shear elastic modulus was lower during the Tlim of the EMS session compared with the control session, our hypothesis that prefatigue of VL would lead to systematic compensation with the agonist muscles through the Tlim was not verified. Instead, a significant increase of shear elastic modulus over time was found, without any difference between the three muscles. Again, this does not mean that no change in load sharing occurred but that these changes (when they occurred) differed between the participants. Indeed, for both the control and the EMS session, about half of the participants exhibited opposite changes in elastic modulus for at least two of the three muscles (Fig. 6), suggesting changes in load sharing during Tlim in the same proportion (i.e., ~50% of the participants) as previously reported (Bouillard et al. 2012a). It is also important to note that these observations are based on differences between start-Tlim and end-Tlim (individual data from Fig. 6) that neglect changes that may have occurred over time during the sustained contraction in some participants (e.g., Fig. 7).

Increase in Shear Elastic Modulus During Tlim

Despite the continual maintenance of the joint torque, a significant increase in shear elastic modulus was reported over time during the Tlim. As the shear elastic modulus can be considered an index of individual muscle force (Bouillard et al. 2011), even when muscle fatigue occurs (Bouillard et al. 2012a), this increase is indicative of an increase in force produced by the recorded muscles (VL, VM, and RF). Two distinct mechanisms might explain this result. First, it is possible that this increase was compensated for by a decrease in force produced by the VI, so that the total knee extension torque was maintained. Nevertheless, considering the high interindividual variability observed in the other muscles, it is unlikely that the vastus muscles would exhibit opposing behaviors in a consistent way between subjects. Second, and more likely, the increase in shear elastic modulus over time during the Tlim may be explained by an increase in activity of the antagonist muscles as previously shown during similar tasks (Enoka and Duchateau 2008; Lévénez et al. 2005; Psek and Cafarelli 1993; Rudroff et al. 2010). For instance, Psek and Cafarelli (1993) observed an increase in EMG activity (≈60%) of the biceps femoris (long head) through an intermittent isometric knee extension performed at 30% of MVC until exhaustion. They concluded that an additional recruitment of the agonist muscles was necessary to counteract the increase in antagonist activation and thus to maintain a constant net torque. However, such an increase in agonist torque during a fatiguing task could not be directly inferred from EMG because the signal is also affected by peripheral manifestation of fatigue (decrease in the muscle fiber conduction velocity, additional motor unit recruitment; Farina et al. 2008; Lindström et al. 1995; De Luca 1984). The present study is the first to provide more direct evidence that an increase in EMG activity during sustained contractions is unlikely to only represent the peripheral manifestations of fatigue but also reflects an increase in force produced by the agonistic muscles.

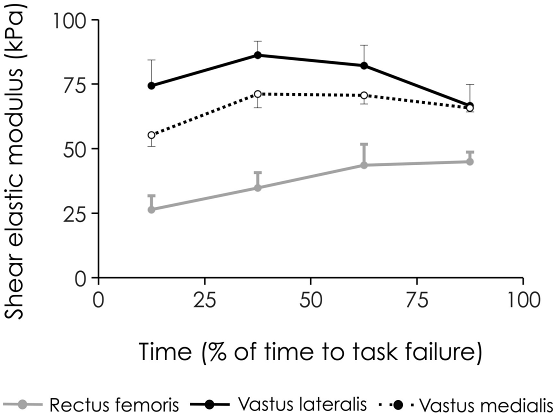


Fig. 7. Example of individual (*participant 2*) changes in shear elastic modulus during Tlim of the EMS session. Analysis of the difference between start-Tlim and end-Tlim modulus values neglects more subtle changes over time as observed in this participant.

Neurophysiological Interpretations

It has been proposed that the CNS uses specific principles to control load sharing (for a review, see Prilutsky and Zatsiorsky 2002). More precisely, the distribution of individual muscle forces should be optimal in the sense that they should minimize costs such as energy expenditure and variability of force. The observed decrease in VL shear elastic modulus (i.e., force) during Tlim of the EMS session compared with the control session appears to be consistent with such an optimal control strategy. When an optimal controller that minimizes energy cost is considered, it seems logical that VL fatigue was associated with a decrease in force produced by this muscle, i.e., a decrease of its contribution to knee extension torque. However, it is not possible to determine whether this decrease was related to decreased activation (and thus to a change in the neural command) or whether the activation level remained the same but force decreased as a result of peripheral fatigue. Recording EMG activity would not have allowed us to answer this question because of the alteration of EMG signals caused by peripheral fatigue.

Other observations made in the present study seem to challenge this optimal control theory. For instance, as VL was prefatigued, an increase of the force produced by VL during Tlim appears to contradict an optimal control based on minimizing energy cost (Tsianos et al. 2012). Interestingly, a similar observation has been reported by De Rugy et al. (2012). They showed that, when the force production capacity of one of the agonist muscles was altered, participants simply increased the recruitment of all agonists, instead of recruiting only the effective muscles, leading to the conclusion that coordination would be more "habitual" than "optimal." In this way, Loeb (2012) proposed an alternative strategy called "good-enough" control in which individuals use trial-and-error learning to acquire a repertoire of sensorimotor behaviors that are not necessarily optimal.

When considering optimal theories, the high variability of individual behaviors reported in the present study could lead one to think that all participants would not optimize the same cost function (e.g., metabolic function as energy consumption, mechanical function as muscle stresses). In contrast, when considering Loeb's theory (2012), it is possible that individuals optimize the same cost function but that the diversity of experiences (history) would have led to different expressions of this optimization.

Finally, as mentioned above, we cannot exclude a contribution of the hip extensors to compensate for the decrease in VL force after EMS (especially because the right thigh could not be strapped). If this occurred, it would mean that the CNS preferentially chooses (when the solution is available) a between-joints compensation strategy rather than compensation between muscles from the same muscle group. Further investigations are needed to address this issue.

Conclusions

This study has demonstrated that prefatiguing a single agonist muscle does not lead to a consistent redistribution of load sharing among the quadriceps muscles between individuals. To better understand the origin of this variability, the reproducibility of such individual strategies over time needs to be considered. A better understanding of how the CNS adapts load sharing during a fatiguing task may provide further insights into musculoskeletal conditions. For example, unbalanced load sharing among synergists has been suggested to represent one of the key causes of some pathologies of the patellofemoral joint (Cerny 1995; Coqueiro et al. 2005). It is thus possible that some strategies are more likely to induce injury than others.

GRANTS

This study was supported by grants from the European Regional Development Fund (ERDF, no. 37400), the French Muscular Dystrophy Association (AFM), and the Region des Pays de la Loire. K. Bouillard received a scholarship from ERDF.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: K.B., M.J., A.N., and F.H. conception and design of research; K.B. performed experiments; K.B. analyzed data; K.B., M.J., A.N., and F.H. interpreted results of experiments; K.B. and F.H. prepared figures; K.B. and F.H. drafted manuscript; K.B., M.J., A.N., and F.H. edited and revised manuscript; K.B., M.J., A.N., and F.H. approved final version of manuscript.

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