

Activation of quadriceps femoris including vastus intermedius during fatiguing dynamic knee extensions

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Abstract

Purpose Fatigue-related muscle activity in the superficial quadriceps femoris (QF) muscles has been widely examined; however, there is no information on the activity of the deep vastus intermedius (VI) muscle during fatiguing dynamic knee extensions. The purpose of this study was to investigate neuromuscular activation patterns of the QF synergists, including the VI, during fatiguing dynamic knee extensions at two submaximal loads.

Methods Nine healthy men performed dynamic knee extensions with loads of 50 and 70 % of one-repetition maximum (1RM) until failure. Muscle activation of the VI, vastus lateralis, vastus medialis (VM) and rectus femoris was recorded using surface electrodes. Root mean square (RMS) amplitude was calculated during the concentric (CON) and eccentric (ECC) phases of each repetition, and normalized to the RMS amplitude during the CON and ECC phases of the 1RM. Each CON and ECC phase was further divided into three subphases according to knee joint angle.

Results The normalized RMS amplitude of the four individual QF muscles during the CON phase linearly increased with fatigue with contractions at both 50 and 70 % 1RM. The highest RMS amplitude was found in VI at

flexed knee joint angles until fatigue. This activation pattern was more prominent at 70 % 1RM than 50 % 1RM. The RMS amplitude of VM at extended knee joint angles was selectively higher at 70 % 1RM than 50 % 1RM.

Conclusions These results suggest that the contribution of the four individual QF muscles to fatiguing dynamic knee extensions differs according to knee joint angle and intensity of load.

Keywords Vastus lateralis · Vastus medialis · Rectus femoris · Surface electromyography · Concentric contraction

Introduction

Muscle fatigue has been a common topic of discussion in the physiology literature for several decades. Muscle fatigue is defined as any exercise-induced reduction in the ability of a muscle to generate force or power (Gandevia 2001). The quadriceps femoris (QF) muscles play a key role in almost all human movements, because they are anti-gravity muscles that support body weight. Thus, they function as the primary activating muscles in human movements such as walking, running, and jumping. From an anatomical point of view, the QF muscles consist of three superficial synergistic muscles [vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF)] and one deep synergistic muscle [vastus intermedius (VI)]. Surface electromyography (EMG) has been used to show the patterns of neuromuscular activation of the three superficial QF muscles during fatiguing tasks (Ebenbichler et al. 1998, 1998; Kouzaki et al. 1999, 2002; Pincivero et al. 2006; Tesch et al. 1990), but there is only limited information on the fatigability of VI. This is primarily due to technical

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difficulties in recording the activation of VI using surface EMG, as the muscle is located deep in the thigh.

We have succeeded in recording the neuromuscular activation of VI using surface electrodes during isometric knee extension tasks (Akima et al. 2012; Watanabe and Akima 2009, 2010, 2011) and dynamic knee extension tasks (Akima and Saito 2013). The main feature of our recording technique is the accurate detection of anatomical characteristics of the superficial region of VI by combining magnetic resonance imaging and/or ultrasonography during rest and muscle contraction (Akima and Saito 2013; Watanabe and Akima 2009, 2010, 2011). Using this innovative technique, we showed that the median frequency of VI activity was significantly higher than that of VL during the final phase of a fatiguing isometric contraction at 50 % of maximum voluntary contraction (MVC) (Watanabe and Akima 2010). This suggests that the fatigue response was different among the synergistic QF muscles. However, as far as we know, there are no studies that report the neuromuscular activation pattern in individual QF muscles during a dynamic fatiguing task. Furthermore, muscle fatigue is heavily dependent on the intensity of muscle contraction (Ebenbichler et al. 1998), which is closely related to the firing pattern of recruited motor units (MUs) within each muscle (Moritani et al. 1986) and the activation strategy among synergistic muscles within a given muscle group (Akima et al. 2012; Kouzaki et al. 1999, 2002; Tamaki et al. 1998). For example, we have shown that the synergistic QF muscles are recruited alternately during low-level sustained static contractions (Akima et al. 2012). This unique neuromuscular adaptation could be associated with modulation by the nervous system to avoid fatigue (Akima et al. 2012).

We recently reported that the pattern of activity in the VI muscle during concentric (CON) and eccentric (ECC) phases of a dynamic contraction was opposite to that of the three superficial QF muscles at knee joint angles of 90°–165° (where 180° represents full extension). In particular, the activation of VI was higher at flexed knee joint angles of 90°–115° (i.e., the initial portion of the CON phase and the final portion of the ECC phase of the dynamic contraction) with loads heavier than 60 % of one-repetition maximum (1RM). If this activation pattern is an intrinsic property of the QF muscle group, it may also be evident with advancing fatigue. However, it is not well understood whether this activation pattern changes with fatigue during contractions of different intensities. Furthermore, the knee joint angle-specific activation pattern of the four individual QF muscles is not well known.

Therefore, the aim of the present study was to investigate the neuromuscular activation patterns of the four individual QF muscles, including VI, during fatiguing dynamic knee extensions performed with loads of 50 and

70 % 1RM. We hypothesized that the neuromuscular activation patterns would differ between loads of 50 and 70 % 1RM, but that angle-specific activation in the four individual QF muscles would be constant throughout the fatiguing tasks.

Materials and methods

Subjects

Nine healthy men participated in this experiment. Before the experiment, the procedure, purposes, risks and benefits associated with the study were explained and written consent was obtained. The mean (\pm standard error of the mean) physical characteristics were as follows: age 24.7 ± 7.7 years; height 174.1 ± 6.1 cm; weight 66.3 ± 10.7 kg. All experimental protocols were approved by the Ethics Committee of the Research Center of Health, Physical Fitness and Sports at Nagoya University, and were in accordance with the Declaration of Helsinki.

Experimental protocol

One week prior to the experiment, all subjects practiced the 1RM test and the fatiguing dynamic knee extensions. For the experiment, the subjects returned to the laboratory and performed fatiguing dynamic knee extensions with a load equal to 50 or 70 % 1RM, while surface EMG was recorded from the four individual QF muscles and one hamstring muscle. On a different day, separated by at least 7 days, the subjects performed the same task with the other load. The order of two loads was random.

Dynamic knee extension task

Dynamic knee extension exercises, consisting of CON and ECC actions, were performed on a weight-loaded leg extension device (Nitro Leg Extension, Nautilus Group Japan, Tokyo, Japan) under isotonic contraction. In the resting position, subjects sat on the device with their hip joint angle at approximately 100°. Knee joint angle at the initial position was $75.5^\circ \pm 1.9^\circ$ for 50 % 1RM and $75.6^\circ \pm 1.3^\circ$ for 70 % 1RM. The ankle padding length was adjusted to the length of the lower limb, and kept constant during the task. After stretching the QF, the subjects performed several repetitions of the dynamic knee extension exercise with submaximal loads to warm up. The 1RM was determined by trial and error, and defined as the maximum amount of weight a subject could lift once with a 3-s CON phase and a 3-s ECC phase, but failed to achieve full knee extension on the second repetition after a 1-s rest period between repetitions. Full knee extension during a 1RM trial

was defined as the completion of $\geq 85\%$ of the range of motion (ROM) achieved during knee extension without any load, as in our previous study (Akima and Saito 2013).

After adequate rest of at least 5 min, the subjects performed dynamic knee extension repetitions with a load of either 50 or 70 % 1RM until fatigue. The number of repetitions for 50 and 70 % 1RM was 15.3 ± 1.2 and 9.1 ± 0.3 , respectively. The number of repetitions performed differed across subjects; therefore, the repetitions corresponding to the 1st, 25th, 50th, 75th and 100th percentiles (initial, 25, 50, 75 % and final, respectively) were analyzed. For example, if a subject completed 15 repetitions, the normalized EMG amplitude was quantified for repetition 1 (initial), 8 (50 %) and 15 (final), and the normalized EMG amplitude was averaged for repetitions 4 and 5 (25 %) and 11 and 12 (75 %). All repetitions were performed a 3-s CON phase and a 3-s ECC phase, with a 1-s rest at the initial position between repetitions. Fatigue was defined as failure to lift the load to the timing of a metronome for two consecutive repetitions, or failure to achieve 85 % of the full ROM of the knee joint as described above. The trajectory of the knee joint angle was assessed using an electrogoniometer (SG150, Biometrics, Ltd., Gwent, UK), and subjects were instructed to perform the movements as smoothly as possible. The knee joint angle was sampled at 2 kHz using an analog-to-digital converter (ADC) (PowerLab 16SP; ADInstruments, Melbourne, Australia), stored on a personal computer (s3740jp/CT; Hewlett-Packard Japan, Tokyo, Japan) using LabChart software (version 7.2.5), and displayed in real time on a computer monitor in front of the subject to provide visual feedback of knee joint angle. The peak knee joint angle of the first and final repetition for 50 % 1RM was $164.8^\circ \pm 3.2^\circ$ and $153.3^\circ \pm 3.5^\circ$, respectively, and for 70 % 1RM was $161.0^\circ \pm 2.3^\circ$ and $147.1^\circ \pm 2.9^\circ$, respectively.

EMG recording

Surface EMG signals from VI, VL, VM, RF and the long head of the biceps femoris (BF) muscles were recorded during the dynamic knee extension exercises using active electrodes, as previously described (Akima and Saito 2013; Akima et al. 2012; Watanabe and Akima 2009, 2010). A single differential electrode (4.1 cm long, 2.0 cm wide, 0.5 cm high) with a 1-cm inter-electrode distance, an input impedance of $>10^{15} \Omega/0.2 \text{ pF}$, and a 90-dB common rejection ratio was used. The sensor pre-amplifier and main amplifier units were set at a gain of 10-fold and 100-fold, respectively. This resulted in a 1000-fold amplification of the original EMG signal and a frequency response of 20 ± 5 to $450 \pm 50 \text{ Hz}$ (sensor DE-2.1; Main Amplifier Unit: Bagnoli-8, Delsys, Boston, MA, USA). Signals from the EMG system were sampled at 2 kHz using the same

ADC and personal computer as for the electrogoniometer, meaning the EMG signal was synchronized with the knee joint angle.

Prior to attaching the electrodes, the skin was shaved, abraded and cleaned with alcohol. The electrodes for VL and BF were placed at the mid-point between the head of the greater trochanter and the inferior edge of the patella. The electrodes for RF and VM were placed at the mid-point of the line joining the anterior superior iliac spine and the superior patellar pole, slightly proximal and medial to the patella, respectively. The VM electrodes, therefore, measured the activity of the VM oblique. All electrodes were placed parallel to the estimated fiber direction.

To measure surface EMG from VI, we used a similar procedure to that of our previous studies (Akima and Saito 2013; Akima et al. 2012; Watanabe and Akima 2009, 2010, 2011). We have previously confirmed the location of the superficial region of the VI muscle at the lateral–distal portion of the thigh in 45 healthy men using magnetic resonance imaging and ultrasonography (Watanabe and Akima 2009). We have also used a combination of surface and intramuscular EMG recordings to confirm that EMG signals recorded from this portion of the muscle are representative of the whole muscle (Watanabe and Akima 2011). Using ultrasonography (Logiq e; GE Healthcare, Wauwatosa, WI, USA), we circled the edge of the superficial region of the VI at knee joint angles of 90° and 165° with different color marker pens. Next, we identified the common region of the VI on the skin surface between the two knee joint angles (Fig. 1). Ultrasonography was used to determine electrode placement within the common region, while noting volume conductance. We have previously demonstrated that the surface EMG signal recorded using this procedure has a negligible amount of cross-talk from the adjacent VL muscle (Watanabe and Akima 2009), and is closely associated with the intramuscular EMG signal from the VI ($r = 0.926\text{--}0.991$) (Watanabe and Akima 2011). In addition, we have confirmed that the superficial region of the VI muscle with a knee joint angle between 90° and 165° is large enough to determine electrode placement (Akima and Saito 2013; Watanabe and Akima 2011), and that deformation by muscle contraction has a minimal effect on the positional relation between the electrode and the common region of the VI during dynamic knee extensions (Akima and Saito 2013). The electrodes for VI were placed parallel to the estimated longitudinal axis of the muscle. The reference electrode was attached to the iliac crest.

Data analysis

The root mean square (RMS) of the EMG signal was calculated during the CON and ECC phases of each repetition when the knee joint angle was between 90° and 165° . A



Fig. 1 Representative image of the superficial region of the vastus intermedius muscle identified with ultrasonography. *Solid* and *dotted* lines represent the region at a knee joint angle of 90° and 165°, respectively. The area denoted by the *solid* and *dotted* lines is 23.0 and 29.9 cm², respectively. The common area denoted by the *solid* and *dotted* lines is 15.5 cm², and the maximal length of the *short* and *long* axes of the region is 2.4 and 9.7 cm, respectively. The *square with the black outline* represents the size and location of the electrode

previously described equation was used to calculate RMS (Basmajian and DeLuca 1985). For the 100 % 1RM load, the EMG signals in two repetitions were used to calculate average RMS value. The RMS during repetitive fatiguing contractions was normalized to this value and expressed as the relative value (%1RM) for each CON and ECC phase and for each muscle (Pincivero et al. 2006). This normalization was performed to minimize the effect of knee joint angle-induced EMG change on normalized EMG amplitude (see Fig. 2) (Watanabe and Akima 2011). The difference in the normalized EMG amplitude between the initial repetition and final repetition was expressed as Δ normalized EMG amplitude. A positive Δ normalized EMG amplitude indicates that the normalized EMG amplitude at the final repetition was larger than that at the initial repetition.

To determine the effect of knee joint angle on EMG amplitude, each CON and ECC phase was further divided into three subphases according to the knee joint angle, as done in our previous study (Akima and Saito 2013): 90°–115°, 115°–140°, and 140°–165° in the CON phase (CON90-115, CON115-140, and CON140-165, respectively), and 165°–140°, 140°–115°, and 115°–90° in the ECC phase (ECC165-140, ECC140-115, and ECC115-90, respectively). If the peak extended knee joint angle did not reach 165°, the ROM was equally divided into three subphases.

Statistical analysis

All data are presented as mean and standard error of the mean. A two-way (repetition \times muscle) analysis of

variance (ANOVA) with repeated measures was used to compare normalized EMG amplitude across repetitions and muscles during CON and ECC phases and each subphase. In the case of a two-factor interaction or a main effect, a Tukey's post hoc test was used to identify significant differences. A one-way ANOVA was used to compare the Δ normalized EMG amplitude across the two loads (50 and 70 % 1RM). A Mauchly's sphericity test was applied and if violated, the Greenhouse–Geisser correction factor was used to control for Type I errors. If a significant difference in one-way ANOVA was found, Tukey's post hoc test was used to identify load difference on Δ normalized EMG amplitude. The level of significance was set at $P < 0.05$. Statistical analysis was performed using IBM SPSS statistics software (version 20.0, IBM, Tokyo, Japan).

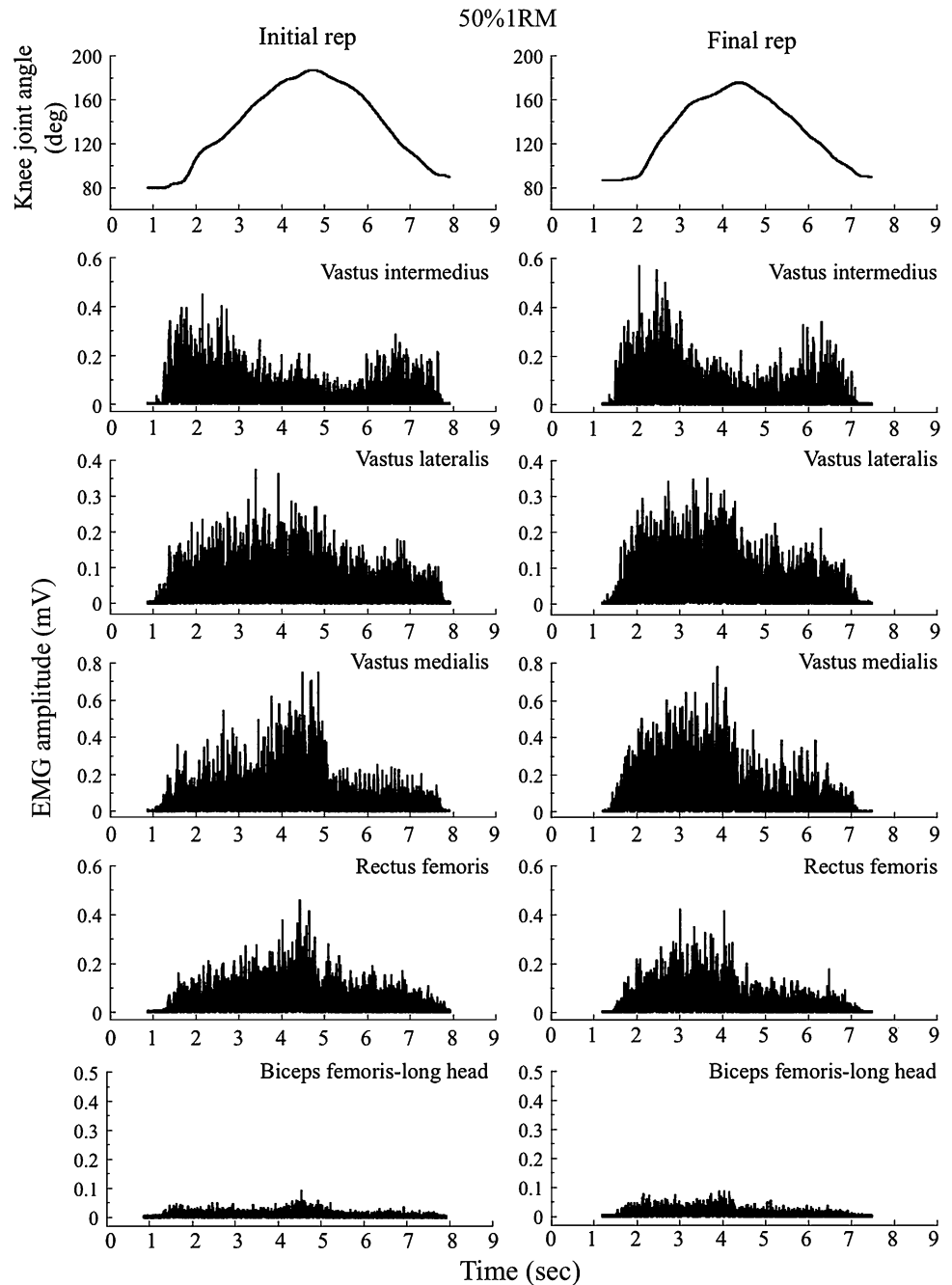
Results

Fatiguing contractions at 50 % 1RM

Rectified EMG signals from each of the four synergistic QF muscles and the BF muscle, and knee joint angle in the initial and final repetitions of the fatiguing knee extension task from one representative subject are shown in Fig. 2. It seems that knee joint angle trajectory was smooth in both the initial and final repetitions, suggesting that the manner of knee extension action had minimal, if any, effect on EMG amplitude. There was larger EMG amplitude in the final repetition than in the initial repetition for each of the four individual QF muscles. The EMG pattern was different between the CON and ECC phases of the task, even during the initial repetition. There was a clear change in EMG amplitude when switching from the CON phase to the ECC phase, especially for VM and RF. BF EMG amplitude was small, but it synchronized with QF EMG. However, it is likely that this had a negligible effect on fatiguing knee extensions; thus, we did not consider BF muscle further in this study.

Figure 3 shows the normalized EMG amplitude of the four individual QF muscles during the CON phase and each CON subphase (CON90-115, CON115-140 and CON140-165) of fatiguing dynamic knee extensions at 50 % 1RM. There was a significant effect of repetition ($P < 0.001$) and a significant repetition-by-muscle interaction ($P < 0.05$) on normalized EMG amplitude in the CON phase and all three CON subphases. Furthermore, there was a significant effect of muscle ($P < 0.01$) in the CON90-115 and CON140-165 subphases. In all CON subphases, the normalized EMG amplitude of VI, VL, VM, and RF significantly increased with the number of repetitions. In pairwise comparisons between muscles, the

Fig. 2 Representative rectified electromyographic (EMG) signals from each of the four individual quadriceps muscles, and the biceps femoris-long head muscle, and knee joint angle during dynamic knee extensions with 50 % of one-repetition maximum (1RM) load



normalized EMG amplitude of VI was significantly higher than RF at all repetitions during the CON90-115 subphase, and was significantly lower than VL and RF from the initial repetition to the 75 % repetition during the CON140-165 subphase. The normalized EMG amplitude of VL was significantly higher than VM at the initial repetition during the CON115-140 subphase and at the initial repetition and the 25 % repetition during the CON140-165 subphase.

Figure 4 shows the normalized EMG amplitude of the four individual QF muscles during the ECC phase and each ECC subphase (ECC165-140, ECC140-115 and ECC115-

90) of fatiguing dynamic knee extensions at 50 % 1RM. There was a significant effect of repetition ($P < 0.001$) on the normalized EMG amplitude in the ECC phase, and the ECC165-140 and ECC140-115 subphases, but not in the ECC115-90 subphase. In addition, there was a significant main effect of muscle ($P < 0.01$) in the ECC phase, and the ECC165-140 and ECC115-90 subphases, and a repetition-by-muscle interaction ($P < 0.01$) in the ECC140-115 subphase. Pairwise comparisons between muscles showed that the normalized EMG amplitude of VL was significantly higher than VI, VM, and RF at all repetitions during the

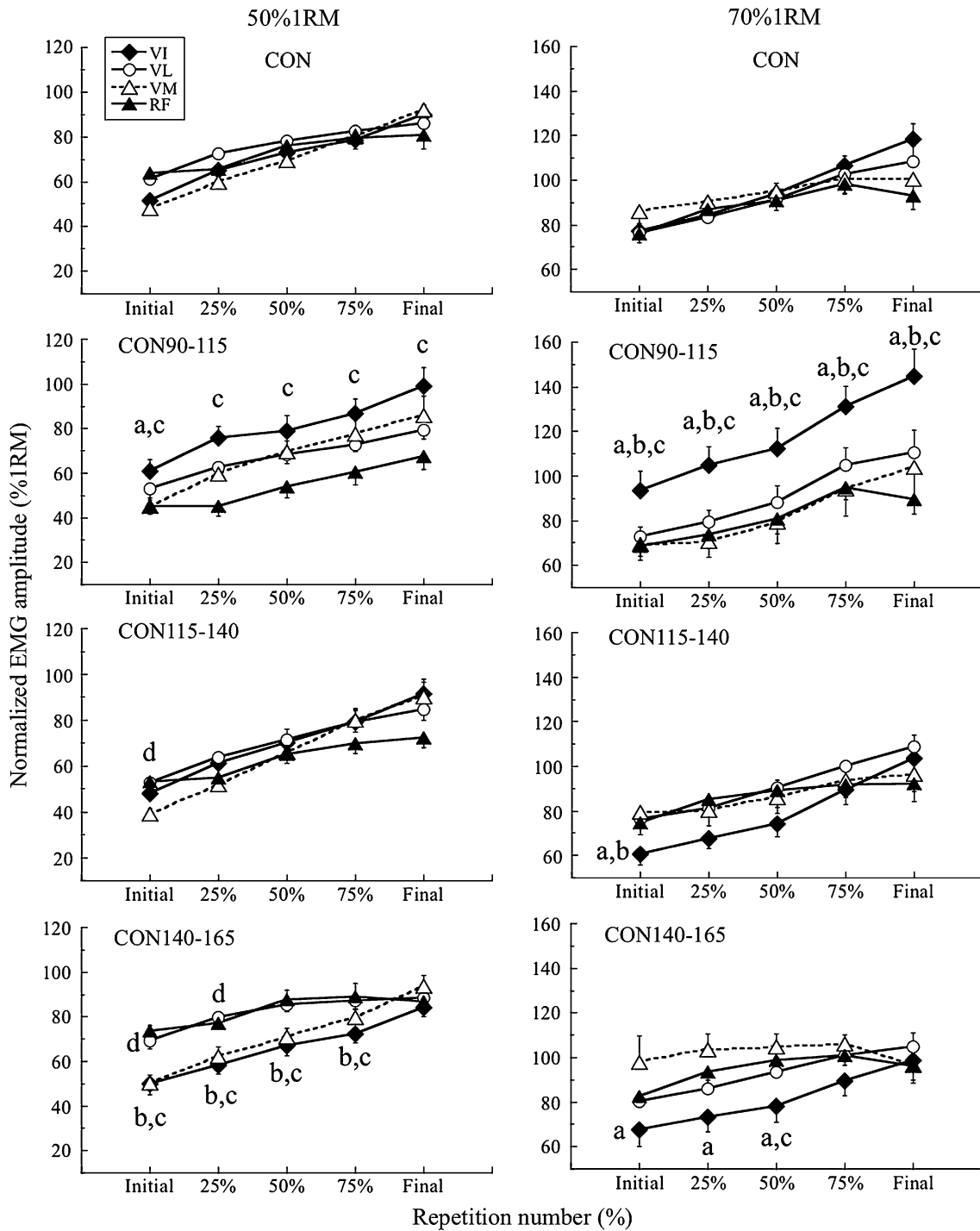


Fig. 3 Normalized electromyographic (EMG) amplitude of vastus intermedius (VI), vastus lateralis (VL), vastus medialis (VM), and rectus femoris (RF) muscles during the concentric phase of dynamic knee extensions with 50 and 70 % of one-repetition maximum (1RM) load. *a* $P < 0.05$ VI vs. VM; *b* $P < 0.05$ VI vs. VL; *c* $P < 0.05$ VI vs.

RF; *d* $P < 0.05$ VL vs. VM. CON90-115, knee joint angle of 90°–115° during a concentric contraction; CON115-140, knee joint angle of 115°–140° during a concentric contraction; CON140-165, knee joint angle of 140°–165° during a concentric contraction

ECC phase, and the ECC165-140 and ECC140-115 sub-phases. During the ECC115-90 subphase, the normalized EMG amplitude of VL and VI was significantly higher than RF at almost all repetitions.

Fatiguing contractions at 70 % 1RM

The activation patterns of the four synergistic QF muscles and the BF muscle, and the knee joint angle trajectory were

essentially similar to those in fatiguing contractions at 50 % 1RM that are shown in Fig. 2. As in fatiguing contractions at 50 % 1RM, the EMG signal of the BF was small, with negligible effect on fatiguing knee extensions, and was not considered further.

Figure 3 shows the normalized EMG amplitude of the four individual QF muscles during the CON phase and each CON subphase (CON90-115, CON115-140 and CON140-165) of fatiguing dynamic knee extensions at 70 % 1RM. There was a significant effect of repetition ($P < 0.001$) in

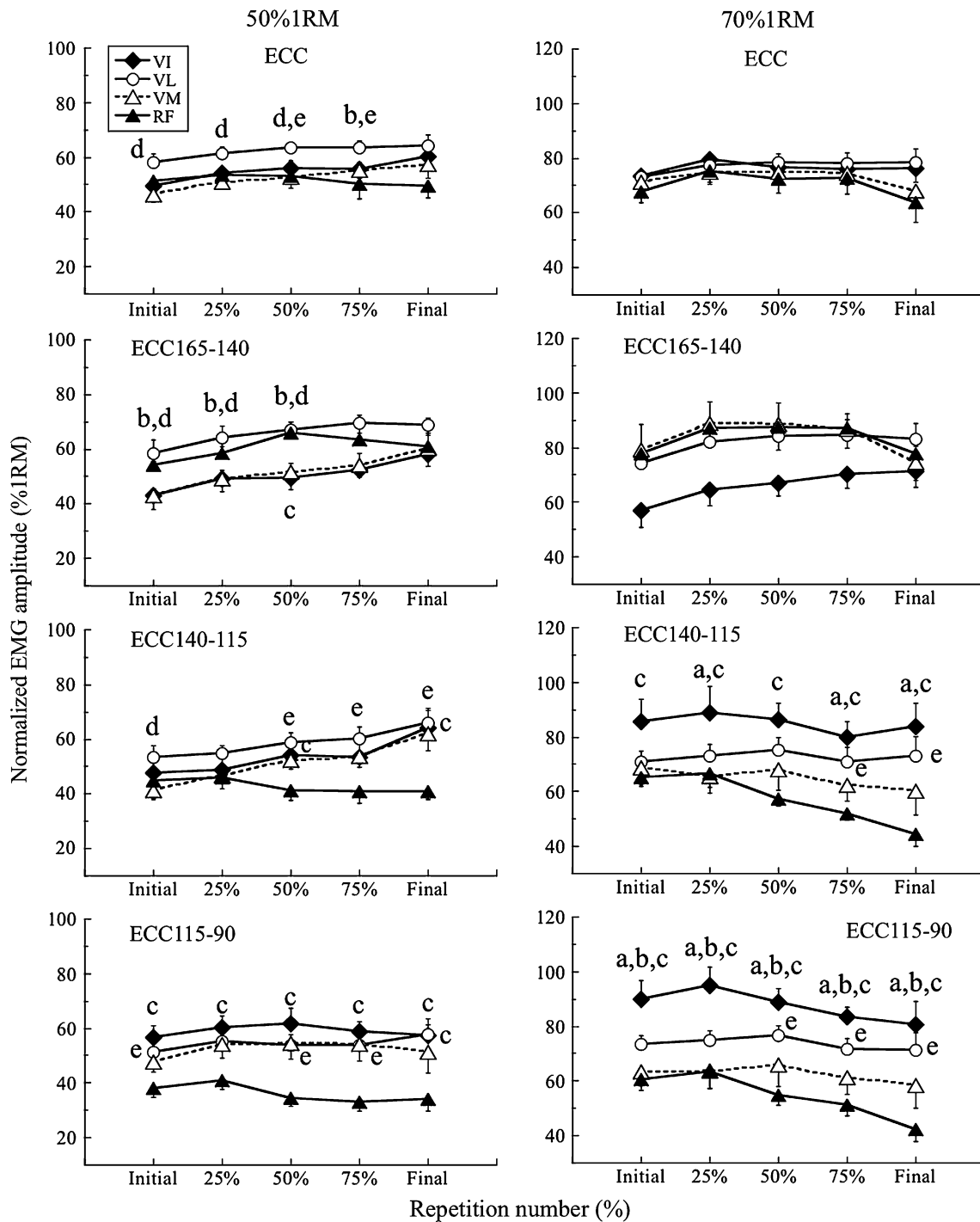


Fig. 4 Normalized electromyographic (EMG) amplitude of vastus intermedius (VI), vastus lateralis (VL), vastus medialis (VM), and rectus femoris (RF) muscles during the eccentric phase of dynamic knee extensions with 50 and 70 % of one-repetition maximum (1RM) load. *a* $P < 0.05$ VI vs. VM; *b* $P < 0.05$ VI vs. VL; *c* $P < 0.05$ VI vs.

RF; *d* $P < 0.05$ VL vs. VM; *e* $P < 0.05$ VL vs. RF. ECC165-140, knee joint angle of 165°–140° during an eccentric contraction; ECC140-115, knee joint angle of 140°–115° during an eccentric contraction; ECC115-90, knee joint angle of 115°–90° during an eccentric contraction

the CON phase and all three CON subphases, a significant effect of muscle ($P < 0.05$) in the CON90-115 subphase, and a repetition-by-muscle interaction ($P < 0.05$) in the CON115-140 subphase. Pairwise muscle comparisons demonstrated that the normalized EMG amplitude of VI was significantly higher than VL, VM, and RF at all repetitions during the CON90-115 subphase. The normalized EMG amplitude of VI was significantly lower than VL and VM at the initial repetition during the CON115-140 subphase, and significantly lower than VM from the initial repetition to the 50 % repetition during the CON140-165 subphase.

Figure 4 shows the normalized EMG amplitude of the four individual QF muscles during the ECC phase and each ECC subphase (ECC165-140, ECC140-115 and ECC115-90) of fatiguing dynamic knee extensions at 70 % 1RM. There was a significant effect of repetition ($P < 0.05$) in the ECC phase and all three ECC subphases, and a significant effect of muscle in the ECC140-115 and ECC115-90 subphases ($P < 0.01$ and 0.001 , respectively). There was no repetition-by-muscle interaction in any phase. Pairwise comparisons between muscles demonstrated that the normalized EMG amplitude of VI was significantly higher than VL, VM, and RF at all repetitions during the ECC140-115 and ECC115-90 subphases. The normalized EMG amplitude of VL was also significantly higher than RF at the 50 % repetition, 75 % repetition and the final repetition during the ECC140-115 and ECC115-90 subphases.

Δ Normalized EMG amplitude

Figures 5 and 6 show Δ normalized EMG amplitude during the CON and ECC phases of fatiguing dynamic knee

extensions at 50 and 70 % 1RM. There was a significant difference in the Δ normalized EMG amplitude of VM between 50 and 70 % 1RM in the CON115-140, CON140-165, and ECC140-115 subphases ($P < 0.05$).

Discussion

We investigated the activation patterns of the four individual QF muscles, including the deeper VI, during dynamic fatiguing knee extensions at 50 and 70 % 1RM. The normalized EMG amplitude of the four muscles linearly increased with fatigue during the CON phase of the movement with both loads. However, the neuromuscular activation patterns that developed with fatigue were specific to the knee joint angle, and these angle-specific neuromuscular activation patterns continued until task failure. In addition, Δ normalized EMG amplitude of VM during both the CON and ECC phases (CON115-140, CON140-165, and ECC140-115) was significantly different between the two loads. This was the only muscle that showed a significant difference in Δ normalized EMG amplitude between the two loads.

Fatiguing contractions at 50 % 1RM

We clearly showed that the level of activation in the four individual QF muscles depended on the knee joint angle during fatiguing contractions at 50 % 1RM. In particular, the level of activation of VI gradually decreased, while that of RF gradually increased as the knee joint extended, i.e., from the CON90-115 subphase to the CON140-165

Fig. 5 The difference in normalized electromyographic (EMG) amplitude in the concentric phase from initial to final repetition of fatiguing dynamic knee extensions performed at 50 and 70 % of one-repetition maximum (1RM). VI vastus intermedius, VL vastus lateralis, VM vastus medialis, RF rectus femoris. * $P < 0.05$, ** $P < 0.01$. CON90-115, knee joint angle of 90°–115° during a concentric contraction; CON115-140, knee joint angle of 115°–140° during a concentric contraction; CON140-165, knee joint angle of 140°–165° during a concentric contraction

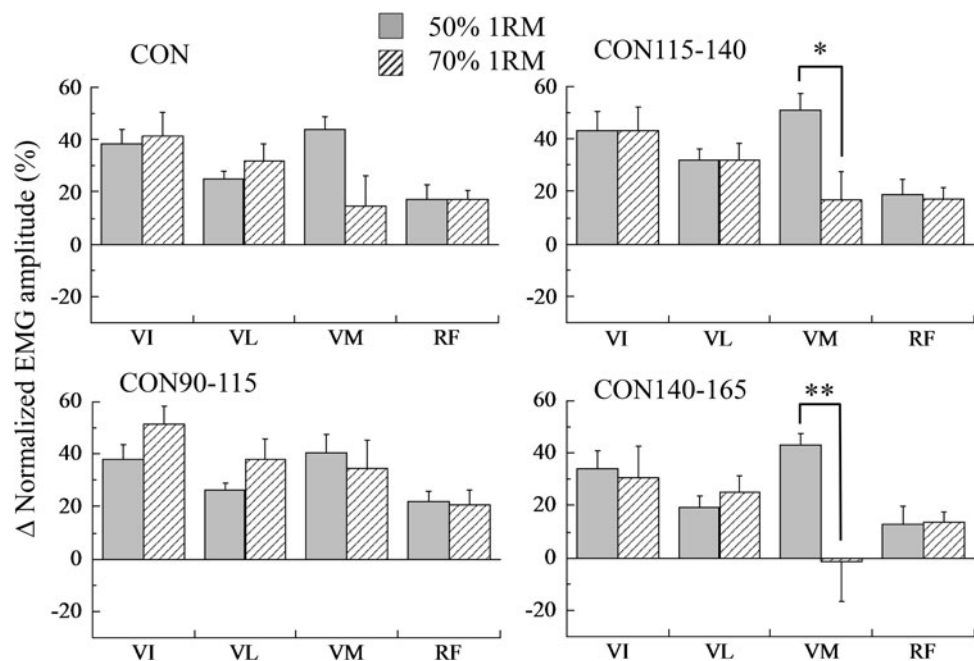
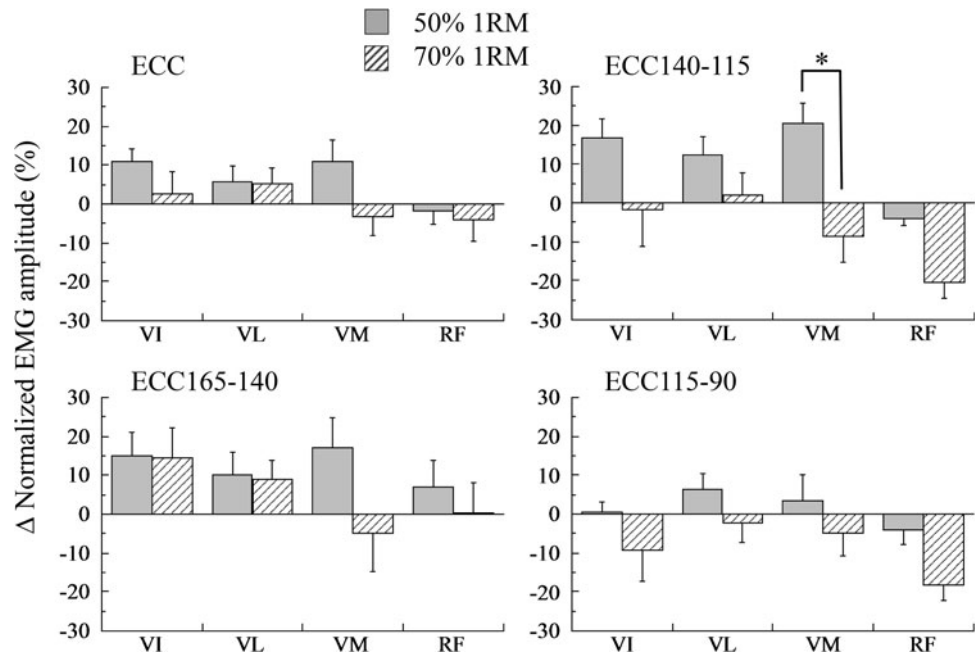


Fig. 6 The difference in normalized electromyographic (EMG) amplitude in the eccentric phase from initial to final repetition of fatiguing dynamic knee extensions performed at 50 and 70 % of one-repetition maximum (IRM). VI vastus intermedius, VL vastus lateralis, VM vastus medialis, RF rectus femoris. * $P < 0.05$. ECC165-140, knee joint angle of 165°–140° during an eccentric contraction; ECC140-115, knee joint angle of 140°–115° during an eccentric contraction; ECC115-90, knee joint angle of 115°–90° during an eccentric contraction



subphase. Furthermore, this activation pattern for the two muscles lasted until task failure, even though these two muscles had very similar activation patterns during the CON phase. From an anatomical point of view, the VI and RF are mono- and bi-articular muscles, respectively, but both muscles are located on a similar line of action to the quadriceps tendon. Nonetheless, the activation pattern was different between VI and RF throughout the fatiguing contractions. Pincivero et al. (2006) demonstrated that the normalized EMG amplitude of VL, VM, and RF in the CON phase significantly increased with the number of repetitions during fatiguing contractions, with no differences between muscles. Thus, the results of our study support those of Pincivero et al. (2006). Recently, we showed higher activation of VI at flexed knee joint angles than at extended knee joint angles in non-fatiguing dynamic knee extensions; thus, the results of the present study also support those of our previous study (Akima and Saito 2013). It is notable that this angle-specific activation pattern remained constant with advancing muscle fatigue, implying that this unique activation pattern is associated with some intrinsic factors.

During the ECC phase, the normalized EMG amplitude of VL was significantly higher than VI, VM, and RF, supporting a previous study (Pincivero et al. 2006). Lower activation in RF than VI was observed for the ECC115-90 phase from the initial to the final repetitions. Furthermore, RF had significantly lower activation than VL and VI in the ECC140-115 subphase during the latter half of the fatiguing task. In some previous studies using surface EMG, mechanomyography, and muscle functional magnetic resonance imaging (Akima et al. 2004, 1999; Ebenbichler

et al. 1998; Kouzaki et al. 1999), RF was more fatigable than VL and VM during isometric or dynamic knee extensions. This study agrees with these previous studies, particularly the results during the ECC140-115 and ECC115-90 subphases.

Fatiguing contractions at 70 % 1RM

The difference in the activation patterns between the four individual QF muscles appeared to be more prominent during fatiguing dynamic knee extensions at 70 % 1RM than at 50 % 1RM. Although the activation patterns were quite similar among four individual QF muscles from the initial repetition to the 75 % repetition during the CON and ECC phases of fatiguing contractions at 70 % 1RM, the activation patterns of the four individual QF muscles during the subphases were also angle specific, as during fatiguing contractions at 50 % 1RM.

We found significantly higher activation in VI than in the three surface QF muscles during the CON90-115 subphase of all repetitions of contractions at 70 % 1RM, whereas the level of activation of VI was lower than in the three surface QF muscles in the CON115-140 and CON140-165 subphases. This angle-specific activation pattern of VI was also observed in contractions at 50 % 1RM, suggesting that the underlying neuromuscular mechanism could be similar. Furthermore, it is notable that during the CON90-115 subphase, the level of muscle activation in VI relative to the other three QF muscles was much higher during contractions at 70 % 1RM than at 50 % 1RM. This implies that VI could greatly contribute to dynamic knee extension when the knee joint angle is flexed

(Akima and Saito 2013). Surprisingly, the normalized EMG amplitude of VI linearly increased with fatigue and finally reached 140 % of 1RM. This higher normalized EMG amplitude in VI corresponded to 10 % increase during dynamic knee extension at 100 % 1RM in non-fatiguing condition (Akima and Saito 2013), suggesting that there was a greater number of active MUs and that active MUs had a higher firing rate (Basmajian and DeLuca 1985) at the end of the fatiguing task in VI at a flexed knee joint angle. We speculate that this higher EMG amplitude in VI at exhaustion may have contributed to the relative high VI EMG amplitude in the CON90-115 subphase, which finally reached up to 140 % 1RM. A gradual increase in VI activation with fatigue could be a compensation for decreased VL and RF activation, particularly in the final quarter of the task (75 % repetition to final repetition). During this final phase, VL and RF appeared to be fatigued. For almost all subjects, the cause of task failure was inadequate ROM of the knee joint during the CON140-165 subphase of the movement. This means that there was capacity for an increase in MU activation in VI during the CON90-115 subphase, even at the final repetition. This may be the main reason for relatively high activation of VI at larger normalized EMG amplitude, which resulted in higher normalized EMG amplitude during the CON phase at the final repetition.

Another notable finding is that the activation of VM was almost maximal throughout fatiguing contractions at 70 % 1RM when the knee joint was in an extended position, which is in contrast to the fatiguing contractions at 50 % 1RM. This increase in the normalized EMG amplitude of VM with advancing fatigue is consistent with our previous study (Watanabe and Akima 2010), in which we showed significant increases in normalized EMG amplitude from the beginning of isometric knee extension at 50 % MVC. On the contrary, Pincivero et al. (2006) reported that the activation of VM was significantly lower than VL when the knee joint was fully extended in an isometric holding phase during dynamic fatiguing knee extensions at 50 % 1RM. This discrepancy may be due to differences in type of contraction, exercise load, and/or exercise procedure between these studies.

When analyzing the ECC phase of fatiguing contractions at 50 and 70 % 1RM, we found a similar activation pattern in each of the four QF muscles. This suggests that VL does not always greatly contribute to the ECC phase of knee extension as suggested by Pincivero et al. (2006). Rather, VI, VM, and RF have the capacity to increase their neuromuscular activation similar to VL. We should pay attention to activation patterns of VI during the ECC140-115 and ECC115-90 subphases of fatiguing contractions at 70 % 1RM, when the normalized EMG amplitude of VI was significantly higher than that of VL, VM, or RF. In

particular, this activation pattern was not seen during the ECC140-115 subphase of fatiguing contractions at 50 % 1RM.

Δ Normalized EMG amplitude in fatiguing contractions at 50 and 70 % of 1RM

In the comparison of Δ normalized EMG amplitude between fatiguing contractions at 50 and 70 % 1RM, we noted two interesting new findings. First, we found a significant difference in the Δ normalized EMG amplitude of VM between 50 and 70 % 1RM during the CON115-140, CON140-165 and ECC140-115 subphases (Figs. 5, 6). This result conflicts with Ebenbichler et al. (1998) who showed that fatigue-related changes in RF EMG activity, not VM EMG activity, were affected by the target forces (30, 50 and 70 % MVC) during fatiguing isometric knee extension. It has been argued that RF is more fatigable than the other QF muscles during knee extension; however, this is likely to be dependent on type of contraction, i.e., isometric, isotonic or isokinetic (Akima et al. 1999; Kellis 1999; Kouzaki et al. 1999; Rochette et al. 2003).

Differences in the metabolic capacity of muscle fibers among the four QF muscles (Saltin and Gollnick 1983) would be expected to influence EMG activation patterns. According to Johnson et al. (1973) and Edgerton et al. (1975), type II fibers ranged from 53 to 71 % across the four QF muscles, which is relatively homogeneous compared to the triceps surae muscles (Saltin and Gollnick 1983). Furthermore, it is necessary to consider the metabolic capacity of muscle fibers, because this can greatly influence muscle fatigue (Enoka and Stuart 1992; Saltin and Gollnick 1983). Based on the study of Edgerton et al. (1975), the relative number of oxidative and glycolytic fibers in VI and VL is quite similar; therefore, there would be no difference in fatigability between these two muscles. Accordingly, we did not observe a difference in fatigability evaluated by normalized EMG amplitude at either exercise intensity.

The central nervous system attempts to compensate for the failing muscle by modulating the number and/or firing rate of active MUs (Basmajian and DeLuca 1985; Housh et al. 1995; Moritani et al. 1986; Stock et al. 2012; Watanabe and Akima 2010). Moritani et al. (1986) clearly showed that EMG amplitude of the biceps brachii muscle significantly increased, with a significant decline in mean power frequency during sustained contractions at 50 % MVC by surface EMG. Furthermore, they simultaneously recorded intramuscular EMG and showed progressive MU recruitment, as evidenced by an increased number of active MUs with relatively large spike amplitude. Kukulka and Clamann (1981) reported that recruitment of additional MUs took place with contraction levels up to 88 % MVC

in large muscles such as biceps brachii and QF muscles. We did not measure recruitment and firing rate of MUs in any of the four QF muscles. However, if there are similar mechanisms as discussed in the previous studies, muscle fatigue would be compensated for by the recruitment of new, unfatigued, and/or larger MUs to prevent the decline of force-generating capacity during fatiguing dynamic QF contractions (Bigland-Richie and Woods 1974). Furthermore, from a motor control point of view, impairment in force-generating capacity by fatigue is compensated by less-fatigued synergistic muscles, which is likely dependent on load and angle (Akima et al. 2012; Kouzaki et al. 1999, 2002; Tamaki et al. 1998).

Another new finding is that VM was the only muscle that showed a significant difference in Δ normalized EMG amplitude across loads. This indicates that the fatigue-induced change in the VM activation is susceptible to the loads lifted. In other words, this muscle may depress the level and/or number of active MUs during the CON115-140 and CON140-165 subphases of fatiguing contractions at 50 % 1RM. In the CON140-165 subphase of the initial repetition at 50 % 1RM, the activation of VM was the lowest, and then it gradually increased. On the other hand, in the CON140-165 subphase of contractions at 70 % 1RM, this muscle maintained the highest activation among the four QF muscles. This load-dependent activation is the primary reason for the significant difference in Δ normalized EMG amplitude across loads in the VM. This compensatory strategy among QF synergists was also shown in our previous study (Akima et al. 2002). An angle-dependent contribution of VM was assessed by de Ruyter et al. (2008), who reported the relative torque contribution of the VM at different knee joint angles using selective functional elimination of the VM by electrical stimulation. During isometric knee extension at 20 % MVC at knee joint angles of 90°–170°, the estimated contribution of the VM to total knee joint torque was 22–25 %. These authors also suggested that the contribution of the VI was similar across all tested knee joint angles. However, from these results it was not clear how the VM engaged in dynamic knee extension tasks at heavier loads. Ebenbichler et al. (1998) showed that, during isometric knee extension, there was an intensity-dependent change in RMS EMG of RF, but not VL or VM. This result conflicts with the present study, because we found an angle-specific EMG activation difference in VM. This discrepancy may be partly associated with the different type of contraction.

RF is more fatigable than other QF muscles (Akima et al. 1999, 2004; Ebenbichler et al. 1998; Kouzaki et al. 1999). We observed larger decreases in Δ normalized EMG amplitude in RF than in other muscles during the ECC140-115 and ECC115-90 subphases, particularly in contractions at 70 % 1RM, suggesting that EMG activity increased with the development of fatigue to compensate for MUs that

were impaired by fatigue Moritani et al. (1986). RF seemed to be activated more than the other QF muscle at extended knee joint angles in both the CON and ECC phases of contractions at 50 and 70 % 1RM. Thus, RF was most active at an extended knee joint angle and reduced its activation to avoid fatigue toward flexed knee joint angle of 90°–140°. During this ROM, the three vastii muscles were highly active to compensate for the reduced activation of RF.

In conclusion, we characterized the neuromuscular activation of four individual QF muscles during fatiguing dynamic contractions at 50 and 70 % 1RM. With both loads, the normalized EMG amplitude of the four individual QF muscles linearly increased with fatigue during the CON phase. Muscle activation patterns with fatigue were specific to the knee joint angle, and angle-specific activation patterns were maintained until task failure. Comparing the two loads, VM had higher activation during the CON115-140, CON140-165, and ECC140-115 subphases of contractions at 50 % 1RM than during contractions at 70 % 1RM. These results suggest that the contribution of the four individual QF muscles to fatiguing dynamic knee extension differs according to knee joint angle and intensity of load.

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

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