Introduction

The physiological demands of fatiguing muscle actions elicit perceptual, neuromuscular, and metabolic changes to the homeostatic conditions of the body. Performance fatigability is the objective measure of muscle performance that characterizes the magnitude of fatigue\(^1\). The mechanisms that underlie performance fatigability have been attributed to neural and mechanical properties of the working muscle\(^1\,2\). The use of electromyographic (EMG) and mechanomyographic (MMG) signal acquisition provide insight regarding the neuromuscular mechanisms of fatigue during dynamic muscle actions\(^4\,7\). The time domain (AMP) of the EMG signal reflects muscle excitation and the frequency domain (MPF) is associated with muscle fiber action potential conduction velocity\(^8\). The MMG signal is the mechanical counterpart of the EMG signal where the AMP provides information regarding motor unit recruitment and the MPF is qualitatively related to the global firing rate of unfused, activated motor units\(^9\,10\). Thus, the neuromuscular mechanisms associated with performance fatigability may be elucidated with the simultaneous assessment of EMG and MMG during fatiguing muscle actions.

Previous investigations have described the mechanisms associated with fatigue-induced changes in muscular function during UL muscle actions. Ebersole et al.\(^4\) reported fatigue-induced increases in muscle excitation (EMG AMP) and motor unit recruitment (MMG AMP), as well
as decreases in muscle fiber action potential conduction velocity (EMG MPF) and motor unit firing rate (MMG MPF) during 50 maximal, isokinetic leg extensions at 60°·s⁻¹ and 300°·s⁻¹. Camic et al.⁹ characterized fatigue by decreased muscle excitation (EMG AMP), muscle fiber action potential conduction velocity (EMG MPF), motor unit recruitment (MMG AMP) and motor unit firing rate (MMG MPF) during 30 maximal, isokinetic leg extensions at 30°·s⁻¹. Smith et al.⁶ reported increased muscle excitation (EMG AMP) and motor unit recruitment (MMG AMP), as well as decreased muscle fiber action potential conduction velocity (EMG MPF) and no change in motor unit firing rate (MMG MPF) during 25 maximal, isokinetic leg extensions at 120°·s⁻¹. The fatigue-induced changes in neuromuscular function during BL muscle actions, however, have only recently been described. Specifically, Anders et al.⁷ characterized bilateral fatigue by decreased muscle fiber action potential conduction velocity (EMG MPF) and motor unit recruitment (MMG AMP), as well as no change in muscle excitation (EMG AMP) and motor unit firing rate (MMG MPF). Thus, the findings of previous studies⁴·⁶·¹¹ suggested BL and UL muscle actions exhibit distinct patterns of neuromuscular fatigue.

Few studies have directly examined the mode-specific differences between BL and UL muscle actions. Matkowski et al.¹² and Rossman et al.¹³ compared the changes in performance fatigability for BL and UL isometric¹² and dynamic cycling¹³ leg extensions. Anders et al.⁷, however, was the first to compare the patterns of neuromuscular responses between BL and UL maximal, isokinetic leg extensions. As their study⁷ was conducted with women, it remains unclear whether the mode-specific differences in performance fatigability and patterns of neuromuscular responses are similarly exhibited in men. Therefore, the purpose of the present study was to compare the performance fatigability and patterns of responses for EMG AMP, EMG MPF, MMG AMP, and MMG MPF for BL versus UL maximal, isokinetic leg extensions in men. Based on previous studies⁷·¹²·¹³, we hypothesized that UL leg extensions would exhibit greater performance fatigability and greater changes in the neuromuscular patterns of responses than BL leg extensions.

**Materials and methods**

**Subjects**

Eleven men (Mean ± SD; age = 22.9 ± 3.7 years; height = 177.8 ± 6.7 cm; weight = 80.4 ± 7.9 kg) volunteered to participate in this study. The subjects were recreationally trained¹⁴ and reported performing 5.5 ± 3.1 hours per week of aerobic and/or anaerobic exercise. Specifically, all of the subjects reported performing resistance training including 1.9 ± 0.9 sessions per week of lower body training (e.g. leg press, back squat) and 10 of the 11 subjects participated in aerobic training in addition to resistance training. All subjects were free from previous injuries that would hinder their performance in the present study. The University Institutional Review Board for Human Subjects approved the present study and prior to participation, all subjects signed a written Informed Consent and completed a health history questionnaire.

**Protocol**

The study was conducted across four visits, each separated by 3-7 days. The first visit was an orientation session where the subjects were familiarized with the exercise protocol and performed BL and UL, submaximal and maximal isometric leg extensions at a knee joint angle of 120° (180° was considered full extension) for 6 s, and concentric, isokinetic leg extensions at 60°·s⁻¹ on a calibrated Cybex 6000 dynamometer (Cybex, Division of Lumex Inc., Ronkonkoma, NY, USA). All UL leg extension muscle actions were performed with the non-dominant limb (determined by kicking preference). For each testing visit, the subjects performed two BL and two UL maximal voluntary isometric contractions (MVICs) for 6 s, in random order. The subjects then performed either 50 consecutive maximal BL or UL (in random order on separate days), isokinetic leg extensions at 60°·s⁻¹.

**Electromyography, mechanomyography, and force acquisition**

Bipolar (30-mm center-to-center) surface EMG electrode (circular 4-mm diameter silver/silver chloride; Biopac Systems, Inc., Santa Barbara, CA, USA) arrangements were placed on the vastus lateralis (VL) of the non-dominant limb in accordance with SENIAM recommendations¹⁵. The bipolar electrodes were placed 66% of the distance between the anterior superior iliac spine and the lateral portion of the patella, orientated at an angle of 20° in order to align with the angle of pennation of the VL muscle fibers¹⁶. A reference
electrode was placed over the anterior superior iliac spine. Electrode placement sites were shaved, carefully abraded, and cleaned with an alcohol wipe prior to application. A miniature accelerometer was placed between the bipolar EMG electrode arrangement (Entras EGAS FT 10, bandwidth 0-200 Hz, dimension 1.0\(\times\)1.0\(\times\)0.5 cm, mass 1.0 g, sensitivity 655.1 mV \cdot g^{-1}) using double-sided adhesive tape to detect the MMG signal.

A 12-big analog-to-digital converter (Model MP 150; Biopac systems, Inc., Goleta, CA, USA) was used to digitize the raw EMG and MMG signal at 2,000 Hz and was stored on a personal computer (G5 Dell Inc., Round Rock, TX, USA) for later analyses. The EMG signal was amplified (gain: \(\times\) 1,000) using differential amplifiers (EMG100C, Biopac Systems, Inc., Goleta, CA, USA; bandwidth 10-500 Hz). The signals were bandpass filtered (fourth-order Butterworth) at 10-500 Hz for EMG and 5-100 Hz for MMG. Customized programs in LabVIEW programming software (version 18.0I2, National Instrument, Austin, TX, USA) were used to process the EMG and MMG signals. For each isokinetic leg extension, the EMG (\(\mu\)V root mean square, \(\mu\)Vrms) and MMG (m\(\cdot\)s\(^{-2}\)) AMP and MPF (Hz) values were calculated for a period of time corresponding to the middle 30° range of motion to avoid the acceleration and deceleration phases of the muscle action\(^7\). The neuromuscular and torque values for the MVICs were determined from the middle 2 s of the muscle action and these values were used to normalize the neuromuscular and torque values from the isokinetic leg extensions. The normalized (to MVIC) neuromuscular parameters and isokinetic torque values from the 50 BL and UL maximal isokinetic leg extensions were averaged across 5 consecutive repetitions (i.e. average of repetitions 1-5=5,

**Figure 2.** Normalized (% of MVIC±SD) EMG amplitude (A), EMG mean power frequency (B), MMG amplitude (C), and MMG mean power frequency (D) for the maximal bilateral (●) and unilateral (○) isokinetic leg extensions. *Significant (\(p<0.005\)) main effects for Repetition: different from repetition 5 when collapsed across bilateral and unilateral leg extensions. **Significant (\(p<0.005\)) main effect for Condition: bilateral was greater than unilateral for EMG MPF and MMG AMP collapsed across repetitions.
Statistical analyses

Mean differences for each normalized neuromuscular parameter (EMG AMP, EMG MPF, MMG AMP, and MMG MPF) and normalized isokinetic torque were examined by separate 2 (Conditions [BL and UL]) × 10 (Repetitions [5, 10, 15, 20, 25, 30, 35, 40, 45, 50]) repeated measures ANOVAs. Follow up 1-way repeated measures ANOVAs and paired samples t-tests were performed when appropriate. The time course of changes in the normalized neuromuscular parameters and normalized isokinetic torque values were examined via paired samples t-tests to determine mean differences between repetition 5 and repetitions 10–50 for both the BL and UL leg extensions. Measures of effect size (Partial eta squared ($\eta^2_p$) and Cohen’s $d$) were calculated for all ANOVAs and paired samples t-tests, respectively. IBM SPSS v. 25 (Armonk, NY) was used for all analyses and an alpha of $p<0.05$ was considered statistically significant for all comparisons.

Results

Isokinetic torque

The initial absolute peak torque values (average of repetitions 1–5) for the fatiguing task were 292.1±42.4 N·m for the BL condition and 210.0±38.1 N·m for the UL condition. The final absolute peak torque values (average of repetitions 45–50) for the fatiguing task were 220.4±31.7 N·m for the BL condition and 113.4±24.9 N·m for the UL condition. Thus, the BL and UL conditions exhibited performance fatigability values of 24.1±8.1 % and 45.1±11.8%, respectively. The changes in BL and UL normalized isokinetic torque across the repetitions are depicted in Figure 1. The 2 × 10 repeated measures ANOVA demonstrated a significant Conditions by Repetitions interaction ($p<0.001$, $\eta^2_p=0.594$). Follow-up 1-way repeated measures ANOVAs demonstrated significant mean differences for normalized isokinetic torque across the repetitions for the BL ($p<0.001$, $\eta^2_p=0.796$) and UL ($p<0.001$, $\eta^2_p=0.884$) leg extensions. For the BL leg extensions, post-hoc pairwise comparisons demonstrated normalized isokinetic torque for repetition 5 (98.0±20.7%) was significantly greater than repetitions 15 (94.±18.5%; $p=0.049$; $d=0.07$), 20 (91.8±20.2%; $p=0.004$; $d=0.21$), 25 (91.0±17.7%; $p=0.004$; $d=0.26$), 30 (85.4±16.6%; $p=0.001$; $d=0.57$), 35 (83.5±17.4%; $p=0.001$; $d=0.65$), 40 (79.8±18.0%; $p<0.001$; $d=0.84$), 45 (75.9±18.1%; $p<0.001$; $d=1.03$), and 50 (74.4±17.1%; $p<0.001$; $d=1.14$). For UL leg extensions, post-hoc pairwise comparisons demonstrated normalized isokinetic torque for repetition 5 (96.8±9.3%) was significantly greater than repetitions 15 (87.5±8.1%; $p=0.002$; $d=1.07$), 20 (80.3±8.9%; $p<0.001$; $d=1.81$), 25 (72.8±10.6%; $p<0.001$; $d=2.41$), 30 (65.1±11.7%; $p<0.001$; $d=3.00$), 35 (68.8±11.5%; $p<0.001$; $d=2.68$), 40 (56.5±10.4%; $p<0.001$; $d=4.09$), 45 (52.9±10.3%; $p<0.001$; $d=4.47$), and 50 (52.7±10.3%; $p<0.001$; $d=4.49$).

Follow-up paired samples t-tests demonstrated that normalized isokinetic torque was significantly greater for BL than the UL condition during repetitions 25 (BL=91.0±17.7%; UL=72.8±10.6%; $p=0.032$; $d=1.25$), 30 (BL=85.4±16.6%; UL=65.9±11.9%; $p=0.022$; $d=1.40$), 35 (BL=83.5±17.4%; UL=58.8±11.5%; $p=0.008$; $d=1.68$), 40 (BL=79.8±18.0%; UL=56.5±10.4%; $p=0.010$; $d=1.59$), 45 (BL=75.9±18.1%; UL=52.9±10.3%; $p=0.011$; $d=1.56$), and 50 (BL=74.4±17.1%; UL=52.7±10.3%; $p=0.014$; $d=1.54$).

Neuromuscular parameters

The changes in neuromuscular parameters across repetitions are depicted in Figure 2. The 2 × 10 repeated measures ANOVA for EMG AMP demonstrated no significant interaction ($p=0.826$; $\eta^2_p=0.053$) or main effect for Conditions ($p=0.990$; $\eta^2_p=0.001$) but a significant main effect for Repetitions ($p<0.001$; $\eta^2_p=0.255$) main effect for Repetitions. When collapsed across Conditions, the normalized EMG AMP was significantly less for repetition 5 (133.4±38.4%) than repetitions 10 (148.7±41.1%; $p<0.001$), 15 (151.7±40.4%; $p<0.001$), 20 (152.9±39.4%; $p=0.001$), 25 (156.2±41.1%; $p=0.016$), 30 (157.7±41.2%; $p=0.012$), 35 (157.2±37.8%; $p=0.003$), 40 (153.5±35.7%; $p=0.018$), 45 (150.6±41.0%; $p=0.047$), and 50 (153.0±45.3%; $p=0.048$; $d=0.47$).

The 2 × 10 repeated measures ANOVA for MMG AMP demonstrated no significant interaction ($p=0.112$; $\eta^2_p=0.141$) but significant main effects for Conditions ($p=0.031$; $\eta^2_p=0.387$) and Repetitions ($p<0.001$; $\eta^2_p=0.650$). When collapsed across Repetitions, the normalized MMG AMP for the BL condition (98.0±8.8%) was significantly greater than the UL condition (89.2±11.3%; $d=0.65$). When collapsed across Conditions, the normalized MMG AMP for repetition 5 (107.1±8.3%) was significantly greater than repetitions 10 (101.4±7.5%; $p=0.001$; $d=0.72$), 15 (97.8±8.0%; $p=0.001$; $d=1.14$), 20 (93.8±8.0%; $p=0.001$; $d=1.63$), 25 (94.3±9.5%; $p=0.002$; $d=1.44$), 30 (90.6±10.1%; $p=0.001$; $d=1.79$), 35 (88.7±7.7%; $p=0.001$; $d=2.30$), 40 (88.0±12.2%; $p=0.001$; $d=1.83$), 45 (87.2±10.8%; $p=0.001$; $d=2.07$), and 50 (86.7±12.7%; $p=0.001$; $d=1.90$).

The 2 × 10 repeated measures ANOVA for MMG MPF demonstrated no significant interaction ($p=0.163$; $\eta^2_p=0.13$), but significant main effects for Conditions ($p=0.002$; $\eta^2_p=0.646$) and Repetitions ($p<0.001$; $\eta^2_p=0.402$). When collapsed across Repetitions, the normalized MMG MPF for the BL conditions (151.9±43.3%) was significantly greater than the UL condition (105.4±24.5%; $p=0.002$; $d=1.32$). When collapsed across Conditions, the normalized MMG MPF for repetition 5 (138.5±32.8%) was significantly greater than repetitions 25 (122.8±28.4%; $p=0.002$; $d=0.51$), 30 (122.2±28.9%; $p=0.012$; $d=0.53$), 35 (116.8±26.1%; $p=0.007$; $d=0.73$), 40 (117.1±29.7%; $p=0.012$; $d=0.68$), and 50 (120.2±39.9%; $p=0.040$; $d=0.50$).

The 2 × 10 repeated measures ANOVA for MMG MPF
demonstrated no significant interaction (p=0.127; \eta^2_p=0.138) or main effect for Conditions (p=0.989; \eta^2_p=0.000) but there is a significant main effect for Repetition (p<0.001; \eta^2_p=0.796). When collapsed across Conditions, the normalized MMG MPF for repetition 5 (117.8±13.0%) was significantly greater than repetitions 10 (107.3±15.5%; p=0.023; d=0.73) 15 (94.8±15.4%; p<0.001; d=1.61), 20 (85.1±13.5%; p<0.001; d=2.47), 25 (81.4±18.9%; p<0.001; d=2.24), 30 (77.7±18.0%; p<0.001; d=2.55), 35 (74.4±16.2%; p<0.001; d=2.96), 40 (67.1±13.7%; p<0.001; d=3.80), 45 (65.3±12.0%; p<0.001; d=4.20), and 50 (68.4±14.3%; p<0.001; d=3.61).

**Discussion**

The purpose of the present study was to compare the fatigue-related isokinetic torque and neuromuscular responses during maximal, BL versus UL leg extensions. The findings demonstrated that UL leg extensions exhibited greater performance fatigability than BL leg extensions. These findings were consistent with previous studies that have reported greater performance fatigability for UL than BL muscle actions following submaximal isometric and dynamic leg extensions. Matkowski et al. reported a 36.6±8.4% decline in MVIC following submaximal (20% of MVIC) UL isometric leg extensions to failure compared to a 22.2±8.5% following BL isometric leg extensions. Rossman et al. reported a 44.0±6.0% decline in MVIC from UL leg extensions during cycle ergometry at 85% peak power output compared to 33.7±7.0% decline following BL cycle ergometry. Furthermore, Anders et al. recently reported a greater fatigue-induced decline in normalized isokinetic peak torque during UL (38.0±12.7%) than BL (17.7±12.9%) leg extensions in women. The current findings in men demonstrated a 45.1±11.8% decline in normalized isokinetic peak torque for UL leg extensions compared to a 24.1±8.1% decline for BL leg extensions. Thus, the results of the present study, as well as previous studies, indicated that submaximal and maximal, isometric and dynamic muscle actions are characterized by greater performance fatigability during UL than BL leg extensions in both men and women.

The time domain of the EMG signal reflects muscle excitation and is influenced by motor unit recruitment, firing rate, and synchronization. In the present study, the EMG AMP exhibited an increase that was maintained during the fatiguing task compared to the initial value (repetitions 10-50 were greater than repetition 5) when collapsed across the BL and UL conditions (Figure 2A). This pattern of response was consistent with previous studies that have demonstrated increases in EMG AMP following UL maximal, fatiguing isokinetic leg extensions. These findings were not consistent, however, with a recent study by Anders et al. who reported no change in EMG AMP during BL and UL maximal, isokinetic leg extensions in women. Thus, the results of the present study and those of Anders et al. suggested there may be initial differences in muscle excitation (EMG AMP) between men and women during maximal, dynamic, isokinetic leg extensions.

The frequency domain of the EMG signal reflects muscle fiber action potential conduction velocity and is influenced by the build up of metabolic byproducts such as extracellular potassium, intracellular calcium, and intracellular hydrogen ions. In the present study, EMG MPF demonstrated a decrease that was maintained during the fatiguing task (repetitions 10-50 were less than repetition 5) and the decline was parallel for UL than BL leg extensions (Figure 2B). The current findings were not consistent with previous studies that reported greater levels of peripheral fatigue for UL than BL conditions during isometric and dynamic leg extensions. Although the patterns of responses for EMG MPF decreased for both the UL and BL conditions, they did not track the greater rate of decrease in normalized isokinetic torque for the UL than BL condition (Figure 1). Overall, the results of the present study indicated that the BL muscle actions were characterized by a greater average motor unit action potential conduction velocity than UL muscle actions but both the BL and UL exhibited the same pattern of fatigue-induced decreases across repetitions.

The MMG signal is the mechanical counterpart to the EMG signal and the amplitude can be influenced by motor unit recruitment, muscle compliance, and muscular stiffness. In the present study, the MMG AMP was less than the initial value (repetitions 25, 30, 35, 45, and 50 were less than repetition 5; collapsed across conditions) during the fatiguing tasks and was significantly greater for the BL than the UL leg extensions when collapsed across repetitions (Figure 2C). These findings for men were not consistent with those of Anders et al. who reported no fatigue-induced changes in MMG AMP during BL and UL leg extensions in women. Decreases in the MMG AMP have been attributed to reduced muscle compliance and increased muscular stiffness, which impair the lateral oscillations of the muscle fibers. Muscular stiffness is associated with the number of attached cross bridges and has been shown to change in accordance with greater force production. Thus, the decrease in the MMG AMP throughout the fatiguing task exhibited by the men in the present study, but not by the women in Anders et al., may have been due to the greater absolute force production in the men. Furthermore, the more attenuated MMG AMP (collapsed across repetitions) and, perhaps, greater muscular stiffness during the UL task in the present study were consistent with the more pronounced performance fatigability for the BL than BL leg extensions.

The frequency domain of the MMG signal represents a qualitative assessment of the global firing rate of activated motor units. In the present study, MMG MPF demonstrated a decrease that was maintained during the fatiguing task (repetitions 10-50 were less than repetition 5) for both the BL and UL leg extensions, however, there was no difference between the two conditions (Figure 2D). These findings were consistent with previous studies that have demonstrated decreases in MMG MPF during...
maximal, UL4-6 and BL7 leg extensions. The fatigue-induced decreases in MMG MPF and global motor unit firing rate were consistent with the Muscle Wisdom Hypothesis as a mechanism to attenuate the magnitude of performance fatigability27-29. The Muscle Wisdom Hypothesis originally described the reduction in motor unit firing rates exhibited during sustained isometric contractions29. Specifically, the Muscle Wisdom Hypothesis proposes that fatiguing muscle actions are characterized by a decrease in motor unit firing rates, elongated relaxation time of activated skeletal muscle, and greater tetanic fusion that attenuates force decrements28,29. Binder-Macleod et al.30 reported 46% greater performance fatigability in isometric force following repeated electrical simulation to the quadriceps femoris at a continuous frequency compared to stimulation with a progressively lower frequency. Although there are conflicting opinions regarding the applicability of the Muscle Wisdom Hypothesis during dynamic muscle actions28, the present study, as well as previous studies, have demonstrated that during maximal, UL4,5,31 and BL7, leg extensions, performance fatigability has similarly been characterized by a reduced MMG MPF and global motor unit firing rate. Thus, the findings of the present study demonstrate that the BL and UL leg extensions exhibited parallel fatigue-induced patterns of decrease for MMG MPF in accordance with the Muscle Wisdom Hypothesis.

Conclusion

In the present study, UL leg extensions exhibited a greater performance fatigability in isokinetic peak torque than BL leg extensions. The greater performance fatigability for the UL than the BL leg extensions was not consistent with the parallel decreases in muscle activation (EMG AMP), muscle fiber action potential conduction velocity (EMG MPF), muscular stiffness (MMG AMP), and global motor unit firing rate (MMG MPF) during the UL and BL leg extensions. In general, the findings of the present study demonstrated that the performance fatigability during both BL and UL dynamic leg extensions were characterized by fatigue-induced patterns of neuromuscular responses that were consistent with the Muscular Wisdom Hypothesis. Further research is warranted to explore the mechanisms associated with differences in performance fatigability from various modes of muscle actions during BL and UL modalities and their corresponding fatigue-induced patterns of neuromuscular responses.

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